

# Utilization of Previously Accumulated and Concurrently Absorbed Nitrogen during Reproductive Growth in Maize<sup>1</sup>

INFLUENCE OF PROLIFICACY AND NITROGEN SOURCE

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## ABSTRACT

A prolific maize (*Zea mays* L.) genotype was grown to physiological maturity under greenhouse conditions to examine the effects of reproductive sink demand on (a) the remobilization of N accumulated during vegetative growth, and (b) the partitioning of N accumulated concurrent with ear development. One- and two-eared plants were treated with either a  $\text{NO}_3^-$  or  $\text{NH}_4^+$  source of  $^{15}\text{N}$ -labeled N during reproductive growth. Plants with two ears enhanced grain production, N remobilization from the stalk and roots, and N translocation to the grain from concurrently assimilated N. But, remobilization of leaf-N was unaffected by ear number. In addition, N uptake and total dry matter accumulation during the reproductive period were also unaffected, although P uptake was greater in the two-eared plants. Less than 15% of the total  $\text{K}^+$  uptake was accumulated after silking while during this time more than 40% of the total N and more than 50% of the total P were absorbed. The data also indicate that with  $\text{NO}_3^-$  nutrition, internal recirculation of  $\text{K}^+$  between shoots and roots may play a prominent role in the transport of nitrogenous solutes during grain development. N source had no effect on dry matter production and N uptake of both one- and two-eared plants. However, slightly greater partitioning of labeled-N from the  $\text{NH}_4^+$  source to the grain was observed in the two-eared plants.

one versus two ears per plant on accumulation and partitioning of dry matter and N during reproductive growth of a prolific maize hybrid. This experimental hybrid produces two comparably sized ears under nonstressed conditions. One-eared plants of this genotype were produced by preventing pollination of the lower earshoot. Controlling ear number in a single genotype by this method avoids the potentially confounding factors encountered in other studies of (a) differences other than ear number between one-eared and two-eared genotypes (15, 19) and (b) differences in microenvironmental conditions that may exist between naturally occurring one- and two-eared plants (1, 15). In contrast to partitioning studies using one-eared genotypes (5, 6) in which reduction of sink size involved complete elimination of grain formation, sink size can be reduced in two-eared genotypes while maintaining, at a reduced rate, the processes involved in grain formation. Utilization of  $^{15}\text{N}$ -labeled urea (together with a nitrification inhibitor) or  $^{15}\text{N}$ -labeled  $\text{Ca}(\text{NO}_3)_2$  applied at the initiation of ear development allowed an assessment of the effects of the second ear and of the two forms of N on remobilization of N accumulated previous to silk emergence and the partitioning of N accumulated after silk emergence. The differential consequences of these treatments on acquisition and distribution of P and  $\text{K}^+$  during reproductive growth were also assessed.

## MATERIALS AND METHODS

The increased sink capacity associated with development of a second ear in prolific maize hybrids tends to increase both total dry matter production and total grain weight (1, 15). Similarly, total N uptake and total grain-N were greater in two-eared plants than one-eared plants (1). During reproductive growth, greater net loss of dry matter and N occurred from the stalks of two-eared plants than one-eared plants (1, 19).

The relative amounts and ratios of  $\text{NO}_3^-$  and  $\text{NH}_4^+$  in the root zone during reproductive development influenced total N uptake and N partitioning in maize (13, 19). Field studies indicated that two-eared genotypes produced more grain and accumulated more grain-N when  $\text{NH}_4^+$  rather than  $\text{NO}_3^-$  was the predominant N form available (19). With  $\text{NH}_4^+$  nutrition, a greater proportion of the accumulated N was translocated to the grain. In contrast, one-eared genotypes performed as well or better with the  $\text{NO}_3^-$  source.

