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Nitrogen uptake and partitioning under alternate- and every-furrow irrigation

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Abstract

Alternate-furrow irrigation, combined with fertilizer placement in the non-irrigated furrow, has the potential to reduce fertilizer leaching in irrigated corn (*Zea mays* L.). The potential also exists, however, for reduced N uptake under alternate-furrow irrigation. This study examined the effects of fertilizer placement and irrigation treatment on N uptake, root→shoot→root circulation, and partitioning between reproductive and vegetative tissues. Rainfall was above average in both years of the study, especially during May and June, so that root growth beneath the non-irrigated furrow was equal to root production beneath the irrigated furrow. Under those conditions, soil NO_3 concentration in the fertilized furrow during late-vegetative and reproductive growth was greater in the alternate-furrow compared with the every-furrow treatment, resulting in increased fertilizer N uptake during reproductive growth and increased N partitioning to reproductive tissues under alternate-furrow irrigation. About 80% of the fertilizer N found in roots had first been translocated to the shoot and then returned via the phloem to the root system. Nitrogen cycling from root to shoot to root was not affected by irrigation treatment. Alternate-furrow irrigation successfully increased N uptake and reduced the potential for NO_3leaching when environmental conditions allowed adequate root development in the non-irrigated furrow, and when the growing season was long enough to allow the crop to reach physiological maturity.

Introduction

Alternate-furrow irrigation, combined with fertilizer placement in the non-irrigated furrow, has the potential to reduce fertilizer leaching in irrigated corn, thus protecting groundwater quality (Benjamin et al., 1994). Alternate-furrow irrigation could also increase water use efficiency. Fischbach and Mulliner (1974) were able to reduce irrigation applications by 30% while maintaining yields using alternate-furrow irrigation. Fertilizer placement in the non-irrigated furrow, however, could reduce nitrate uptake because mass flow transfer of mobile nutrients, such as nitrate, to the root system depends on root water absorption (Barber, 1977). Because of this, low soil water availability can reduce nitrate uptake even when soil N is not limiting (Abreu et al., 1993; Karrou and Maranville, 1994).

In a dry year, fertilizer N accumulation in corn was reduced 50% when fertilizer was placed in the non-irrigated furrow (Benjamin et al., 1997). In the same study, fertilizer N accumulation was similar under alternate- or every-furrow irrigation during a relatively wet year. The pattern of N accumulation, however, was affected by irrigation treatments in both years. With every-furrow irrigation, only 6% of the fertilizer N uptake occurred after the beginning of reproductive development, while 35% occurred during reproductive growth under alternate-furrow irrigation.

Much of the N that is taken up by plants enters a circulating pool that cycles back and forth between roots and shoots before being incorporated in structural materials. This circulating pool could control both N uptake and partitioning among different plant tissues (Agrell et al., 1994; Cooper and Clarkson, 1989; Lambers et al., 1982). The delayed aboveground N accumulation observed by Benjamin et al. (1997)

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during a dry year under alternate-furrow irrigation could have resulted from reduced root uptake capacity early in the season or from increased partitioning to below ground tissues. This paper follows up on the work of Benjamin et al. (1997) by examining the effects of fertilizer placement and irrigation treatment on N uptake, partitioning, root→shoot→root circulation, and remobilization from vegetative to reproductive tissues.

Materials and methods

This study was conducted at the Agricultural Research, Development, and Education Center (ARDEC) near Ft. Collins, CO in 1995 and 1996, on a Ft Collins loam soil (fine-loamy, mixed, superactive, mesica Aridic Haplusalf). Plots were 9.1 m long by 3 m wide (4 rows) and were replicated four times. Irrigation water was supplied to every furrow or to alternate furrows with a linear-move irrigation system modified to apply water directly to the center of the furrows (Benjamin et al., 1997). Plots were irrigated weekly at 100% of estimated evapotranspiration calculated by the Kimberly modified Penman technique (Jensen, 1973) from station meteorological data . Twice as much water was applied to the irrigated furrow in alternate-furrow plots compared with furrows in the every-furrow treatment so that the total amount of water was the same for all plots. Soil water content was measured to a depth of 1.5 m with neutron probes placed within each furrow and within the row. Water content was measured 24 h before and 48 h after each irrigation.

Nitrogen-15-depleted fertilizer as $(NH_4)_2SO_4$ (99.39 atomic percent ^{14}N) was dissolved in water and applied at the rate of 145 kg ha^{-1} (4 L of fertilizer solution for each 3-m length of row) with a hand sprayer to the bottom of an approximately 0.1-m deep trench dug by hand in the center of one of the two furrows adjacent to each row. In both years, fertilizer was applied after seedling emergence at about the V1 growth stage (one collared leaf, Ritchie and Hanway, 1982). In the alternate-furrow treatment, fertilizer was placed in the non-irrigated furrow. In the every-furrow treatment, fertilizer was placed in only one of the two irrigated furrows.

In 1995, corn (var. 'Pioneer 3790') was planted on 11 May at a seeding rate of 81,500 plants ha^{-1}. Plots were subsequently thinned to 71,600 plants ha^{-1} after emergence. Fertilizer application did not occur until 7 June because of delayed emergence due to cool temperatures. A killing frost on 21 September terminated plant development before physiological maturity was reached (about the R5 growth stage). In 1995, 1042 growing degree days (GDD) accumulated between planting and the killing frost. Sampling occurred on 5 July (298 GDD, V5), 31 July (559 GDD, V12), 16 August (723 GDD, R1), and 28 September (1042 GDD, R5). Growing degree days were calculated from average daily temperatures with a minimum of 10 ° C and a maximum of 30 ° C.