In this investigation, comparisons were made of the effects of

**Plant Culture.** An experimental prolific genotype of maize (*Zea mays* L.) was selected for this study. In previous studies, this genotype exhibited increased grain production when  $\text{NH}_4^+$  rather than  $\text{NO}_3^-$  was supplied during reproductive growth (genotype D) (19). This single-cross hybrid was made from unselected inbred lines derived from 'Jarvis Golden Prolific' and 'Indian Chief' cultivars. Plants were grown to physiological maturity under greenhouse conditions. Maize seeds were planted on February 23, 1984, in each of 29 pots. Each pot contained 45 kg of sandy loam soil. Plants were thinned to one per pot 5 d after germination. Plants were harvested June 4 (103 DAP<sup>2</sup>) after the black layer formed in the grain. Maximum daytime temperatures were maintained below 39°C by evaporative cooling. Plants were watered before visible water stress, but not excessive enough to cause leaching of nutrients from the pots. The soil used was composed of the surface horizons from several soil series belonging to the Paleudult soil order. Prior to amendment the soil had a pH of 5.0, and contained 0.50 meq  $\text{Al}^{3+}$  100 g<sup>-1</sup> soil, 0.14 meq  $\text{Mg}^{2+}$  100 g<sup>-1</sup> soil, 0.44 meq  $\text{Ca}^{2+}$  100 g<sup>-1</sup> soil, 0.09 meq  $\text{K}^+$  100 g<sup>-1</sup> soil, and 13  $\mu\text{g}$  available P g<sup>-1</sup> soil. Effective cation exchange

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<sup>2</sup> Abbreviation: DAP, days after planting.

capacity was 1.17 meq 100 g soil<sup>-1</sup> and organic matter content was 1.1%. In accord with soil analysis 0.4 g KH<sub>2</sub>PO<sub>4</sub> kg<sup>-1</sup> soil and 0.73 g dolomitic lime (21% Ca, 12% Mg) kg<sup>-1</sup> soil were thoroughly mixed into the soil prior to planting. Soil acidity at planting was pH 6.2.

At time of planting 0.66 g N plant<sup>-1</sup> was surface-applied as (NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub> in solution. Ammonium is completely nitrified within 14 d under these soil conditions (4). Additional N was supplied during vegetative growth as Ca(NO<sub>3</sub>)<sub>2</sub> at 2.47 g N plant<sup>-1</sup> application<sup>-1</sup> at 26 and 52 DAP.

At silk emergence (70 DAP), 5 plants were sampled for determination of dry matter and nutrient composition in the leaves, stalks, roots, and earshoots. The remaining plants were divided into two groups (12 plants each) that were fertilized at 70 and 90 DAP with either of two N sources. At each time interval, 1.64 g N were applied to each pot as solutions of either Ca(NO<sub>3</sub>)<sub>2</sub> or urea + nitrapyrin. Both sources were enriched with 5 atom % <sup>15</sup>N. Nitrapyrin, a nitrification inhibitor, was supplied at a rate of 52 mg plant<sup>-1</sup> application<sup>-1</sup> in solution with the dissolved urea. All N treatments were surface applied as solutions during daily watering (~1.5 L plant<sup>-1</sup> day<sup>-1</sup>). Two applications of N and nitrapyrin were made during ear development to maintain the efficacy of nitrapyrin (19).

Within each N treatment, 6 plants were allowed to fully pollinate both top and bottom earshoots, while pollination of the bottom earshoot of 6 plants was prevented by covering the shoot with a paper bag prior to silk emergence. The 6 replicates of each of 4 N source-ear number combinations were arranged in a randomized complete block design.

**Plant Analyses.** Leaves, stalks, roots, grain, and cob + husk were separated, oven dried at 70°C, weighed, and analyzed for nutrient composition. Nitrogen values reported herein include NO<sub>3</sub><sup>-</sup>-N reduced with salicylic acid/sulfuric acid prior to Kjeldahl digestion (16). Ammonium in the digest was determined spectrophotometrically (3). Ammonium was then recovered from the digest by diffusion and analyzed for <sup>15</sup>N enrichment by mass spectrometry (22). Nitrogen accumulation in each plant part derived from the <sup>15</sup>N-labeled fertilizer was determined by multiplying A% excess <sup>15</sup>N by the total N in each plant part and dividing by the A% excess <sup>15</sup>N of the applied fertilizer. Nitrate in stalk tissue was extracted with hot water (97°C) for 1 h and determined by a manual modification of the procedure of Lowe and Hamilton (12). Potassium was determined by flame photometry, and Ca<sup>2+</sup> and Mg<sup>2+</sup> were analyzed by atomic absorption spectrometry.

## RESULTS

**Dry Matter Production and Partitioning.** Fifty percent of the total dry matter at maturity was accumulated after silking (Table I). Ear number altered dry matter partitioning, although total dry matter accumulation was unaffected. Two-eared plants produced 63% more grain plant<sup>-1</sup> than one-eared plants. Net increase in stalk weight between silk emergence and maturity were less than 13% for the two-eared plants, but greater than 65% for the one-eared plants. Root weight of two-eared plants was greater at silk emergence than at maturity. In contrast, one-eared plants exhibited similar root weights at silking and maturity. Changes in leaf dry matter between silk emergence and maturity were relatively small and not altered by differences in ear number. The form of N had no effect on total dry matter accumulation or yield of grain for either one- or two-eared plants.

**Uptake and Partitioning of N Absorbed after Silk Emergence.** For the four treatments, the <sup>15</sup>N-labeled sources provided from 73 to 78% of the total N accumulated by the plants between silk emergence and maturity (Table II). The remainder of the N that accumulated during this period was derived from mineralization of soil organic matter and/or unlabeled-N that was applied prior

to silk emergence and that remained in the soil by silk emergence.

Although 41 to 43% of the total N accumulation occurred after silk emergence, N uptake was unaffected by ear number or N source (Table II). However, significant N source × ear number interaction occurred for labeled -N partitioning to the top ear (Table III). Thus, two-eared plants partitioned to the grain 76 and 69% of total N absorbed from <sup>15</sup>N-labeled sources when grown on NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup>, respectively (Table III). In contrast, one-eared plants partitioned only 51% to the grain, regardless of N source, while accumulating a greater proportion in the stalk and roots. Only 6% of the total N absorbed from <sup>15</sup>N-labeled sources was retained in the leaves, and neither ear number nor N source affected leaf accumulation.

**Redistribution of N Accumulated Prior to Silk Emergence.** During reproductive growth leaves, stalks, and roots lost previously accumulated N (Table IV). Whereas the amount lost from the leaves was not affected by ear number or N source, the development of a second ear stimulated greater remobilization of N from the stalk and roots. This resulted in greater overall remobilization of N from vegetative tissues in two- versus one-eared plants, 2.52 versus 1.84 g plant<sup>-1</sup>, respectively.

Accumulation of N in the stalk and roots of one-eared plants after silking was more than sufficient to replace the previously accumulated N remobilized to the grain, resulting in a net gain of N in these tissues (Table II). In comparison, the loss of 0.91 g of previously accumulated N from the leaves (Table IV) far outweighed the 0.19 g N that accumulated during ear development, which resulted in a net loss of 0.72 g from the leaves (Table II). A similar balance of leaf-N was exhibited by two-eared plants. However, the stalk and roots of the two-eared plants showed a net loss of N during ear development due to both greater remobilization of N accumulated prior to silking (Table IV) and lower deposition of concurrently accumulated N (Table III).

**Origin of Grain-N.** Second ear development stimulated a 46 and 39% increase of total grain-N accumulation of NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup> exposed plants, respectively (Table V). Nitrogen accumulated prior to silking contributed 1.62 g N plant<sup>-1</sup> to the grain of one-eared plants, which represented 53% of the total grain-N. Increased grain-N accumulation in two-eared plants resulted from greater contributions from both N accumulated prior to silking and N absorbed concurrent with grain fill. Consequently, the proportion of grain-N derived from N absorbed during the two developmental stages were similar in both one- and two-eared plants. There was no difference between the two N sources in the contribution of previously accumulated N to the grain (2.52 g N plant<sup>-1</sup>) whereas 2.65 and 2.18 g N plant<sup>-1</sup> in the grain was derived from concurrently absorbed N for the NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup> sources, respectively.