In 1996, planting occurred on 6 May and plots were fertilized on 22 May. Seeding rate and final plant population were the same as in 1995. The experiment was again terminated by a killing frost on 27 September. However, the crop was near maturity (R6) when the frost occurred. In 1996, 1186 GDD accumulated between planting and the killing frost. Sampling in 1996 occurred on 1 July (426 GDD, V9), 22 July (648 GDD, V16), 6 August (790 GDD, R1), and 1 October (1186 GDD, R6).

At each harvest, four adjacent plants were cut near the soil surface and separated into leaves, stems and ears (when present). Root and soil samples were then collected by removing 5-cm diameter by 120-cm deep soil cores from six positions around one of the plants from which the shoot had been removed. The six positions were: (1) directly over the crown of the plant; (2) in the row half way between the crown and an adjacent plant; (3) and (4) the center of each furrow perpendicular to the crown; (5) and (6) the center of each furrow perpendicular to the interplant space within the row . Soil cores were separated into 0–30, 30–60, 60–90, and 90–120 cm depths and a 10–15 g subsample was removed for soil NO_3 determination. Nitrates were extracted from the soil with a 2 *M* KCl solution for 30 min, then analyzed using an Alpkem autoanalyzer (Alpkem, Wilsonville, Oregon, USA). Roots were then washed free of soil and live roots were hand separated from dead roots and debris based on color and structural integrity.

The plant parts were weighted for biomass determination and analyzed for total N and for atom percent ^{15}N on a continuous flow combustion analyzer (Carlo Erba, Milan, Italy) coupled with an isotope-ratio mass-spectrometer (Europa Scientific Limited, Crewe, UK). Root samples from each furrow and from the row were pooled for N analysis. Fertilizer N (N_F) content of the plant samples was determined by the following

Table 1. Comparison of 1995 and 1996 monthly rainfall during the growing season with 30 year (1965–1994) average monthly rainfall at Ft. Collins, CO

	May	June	July	August	Total
			mm		
30-year average	68	50	46	33	197
1995	185	136	79	20	420
1996	115	72	55	14	256

equation:

$$N_F = N_{tot}(^{15}N_S - 0.372)/(0.0061 - 0.372) \quad (1)$$

where N_{tot} = total N in the sample, $^{15}N_S$ = atom% ^{15}N in the sample, 0.0061 = atom% ^{15}N in the fertilizer, and 0.372 = background atom% ^{15}N from plant samples collected outside the fertilized plots.

Nitrogen remobilization from roots, stalks and leaves was determined by subtracting tissue N content at the final harvest from tissue N content at the harvest where total vegetative N content was the greatest, which occurred at the R1 growth stage in 1995 and at the V16 growth stage in 1996. Leaves accumulated N throughout the growing season in 1995, resulting in negative remobilization rates.

Root→shoot→root N circulation was estimated based on the following assumptions. First, all fertilizer N remained in the fertilized furrow (Benjamin et al., 1994) and was taken up by roots growing in that furrow. Any fertilizer N found in roots beneath the row or unfertilized furrow, therefore, must have first cycled through the shoot. Second, fertilizer N returned to source roots at the same rate as it was cycled to non-fertilized roots (Agrell et al., 1994; Lambers et al., 1982). Finally, non-labeled N cycled between roots and shoots at the same rate as labeled N.

Results

Detailed root growth data have been presented by Skinner et al. (1998). This paper will concentrate on root production beneath the irrigated and non-irrigated furrows that received N fertilization. Plants were harvested at different growth stages in 1995 and 1996. Therefore, data are presented for early-vegetative (V5 and V9 harvests in 1995 and 1996, respectively), late-vegetative (V12 and V16), early-reproductive (R1 both years), and late-reproductive (R5 and R6) growth. Root dry weights beneath the fertilized furrows were similar regardless of whether or not the furrows were irrigated (Figure 1). Root growth patterns were similar in both years of the study. Both years received greater than normal precipitation, especially during May and June (Table 1), so that root growth during vegetative development occurred while soil moisture was high in all furrows. Adequate moisture also remained available at lower depths in the non-irrigated furrow throughout the growing season (Skinner et al., 1998).

Irrigation treatments had no effect on whole plant N accumulation (Figure 2), although there was a trend in both years for total N content to be greater under alternate-furrow irrigation at the final harvest. Fertilizer N accumulation under alternate-furrow irrigation tended to lag behind every-furrow irrigation during vegetative and early-reproductive growth although differences were not significant. After R1, however, fertilizer N uptake ceased under every-furrow but continued under alternate-furrow irrigation, so that total fertilizer N accumulation over the growing season was greatest in the alternate-furrow treatment ($p < 0.05$).