Although N source did not affect the amount of grain produced (Table I), the NH<sub>4</sub><sup>+</sup> source resulted in slightly greater grain-N concentration than the NO<sub>3</sub><sup>-</sup> sources, 2.35% N versus 2.27% N, respectively for one-eared plants and 2.11% N versus 1.93% N, respectively for two-eared plants (data not shown). Hence for each N source, N concentration as well as total N (Table V) of the top ear was decreased slightly by the formation of a second ear. Total grain-N showed a tendency to be greater when NH<sub>4</sub><sup>+</sup> was the N source, 3.52 g N plant<sup>-1</sup> versus 3.39 g N plant<sup>-1</sup> for one-eared plants, and 5.15 g N plant<sup>-1</sup> versus 4.72 g N plant<sup>-1</sup> for two-eared plants (Table V). The differences due to N treatment were significant at the 0.07 level of probability.

**Uptake and Partitioning of Phosphorus.** Fifty-one to 63% of the total P uptake occurred between silk emergence and maturity (Table VI). Development of a second ear influenced both uptake and partitioning of P. With both N sources, total uptake of P of two-eared plants during reproductive growth was greater than that of one-eared plants (Table VI), in spite of the decrease in

Table I. Plant Part Weights at Silk Emergence and Change in Total Plant Part Weight ( $\Delta W_i$ ) between Silk Emergence ( $W_s$ ) and Physiological Maturity ( $W_m$ ), where  $\Delta W_i = W_m - W_s$ 

N Source	Ears Plant <sup>-1</sup>	Leaves	Stalk	Roots	Top Ear		Bottom Ear		Total
					Grain	Cob + husk	Grain	Cob + husk	
$W_s$									
<i>g dry wt part<sup>-1</sup></i>									
		61	136	105		12 <sup>a</sup>			314
$\Delta W_i$									
<i>Δ g dry wt part<sup>-1</sup></i>									
Ammonium	1	+9	+93	+12	+150	+53			+317
	2	+9	+17	-31	+152	+40	+92	+33	+312
Nitrate	1	+7	+89	-2	+149	+48			+291
	2	+17	+9	-25	+141	+37	+103	+31	+313
N source		NS <sup>b</sup>	NS	NS	NS	NS	NS	NS	NS
Ear No.		NS	— <sup>c</sup>	—	NS	—			NS
N source × ear No.		NS	NS	NS	NS	NS			NS

<sup>a</sup> Sample comprises entire earshoot, husk, and silks.

<sup>b</sup> Not significant.

<sup>c</sup> — = Significant F test at the 0.05 level.

total root mass during this time (Table I). The development of a second ear resulted in the net loss of 0.10 g P plant<sup>-1</sup> from the stalk between silk emergence and maturity. In the roots the P content of one-eared plants increased while the P content of two-eared plants decreased. The P content of leaves decreased by only 0.05 g P plant<sup>-1</sup> between silk emergence and maturity, and there were no differential effects of N source or ear number on this movement.

Nitrogen source affected the total uptake of P during reproductive growth. Uptake by plants receiving NO<sub>3</sub><sup>-</sup> averaged 0.65 g P plant<sup>-1</sup> whereas plants receiving NH<sub>4</sub><sup>+</sup> averaged 0.80 g P plant<sup>-1</sup> (Table VI). In plants receiving NH<sub>4</sub><sup>+</sup> the concentration of P was greater in the leaves, stalks, and grain than in plants receiving NO<sub>3</sub><sup>-</sup> (data not shown).

**Uptake of Potassium.** Uptake of K<sup>+</sup> during ear development was relatively small, although it was increased significantly by presence of the second ear (Table VII). Only 5 and 14% of the total K<sup>+</sup> content was absorbed after silk emergence for one- and two-eared plants, respectively. No significant changes in K<sup>+</sup> content of leaves or stalks occurred in any of the four treatment combinations. In roots, one-eared plants increased slightly in K<sup>+</sup> content, whereas a slight decrease occurred in two-eared plants.