More soil NO_3 was availabile in the fertilized furrow during late-vegetative and early-reproductive growth under alternate-furrow irrigation (Table 2). Irrigation treatments, which began about 1 wk after the first harvest in 1995, and 1 wk before the first harvest in 1996, had no significant effect on soil NO_3 at the early-vegetative harvest. By the late-vegetative stage, soil NO_3 concentration was significantly greater under alternate- compared with every-furrow irrigation. Both, however, remained elevated compared with the non-fertilized furrow. By the beginning of reproductive development, NO_3 concentration in the fertilized furrow under every-furrow irrigation was only marginally greater than in the non-fertilized furrow, while NO_3 levels remained high under alternate-furrow irrigation. Differences in N uptake between irrigation treatments were not significant (Figure 2). Therefore, reduced soil NO_3 under every-furrow irrigation may have resulted, at least in part, from increased leaching below the root zone. Most of the additional NO_3 available under alternate-furrow irrigation at the beginning of reproductive growth had been taken up by the plants by the final harvest, so that differences between treatments were again non-significant.

Whole plant total N content was similar in 1995 and 1996 (Table 3). Because an early frost in 1995 terminated development before maturity was reached, more than half of the plant N at the final harvest remained in vegetative tissues in 1995, while 75 to 80%

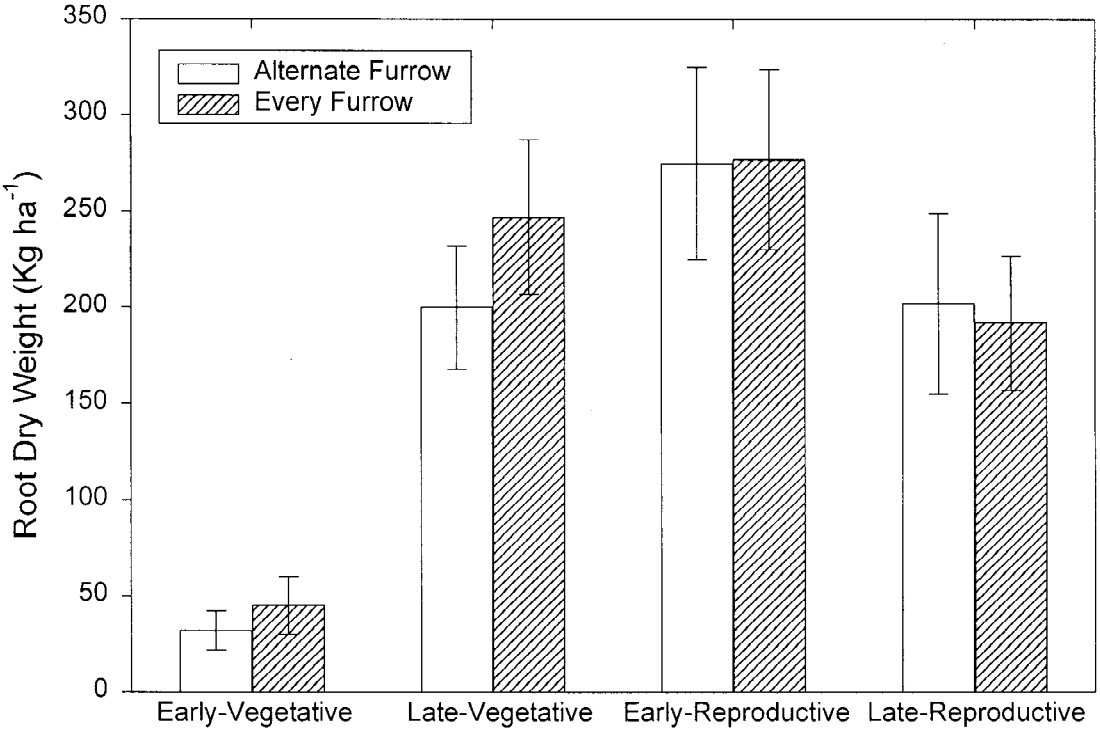

Figure 1. Root production under fertilized furrows which received irrigation water (every-furrow) or received only natural precipitation (alternate-furrow) during the growing season. Error bars represent ± 1 SE. Data have been combined across years.

was found in reproductive structures in 1996. More fertilizer N was partitioned to reproductive growth under alternate- compared with every-furrow irrigation in both years. In 1996, more total N was also found in reproductive tissues under alternate-furrow irrigation. A similar trend for total N also existed in 1995, although difference were not significant.

Fertilizer N concentration in roots beneath the fertilized furrow was greater than the concentration in roots collected beneath the row or from the unfertilized furrow (Table 4). With the exception of the final harvest, fertilizer N concentration also tended to be greater in roots beneath the row compared to the unfertilized furrow. The greatest total amount of fertilizer N in the roots was found beneath the row because of the greater concentration of roots directly beneath the plant. The remobilization of fertilizer N during reproductive development was also greatest from roots beneath the row.

Between 18 and 71% of the vegetative N was remobilized during reproductive development, depending on treatment and year (Table 5). Remobilized N from vegetative tissues could have contributed as much as 33% of the total N found in ears in 1995 and 67% in 1996. In 1995, stalks were the first plant part to begin exporting N to the ear (Figure 3), beginning after V12. Roots accumulated N for a longer period of time before remobilization began, while no net remobilization from leaves was observed. In 1996, clear distinctions between vegetative tissues for N remobilization were not observed, although remobilization from leaves may have been slightly delayed compared with other tissues. Root remobilization also appeared to be delayed under every-furrow irrigation, but the initial accumulation was also much less than in the previous year, or in the alternate-furrow irrigation treatment.