**Cation and Anion Uptake.** Exposure to the two N sources during ear development altered appreciably the relative proportion of cation and anion uptake during this period (Table VIII). Estimates of the extent of this difference can be made on the following assumptions: (a) N uptake prior to silk emergence was entirely as NO<sub>3</sub><sup>-</sup>. Nitrification of initially applied (NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub> is sufficiently rapid; it was 100% complete in the period 7 to 14 d after application (4), so that little NH<sub>4</sub><sup>+</sup> remained shortly after germination (5 DAP). In addition uptake of NH<sub>4</sub><sup>+</sup> shortly after germination is minor when compared to total N uptake between germination and silking; (b) N uptake after silk emergence in the NO<sub>3</sub><sup>-</sup> treatment was entirely as NO<sub>3</sub><sup>-</sup>; (c) N uptake after silking of soil-N in the urea (+ nitrapyrin) treatment was as NO<sub>3</sub><sup>-</sup>; (d) N uptake after silking of the applied <sup>15</sup>N-labeled urea (+ nitrapyrin) treatment was as NH<sub>4</sub><sup>+</sup>. Urea hydrolysis is complete after 2 d in soils of this type, but nitrification is effectively inhibited by the rates of nitrapyrin used (4) so that the NH<sub>4</sub><sup>+</sup> produced by the rapid hydrolysis of urea remained in the NH<sub>4</sub><sup>+</sup> form; and (e) the quantities of ions (e.g. Na<sup>+</sup>, Cl<sup>-</sup>, SO<sub>4</sub><sup>-2</sup>) taken up other than

those measured were not sufficiently large to alter appreciably the cation/anion uptake ratio established by the measured ions.

During vegetative growth cation uptake was significantly less than anion uptake primarily due to the large uptake of NO<sub>3</sub><sup>-</sup> (Table VIII). When NO<sub>3</sub><sup>-</sup> fertilization was continued through grain formation, this tendency became even more pronounced as relatively little K<sup>+</sup> was absorbed and NO<sub>3</sub><sup>-</sup> uptake remained substantial. When urea was supplied after silking, significant NH<sub>4</sub><sup>+</sup> uptake resulted in cation uptake substantially exceeding anion uptake, although the effect may have been slightly less in two-eared plants.

## DISCUSSION

The reproductive sink size of this prolific maize genotype was decreased by preventing the pollination of the lower earshoot. This alteration had no effect on total dry matter production, although the partitioning of dry matter among leaves, stalks, roots, and grain changed dramatically (Table I). In contrast, other studies of maize have indicated that net photosynthesis can be affected by changes in source-sink relationships between leaves and developing grain. Earshoot removal from nonprolific maize has resulted in decreased total dry matter production (5, 6) and decreased leaf carbon exchange rates (2, 14, 21), while enhancing the storage of stalk carbohydrates (5, 6) and the flux of photosynthate to plant roots (18). Similarly, comparisons of prolific and nonprolific maize genotypes have revealed positive relationships between reproductive sink size and total dry matter production (15). In addition, a study comparing naturally occurring one- and two-eared plants of two semiprofitic genotypes suggested an increase in reproductive sink demand may enhance net photosynthesis (1). The present experiment did not demonstrate an effect of ear number on dry matter accumulation between artificially manipulated one- and two-eared plants (Table I). Similar results have also been obtained under field conditions (WL Pan, unpublished data). In both instances an increase in sink demand only changed the proportional partitioning of dry matter among plant tissues, with two-eared plants exhibiting greater dry matter translocation to the grain at the expense of dry matter accumulation in the stalk and roots (Table I).

Similarly, the formation of a second ear did not enhance total N uptake, but did alter the partitioning of N within the plant

Table II. Total N in Each Plant Part at Silk Emergence ( $N_r$ )

The net change in total N content ( $\Delta N$ ) between silk emergence (S) and physiological maturity (M), where  $\Delta N = M - S$ . Total N in each plant part derived from the  $^{15}\text{N}$ -labeled N source<sup>a</sup> is given in parentheses. The latter represent absolute values measured at physiological maturity as the  $^{15}\text{N}$ -labeled N sources were first applied at silk emergence.