Discussion

Nitrogen uptake and remobilization

Alternate-furrow irrigation of corn, with fertilizer placement in the non-irrigated furrow, increased fertilizer N uptake and partitioning to reproductive growth compared with every-furrow irrigation. This occurred

Table 2. Effect of alternate- or every-furrow irrigation on NO_3 concentration in the top 120 cm of the soil profile during corn development. Fertilizer N was placed in the non-irrigated furrow under alternate-furrow irrigation or in one of the two irrigated furrows under every-furrow irrigation. Data are combined across years

Growth stage	Fertilized Furrow		Non-Fertilized Furrow	
	Alternate-Furrow	Every-Furrow	Alternate-Furrow	Every-Furrow
	Soil NO_3-N (mg/kg $\pm$ 1 SE)			
Early-Vegetative	38.5 ± 7.0	30.1 ± 5.6	5.1 ± 1.4	3.6 ± 0.2
Late-Vegetative	23.8 ± 5.1	10.9 ± 1.3	3.2 ± 0.2	3.0 ± 0.2
Early-Reproductive	12.1 ± 1.9	4.2 ± 0.4	2.6 ± 0.2	2.5 ± 0.1
Late-Reproductive	3.9 ± 0.4	3.4 ± 0.4	3.0 ± 0.4	2.7 ± 0.3

Table 3. Nitrogen partitioning between vegetative (roots, stalks and leaves) and reproductive (grain, cobs and husks) tissues at the final harvest. An early frost in 1995 killed the plants before maturity was reached. Means within a column followed by the same letter are not significantly different at $p < 0.05$

	Total N			Fertilizer N		
	Whole Plant	Vegetative	Reproductive	Whole Plant	Vegetative	Reproductive
1995			kg/ha			
Alternate-Furrow	198 a	103 a	96 c	82 b	36 a	46 c
Every-Furrow	187 a	99 a	88 c	72 b	36 a	36 d
1996						
Alternate-Furrow	196 a	42 b	154 a	103 a	18 b	85 a
Every-Furrow	179 a	45 b	134 b	84 b	19 b	65 b
$LSD_{0.05}$	25	18	13	18	13	9

Table 4. Fertilizer N partitioning among roots from different positions (fertilized furrow, unfertilized row and unfertilized furrow) beneath the corn plant. Data from 1995 and 1996 have been combined

	Alternate-Furrow Irrigation				Every-Furrow Irrigation			
Position	Early Vegetative	Late Vegetative	Early Reproductive	Late Reproductive	Early Vegetative	Late Vegetative	Early Reproductive	Late Reproductive
	mg N/g root dry weight $\pm$ 1 SE							
Fertilized	2.1 ± 0.9	4.8 ± 0.8	3.1 ± 0.4	1.9 ± 0.6	3.8 ± 1.6	5.8 ± 0.5	4.0 ± 0.4	2.0 ± 0.4
Row	1.7 ± 0.5	2.3 ± 0.6	1.3 ± 0.3	0.6 ± 0.2	2.1 ± 0.5	3.3 ± 0.3	1.7 ± 0.4	1.1 ± 0.2
Unfertilized	1.3 ± 0.5	1.6 ± 0.2	1.1 ± 0.2	1.3 ± 0.4	0.9 ± 0.4	2.0 ± 0.3	1.3 ± 0.1	1.1 ± 0.2
Mean	1.7 ± 0.4	2.9 ± 0.4	1.8 ± 0.3	1.3 ± 0.3	2.3 ± 0.6	3.7 ± 0.4	2.3 ± 0.3	1.4 ± 0.2
	kg N/ha $\pm$ 1 SE							
Fertilized	0.3 ± 0.1	3.3 ± 0.8	2.8 ± 0.5	1.0 ± 0.6	0.4 ± 0.1	4.3 ± 0.7	3.1 ± 0.5	1.3 ± 0.3
Row	0.9 ± 0.3	6.3 ± 2.6	3.8 ± 0.9	0.4 ± 0.1	1.1 ± 0.4	7.4 ± 2.6	4.2 ± 1.5	0.9 ± 0.7
Unfertilized	0.2 ± 0.1	1.3 ± 0.3	1.2 ± 0.3	0.8 ± 0.3	0.3 ± 0.1	1.8 ± 0.4	1.3 ± 0.3	0.7 ± 0.2
Total	1.4 ± 0.4	10.9 ± 2.9	7.6 ± 1.2	2.3 ± 0.9	1.8 ± 0.5	13.4 ± 3.0	8.6 ± 1.7	2.9 ± 0.8

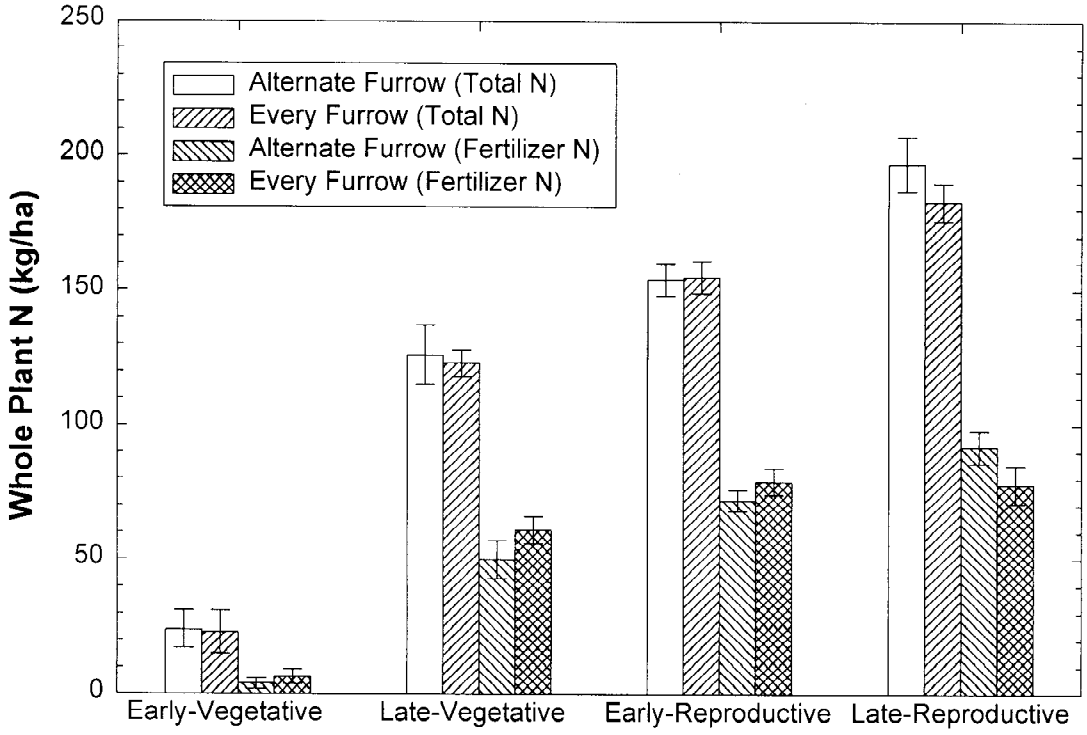

Figure 2. The effect of alternate- and every-furrow irrigation on whole plant N uptake by corn. Error bars represent ± 1 SE. Data have been combined across years. Treatment differences were only significant for fertilizer N at the last harvest.

because of increased N uptake during reproductive growth, which appeared to be related to increased soil NO_3 availability during that same period. Most studies suggest that the majority of N uptake in corn occurs prior to anthesis (Below et al., 1985; Pan et al., 1995; Swank et al., 1982; Tsai et al., 1984), and this was true in our study as well. Even though most N accumulates before anthesis, some researchers have suggested that it is the N taken up during reproductive growth that is most important in determining yield differences due to genetics or the environment (Below et al., 1981; Tsai et al., 1984). One reason might be that the later N is absorbed by corn, the more likely it is to end up in the ear (Mattsson et al., 1993; Ta and Weiland, 1992; Weiland, 1989). We found that 56 and 83% of the fertilizer N was partitioned to reproductive growth under alternate-furrow irrigation in 1995 and 1996, respectively, compared with 50 and 77% under every-furrow irrigation, supporting the contention that increased N uptake during grain filling under alternate-furrow irrigation increased partitioning to ears.

Results are mixed concerning how important the role of remobilized vegetative N is in contributing to ear development. Studies have found that remobilization can contribute anywhere from only a small percentage to the majority of total grain N (Below et al., 1981; Friedrich and Schrader, 1979; Reed et al., 1980; Uhart and Andrade, 1995). When a killing frost terminated growth at R5 in 1995, 83% of total plant N had been taken up prior to R1, yet remobilization contributed only 33% of the total N in ears at the final harvest. In 1996, when the crop reached maturity, we found 75 to 80% of the total N content at maturity had accumulated during vegetative growth, while 67% of the N in ears was remobilized from vegetative tissues. In 1996, when the crop was able to fully mature, the 15% increase in N content of reproductive tissues under alternate-furrow irrigation was the result of a 16% increase in remobilized N from vegetative tissues, and a 13% increase in direct incorporation of newly acquired N. Thus, both processes were enhanced by alternate-furrow irrigation, and appeared to be equally important in increasing N availability to ears.

The calculated values for N remobilization represent the maximum possible contribution of remobilized N to reproductive growth. Some of the N lost from

Table 5. Apparent N remobilization from individual plant parts and from root fractions at different locations beneath the plant

	1995				1996			
	Alternate-Furrow		Every-Furrow		Alternate-Furrow		Every-Furrow	
Plant Part	Amount (Kg/ha)	% Remobilized	Amount (Kg/ha)	% Remobilized	Amount (Kg/ha)	% Remobilized	Amount (Kg/ha)	% Remobilized
Leaves	−14	−27	−12	−22	30	57	34	61
Stalks	22	69	27	78	40	82	42	82
Roots	15	33	23	50	33	77	13	50
Fertilized	2	16	2	24	6	72	4	53
Row	12	50	20	65	25	90	5	52
Unfertilized	1	9	1	14	2	30	4	46
Total Vegetative	23	18	38	27	103	71	89	66