N Source	Ears Plant <sup>-1</sup>	Leaves		Stalk	Roots	Top Ear		Bottom Ear		Total
		Grain	Cob + husk			Grain	Cob + husk			
		$N_r$								
		$g\ N\ part^{-1}$								
		$\Delta N$								
		$\Delta\ g\ N\ part^{-1}\ (g\ ^{15}\text{-labeled}\ N\ part^{-1})$								
Ammonium	1	-0.72 (0.14)	+0.05 (0.56)	+0.36 (0.38)	+0.36 (0.38)	+3.52 (1.20)	+0.03 (0.08)	+1.92 (0.69)	+0.15 (0.04)	+3.24 (2.36)
	2	-0.71 (0.16)	-0.95 (0.18)	-0.16 (0.15)	-0.16 (0.15)	+3.23 (1.24)	+0.00 (0.07)			+3.48 (2.53)
Nitrate	1	-0.73 (0.14)	+0.21 (0.62)	+0.22 (0.34)	+0.22 (0.34)	+3.39 (1.23)	+0.01 (0.08)	+1.95 (0.71)	+0.13 (0.03)	+3.10 (2.41)
	2	-0.74 (0.13)	-0.81 (0.25)	-0.08 (0.28)	-0.08 (0.28)	+2.77 (0.94)	-0.08 (0.04)			+3.14 (2.38)
N source		NS <sup>c</sup>	NS	NS	NS	NS	NS	NS	NS	NS
Ear No.		NS	NS	NS	NS	NS	NS	NS	NS	NS
N source x Ear No.		NS	NS	NS	NS	NS	NS	NS	NS	NS

<sup>a</sup> Labeled N =  $N_r$  ( $A\% \ ^{15}\text{N}_r - 0.358$ ), where  $N_r$  = total N in each plant part;  $A\% \ ^{15}\text{N}_r$  and  $A\% \ ^{15}\text{N}_r$  = the atom percent  $^{15}\text{N}$  measured in  $N_r$  and the original labeled N sources applied during ear development, respectively. The atom percent  $^{15}\text{N}$  measured in plant material not exposed to  $^{15}\text{N}$ -labeled fertilizer, *i.e.* plants harvested at silking, was 0.358 %  $^{15}\text{N}$ .

<sup>b</sup> Sample compromise entire earshoot, husk, and silks.

<sup>c</sup> Not significant.

<sup>d</sup> = Significant *F* test at the 0.05 level.

(Table II). In comparison to one-eared plants, two-eared plants partitioned more concurrently absorbed N to the grain, 73 versus 51%, and less N to the stalk, 9 versus 25% (Table III). The remobilization of root- and stalk-N accumulated prior to silk emergence was also increased by the formation of a second ear. Two-eared plants remobilized 0.41 g N plant<sup>-1</sup> from the roots, whereas one-eared plants only remobilized 0.19 g N plant<sup>-1</sup> (Table IV). In addition 1.17 g N plant<sup>-1</sup> were remobilized from the stalks of two-eared plants, nearly double the amount (0.66 g N plant<sup>-1</sup>) remobilized from the stalks of one-eared plants. Unlike the roots and stalks, remobilization from the leaves of the N accumulated prior to silk emergence was not stimulated by the presence of a second ear; both one-eared and two-eared plants remobilized a large amount of leaf-N, 0.92 g N plant<sup>-1</sup> (Table IV).