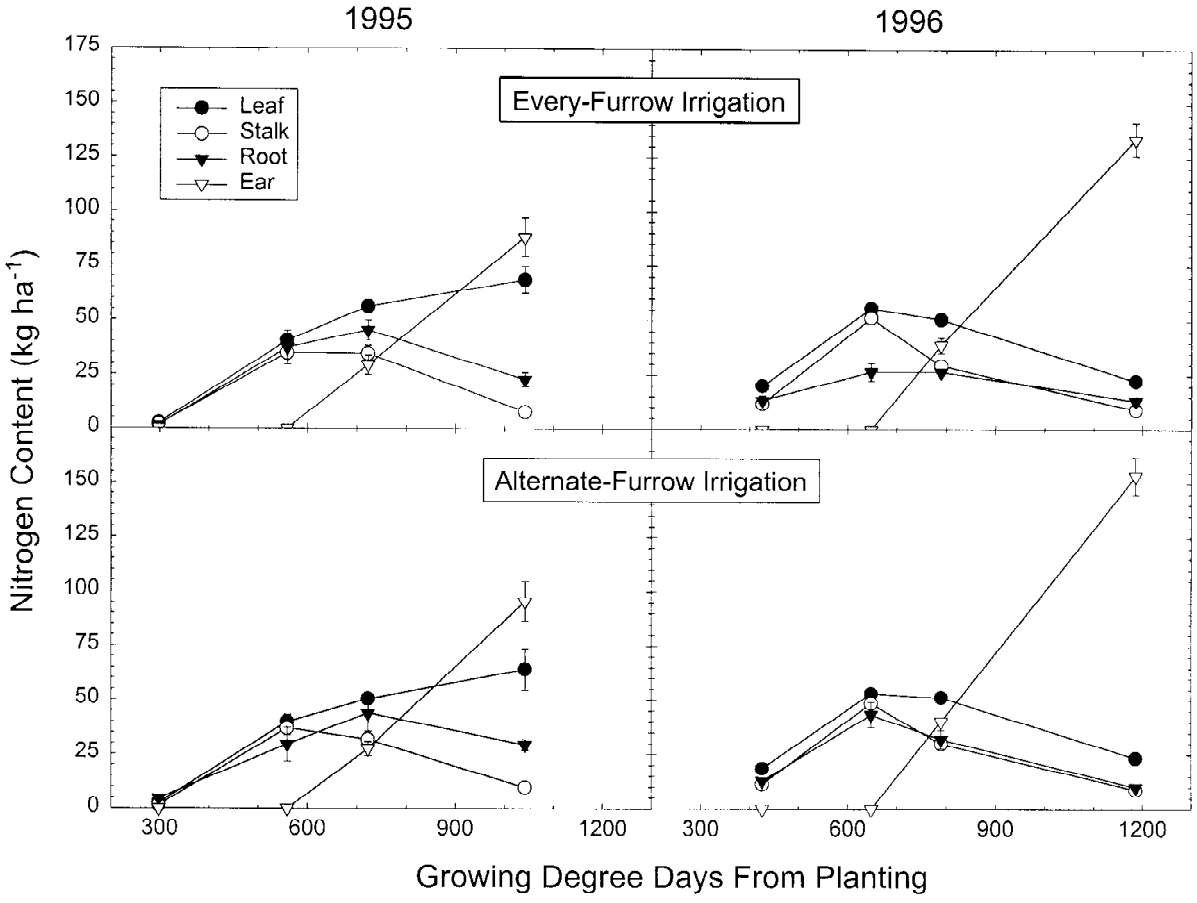

Figure 3. Nitrogen partitioning and remobilization among vegetative and reproductive tissues during corn development. Error bars represent ± 1 SE.

vegetative tissues may have been completely lost from the plant through root decay or volatilization into the atmosphere. Nitrogen losses from volatilization were probably minor. Harper and Sharpe (1995) found that irrigated corn can both emit and absorb NH_3 from the atmosphere during the growing season with a relatively small total net loss of 4 kg N ha^{-1}. Root decay could have potentially caused a greater loss of N from the plant. Combined across treatments, about 25% of total root biomass was lost during reproductive development in 1995 and 55% in 1996. Although extensive research has been conducted on N remobilization from senescing leaves (Martin del Molino et al., 1995; Wittenbach et al., 1980), little is known about remobilization from senescing roots. If we assume that 50% of the nitrogen in those roots was remobilized to younger tissues prior to senescence, then the apparent remobilization from roots in Table 5 would be reduced by about 33% or 3 to 12 kg ha^{-1}. When both potential sources of N loss from the plant are considered together, then the apparent contribution of remobilized N from vegetative tissues could have been reduced by about 30 to 40% in 1995 when remobilization was limited, and by 10 to 15% in 1996.

Remobilization from individual plant parts

The percentage of tissue N that was remobilized was greatest from stalks and least from leaves (Table 5). Some disagreement in the literature exists over the relative importance of remobilization from leaves and stalks. Some reports suggest that remobilization from stalks is relatively unimportant, and that leaves contribute about 90% of the N remobilized from aboveground tissues (Below et al., 1981; Pan et al., 1995). Others have found a more even balance, with stalks and leaves each contributing about 50% of aboveground remobilized N (Ta and Weiland, 1992; Uhart and Andrade, 1995; Zhou et al., 1997). Upon closer examination, remobilization from leaves appeared to be fairly constant at about 35 to 47 kg ha^{-1} in all experiments. Remobilization from stalks was much more variable, ranging from 1 (Pan et al., 1995) to 60 kg ha^{-1} (Zhou et al., 1997).

Planting density appeared to be the most important factor controlling the relative importance of remobilization from leaves and stalks. Stalk remobilization was low when planting densities were less than 40,000 plants ha^{-1} (Below et al., 1981; Pan et al., 1995). When planting density ranged from 60,200 to 88,000 plants ha^{-1}, remobilization from stalks played a more significant role in grain N accumulation (Ta and Weiland, 1992; Uhart and Andrade, 1995; Zhou et al., 1997). Our planting density was in the latter range and the amount of remobilization from stalks that we observed was consistent with the higher plant populations.

The total contribution of remobilized N to grain N tends to be heavily influenced by remobilization from stalks. Thus, only about 33% of the total N in ears came from aboveground remobilization when the contribution from stalks was low (Below et al., 1981; Pan et al., 1995), but nearly 60% was derived from remobilized N when remobilization from stalks was more significant (Ta and Weiland, 1992; Uhart and Andrade, 1995; Zhou et al., 1997). We found that remobilized N contributed 67% of the N found in ears, with about 50% of the N in ears coming from aboveground tissues, in 1996 when remobilization had the chance to be fully expressed.

Few studies have looked at the contribution of root remobilization to N accumulation in ears. Friedrich and Schrader (1979) found that little N was remobilized from roots under high fertility conditions. When they removed N from the nutrient solution at anthesis, however, the amount of N remobilized from roots increased about 5-fold. In contrast, in a study where high and low N levels were maintained throughout the growing season, remobilization was greatest from the well-fertilized roots (Ta and Weiland, 1992).

Continued N uptake during reproductive growth depends on the continual health and integrity of the root system during that period. This would be especially important when soil fertility was low. We found that the greatest percent tissue N loss, and the greatest total remobilization was from roots located beneath the row (Table 5). This was especially true in 1995, suggesting that initial remobilization was predominantly from those roots. This fraction included brace roots, which are functionally similar to stalks, providing support and serving as storage tissues for N and labile carbohydrates with little role in nutrient and water uptake. Large amounts of N could be remobilized from these tissues without having an effect on root uptake functions.

Remobilization was also greater beneath the fertilized compared to the unfertilized furrow. The uptake of NO_3 by corn roots is most likely dependent on the activity of transport proteins (Hole et al., 1990), and is reduced in the presence of the protein synthesis inhibitor, cycloheximide (Laine et al., 1995). Reduced remobilization from roots during reproductive growth

could help maintain root uptake capabilities by maintaining the integrity of transport proteins. Maintenance of the active N uptake system was apparently not as crucial beneath the fertilized furrow as it was beneath the unfertilized furrow, perhaps because higher soil NO_3 concentrations facilitated N uptake.

Vegetative circulation and partitioning

At the late-vegetative harvest, 78% of the fertilizer N was partitioned to aboveground tissues, regardless of irrigation treatment. About 70% of the fertilizer N in roots was found beneath the row or unfertilized furrow. No difference in N partitioning was detected between alternate- or every-furrow irrigation. Benjamin et al. (1994) have suggested that very little lateral movement of mobile chemicals occurs following placement in the dry furrow of an alternate-furrow irrigation system. They found that in heavy textured soils, lateral movement under every-furrow irrigation was greater then under alternate-furrow irrigation, but did not extend beyond the area beneath the furrow of application If roots beneath the row and unfertilized furrow had no direct access to fertilizer N from the soil, then any labeled N must have first been translocated to shoots then returned to the root system via the phloem.

We calculated that 95 to 96% of the N taken up by roots during vegetative growth was translocated to the shoot while only 4 to 5% was incorporated directly into the root system. About 18% of the N supplied to the shoot was then returned to the roots. This cycled N made up 80% of the total N found in roots. There was no difference between alternate- and every-furrow irrigation in the percentage of total N that was cycling between roots and shoots. Cheeseman (1993) suggested that this cycling was necessary for the integration of root and shoot activity. Thus, root growth can be enhanced by deficiencies of N and P, which are readily translocated in the phloem, but not under deficiencies of nutrients with low phloem mobility (Marschner et al., 1996). Cooper and Clarkson (1989) have also suggested that this pool of cycling amino-N could act to control N uptake at the whole plant level.

Alternate- compared with every-furrow irrigation had no effect on cycling in our experiment. When considered along with similarities in root growth and N uptake, it appears that placing fertilizer in the non-irrigated furrow had no adverse effect on N availability or on root N uptake capacity during vegetative growth. With a well established, active root system in the non-irrigated furrow, plants were well situated to take advantage of the additional soil NO_3 which was available during reproductive growth under alternate-furrow irrigation.

The potential increase in productivity from alternate-furrow irrigation could be accompanied by increased risks. Much of the advantage of alternate-furrow irrigation disappeared when a cold, wet spring combined with an early frost in 1995 prevented crop development from being completed. Also, the lack of early season moisture in 1994 led to a 50% decrease in fertilizer uptake under alternate-furrow irrigation (Benjamin et al., 1997). Alternate-furrow irrigation will be most successful when steps are taken to ensure root establishment in the non-irrigated furrow, and when conditions allow full utilization of the additional soil NO_3 made available during reproductive growth.

References

Abreu J P, DE M E, Flores I, De Abreu F M G and Madeira M V 1993 Nitrogen uptake in relation to water availability in wheat. Plant Soil 154, 89–96.

Agrell D, Oscarson P and Larsson C-M 1994 Translocation of N to and from barley roots: its dependence on local nitrate supply in split-root culture. Physiol. Plant. 90, 467–474.

Barber S A 1977 Nutrients in the soil and their flow to plant roots. *In* The below ground ecosystem: a synthesis of plant associated processes. Range Science Department Science Series No 26. Colorado State University, Fort Collins. pp. 161–168.

Below F E, Christensen L E, Reed A J and Hageman R H 1981 Availability of reduced N and carbohydrates for ear development of maize. Plant Physiol. 68, 1186–1190.