Analyses of the stalks for  $\text{NO}_3^-$  as well as total N permits estimates of the removal during reproductive growth of both  $\text{NO}_3^-$  and reduced-N which had accumulated by silk emergence. Because  $^{15}\text{N}$  enrichment in  $\text{NO}_3^-$  was not determined, precise values cannot be obtained. However, calculations based on either of two boundary conditions permit the definition of a range of values for the removal of the two N fractions. The range of values is sufficiently narrow that the numbers can be meaningfully interpreted. The boundary conditions are (a) all of the  $\text{NO}_3^-$ -N accumulated prior to silking was removed from the stalk, and accumulation of  $\text{NO}_3^-$ -N after silking accounted for the  $\text{NO}_3^-$ -N present in the stalk at maturity. The accumulation of  $\text{NO}_3^-$ -N after silking may have originated from  $\text{NO}_3^-$  previously stored in the roots or from concurrently absorbed  $\text{NO}_3^-$ . For the opposing extreme possibility, it is assumed in boundary condition (b) that  $\text{NO}_3^-$ -N in the stalk at harvest originated from  $\text{NO}_3^-$ -N accumulated in the stalk prior to silking, *i.e.* no  $\text{NO}_3^-$ -N translocated to the stalk during ear development remained in the stalk at maturity.

The data for the one-eared plants with the  $\text{NH}_4^+$  source (Table IX) may be used to illustrate the calculations, all in g N plant<sup>-1</sup>. For the total N ( $\text{NO}_3^-$ -N + reduced-N), the labeling data show an accumulation of 0.77 g N after silking ( $N_a$ , as described in Table IV) and a loss of 0.72 g of previously accumulated N ( $\Delta N_r$ , Table IV) for a net total gain of 0.05 g N. Concomitantly, there was a net loss of 0.58 g as  $\text{NO}_3^-$ -N which can be accounted for either by a loss of all  $\text{NO}_3^-$ -N present at silking, 0.67 g, and a gain of 0.09 g  $\text{NO}_3^-$ -N after silking (boundary condition a), or by a loss of 0.58 g previously accumulated  $\text{NO}_3^-$ -N with no accumulation of  $\text{NO}_3^-$ -N after silking (boundary condition b). Therefore between 87 to 100% of the previously accumulated  $\text{NO}_3^-$ -N was removed from the stalks during reproductive growth. In addition, a net gain in total N of 0.05 g and a net loss of  $\text{NO}_3^-$ -N of 0.58 g indicates there must have been a net accumulation of 0.63 g of reduced-N. Again, upper and lower boundaries may be calculated for the extent to which N accumulation after silking and loss of N accumulated prior to silking contributed to the net change in reduced-N. For boundary condition (a), 0.05 g of previously accumulated reduced-N was remobilized and 0.68 g of reduced-N was accumulated after silking. For boundary condition (b) the two values are 0.14 and 0.77 g. Hence from 4 to 12% of the reduced-N accumulated prior to silking was removed from the stalks of the one-eared plants during reproductive growth when treated with urea (+ nitrapyrin). In spite of only being able to calculate a range of values for the remobilization of  $\text{NO}_3^-$ -N and reduced-N from the stalk, it is clear that  $\text{NO}_3^-$ -N was removed considerably more effectively than reduced-N under these experimental conditions.

Presence of the second ear had no significant effect on removal of previously accumulated  $\text{NO}_3^-$ -N from the stalks but increased appreciably the removal of reduced-N accumulated prior to silking (Table IX). In addition, substantially less reduced-N was accumulated during reproductive growth in the stalks of the two-

Table III. Proportion of Total N Absorbed from <sup>15</sup>N-Labeled N Sources Contained in Each Plant Part at Maturity

N Source	Ears Plant <sup>-1</sup>	Leaves	Stalk	Roots	Top Ear		Bottom Ear		Total Grain
					Grain	Cob + husk	Grain	Cob + husk	
						%			
Ammonium	1	6	24	16	51	3			51
	2	6	7	6	49	3	27	2	76
Nitrate	1	6	26	14	51	3			51
	2	5	11	12	39	2	30	1	69
N source		NS <sup>a</sup>	NS	NS	NS	NS	NS	NS	NS
Ear No.		NS	— <sup>b</sup>	—	—	NS			*
N source × ear No.		NS	NS	NS	—	NS			NS

<sup>a</sup> Not significant. <sup>b</sup> — = Significant *F* test at the 0.05 level.