Below F E, Crafts-Brandner S J, Harper J E and Hageman R H 1985 Uptake, distribution, and remobilization of ^{15}N-labeled urea applied to maize canopies. Agron. J. 77, 412–415.

Benjamin J G, Havis H R, Ahuja L R and Alonso C V 1994 Leaching and water flow patterns in every-furrow and alternate-furrow irrigation. Soil Sci. Soc. Am. J. 58, 1511–1517.

Benjamin J G, Porter L K, Duke H R and Ahuja L R 1997 Corn growth and nitrogen uptake with furrow irrigation and fertilizer bands. Agron. J. 89, 609–612.

Cheeseman J M 1993 Plant growth modelling without integrating mechanisms. Plant, Cell Environ. 16, 137–147.

Cooper H D and Clarkson D T 1989 Cycling of amino-nitrogen and other nutrients between shoots and roots in cereals: a possible mechanism integrating shoot and root in the regulation of nutrient uptake. J. Exper. Bot. 40, 753–762.

Fischbach P E and Mulliner H R 1974 Every-other furrow irrigation of corn. Trans. ASAE 17, 426–428.

Friedrich J W and Schrader L E 1979 N deprivation in maize during grain-filling. II. Remobilizaton of ^{15}N and ^{35}S and the relationship between N and S accumulation. Agron. J. 71, 466–472.

Harper L A and Sharpe R R 1995 Nitrogen dynamics in irrigated corn: soil-plant nitrogen and atmospheric ammonia transport. Agron. J. 87, 669–675.

Hole D J, Emran A M, Fares Y and Drew MC 1990 Induction of nitrate transport in maize roots, and kinetics of influx, measured with nitrogen-13. Plant Physiol. 93, 642–647.

Jensen M E 1973 Consumptive use of water and irrigation water requirements. Irrigation and Drainage Division, American Society of Civil Engineers, New York. 215 p.

Karrou M and J W Maranville 1994 Response of wheat cultivars to different soil nitrogen and moisture regimes: II. Nitrogen uptake, partitioning and influx. J. Plant Nutr. 17, 745–761.

Laine P, Ourry A and Boucaud J 1995 Shoot control of nitrate uptake rates by roots of *Brassica napus* L.: effects of localized nitrate supply. Planta 196, 77–83.

Lambers H, Simpson R J, Beilharz V C and Dalling M J 1982 Growth and translocation of C and N in wheat (*Triticum aestivum*) grown with a split root system. Physiol. Plant. 56, 421–429.

Marschner H, Kirkby E A and Cakmak I 1996 Effect of mineral nutritional status on shoot-root partitioning of photoassimilates and cycling of mineral nutrients. J. Exper. Bot. 47, 1255–1263.

Martin del Molino L M, Martinez-Carrasco R, Perez P, Hernandez L, Morcuende R and Sanchez de la Puente L 1995 Influence of nitrogen supply and sink strength on changes in leaf nitrogen compounds during senescence in two wheat cultivars. Physiol. Plant. 95, 51–58.

Mattsson M, Lundborg T and Larsson C-M 1993 Nitrogen utilization in N-limited barley during vegetative and generative growth. J. Exper. Bot. 44, 537–546.

Pan W L, Camberato J J, Moll R H, Kamprath E J and Jackson W A 1995 Altering source-sink relationships in prolific maize hybrids: consequences for nitrogen uptake and remobilization. Crop Sci. 35, 836–845.

Reed A J, Below F E and Hageman R H 1980 Grain protein accumulation and the relationship between leaf nitrate reductase and protease activities during grain development in maize (*Zea mays* L.). I. Variation between genotypes. Plant Physiol. 66, 164–170.

Ritchie S W and Hanway J J 1982 How a corn plant develops. Special Report 48. Revised Edition. Iowa State University Cooperative Extension Service, Ames IA.

Skinner R H, Hanson J D and Benjamin J G 1998 Root distribution following spatial separation of water and nitrogen supply in furrow irrigated corn. Plant Soil 199, 187–194.

Swank J S, Below F E, Lambert R J and Hageman R H 1982 Interaction of carbon and nitrogen metabolism in the productivity of maize. Plant Physiol. 70, 1185–1190.

Ta C T and Weiland R T 1992 Nitrogen partitioning in maize during ear development. Crop Sci. 32, 443–451.

Tsai C Y, Huber D M, Glover D V and Warren H L 1984 Relationship of N deposition to grain yield and N response of three maize hybrids. Crop Sci. 24, 277–281.

Uhart S A and Andrade F H 1995 Nitrogen and carbon accumulation and remobilization during grain filling in maize under different source/sink ratios. Crop Sci. 35, 183–190.

Weiland R T 1989 Maize (*Zea mays* L.) hybrid use of ^{15}N-nitrate absorbed vegetatively by roots. Can. J. Plant Sci. 69, 383–393.

Wittenbach V A, Ackerson R C, Giaquinta R T and Hebert R R 1980 Changes in photosynthesis, ribulose bisphosphate carboxylase, proteolytic activity, and ultrastructure of soybean leaves during senescence. Crop Sci. 20, 225–231.

Zhou X M, Madramootoo C A, MacKenzie A F and Smith D L 1997 Biomass production and nitrogen uptake in corn-ryegrass systems. Agron. J. 89, 749–756.

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