Table IV. Mobilization between Silk Emergence and Physiological Maturity of N Accumulated Prior to Silk Emergence ( $\Delta N_v$ )

These calculations are based on the assumption that all N absorbed after silk emergence was distributed among the plant parts in the same proportion as the <sup>15</sup>N accumulated from the labeled sources. *Example calculation:* Values given in Table II for one-eared plants exposed to the NH<sub>4</sub><sup>+</sup> source (all values in g N plant<sup>-1</sup>):  $\Delta N$  (stalk) = +0.05, <sup>15</sup>N-labeled N (stalk) = 0.56,  $\Delta N$  (whole plant) = 3.24, and <sup>15</sup>N-labeled N (whole plant) = 2.36. Based on this assumption, N in the stalk at maturity that was derived from N absorbed after silking (*N<sub>a</sub>*) is calculated as *N<sub>a</sub>* = 0.56 (3.24/2.36) = 0.77. Then  $\Delta N_v$  =  $\Delta N$  (stalk) -  $\Delta N_a$  = 0.05 - 0.77 = -0.72 g N.

N Source	Ears Plant <sup>-1</sup>	Leaves	Stalk	Cob + Husk	Roots	Total
						<i>g N part<sup>-1</sup></i>
Ammonium	1	-0.91	-0.72	-0.08	-0.16	-1.87
	2	-0.93	-1.20	0.00 <sup>a</sup>	-0.37	-2.50
Nitrate	1	-0.91	-0.59	-0.09	-0.22	-1.81
	2	-0.91	-1.14	-0.04 <sup>a</sup>	-0.45	-2.54
N source		NS <sup>b</sup>	NS	NS	NS	NS
Ear No.		NS	— <sup>c</sup>	—	—	—
N source × ear No.		NS	NS	NS	NS	NS

<sup>a</sup> Represents summation of top and bottom ears. <sup>b</sup> Not significant. <sup>c</sup> — = Significant *F* test at the 0.05 level.

Table V. Quantities of Grain-N Derived from N Accumulated during Reproductive Growth (*N<sub>a</sub>*) and N Accumulated Prior to Silk Emergence (*N<sub>v</sub>*)

See Table IV for equations derived for calculating *N<sub>a</sub>* and *N<sub>v</sub>*.

N Source	Ears Plant <sup>-1</sup>	<i>N<sub>a</sub></i>	<i>N<sub>v</sub></i>	Total N	$\frac{N_v}{Total\ N} \times 100$
					%
Ammonium	1	1.65	1.87	3.52	53
	2-T <sup>a</sup>	1.70	1.53	3.23	47
	2-B <sup>b</sup>	0.95	0.97	1.92	51
	2-total	2.65	2.50	5.15	49
Nitrate	1	1.58	1.81	3.39	53
	2-T	1.24	1.53	2.77	55
	2-B	0.94	1.01	1.95	52
	2-total	2.18	2.54	4.72	54

<sup>a</sup> Top ear. <sup>b</sup> Bottom ear.

eared plants. Thus, for the NH<sub>4</sub><sup>+</sup> treatment, from 45 to 53% of the reduced-N accumulated prior to silking was removed from the stalks of the two-eared plants compared with 4 to 12% for the one-eared plants.

The effects of ear number on remobilization of NO<sub>3</sub><sup>-</sup>-N and reduced-N accumulated prior to silking from the stalks of plants treated with NO<sub>3</sub><sup>-</sup> (Table IX) were less definitive because wider ranges result from the two contrasting assumptions used to provide the estimates. Nevertheless, the patterns were similar; presence of the second ear had little effect on the net removal of NO<sub>3</sub><sup>-</sup> but increased the remobilization of reduced-N accumu-

lated prior to silking and decreased the accumulation of reduced-N during reproductive growth. The data do not indicate any measurable differences between the two N sources in the relative loss of previously accumulated reduced-N from the stalks.

The data clearly emphasize the importance of remobilization of N accumulated prior to silking in providing N to the developing grain (1, 7, 8, 19, 20). The remobilization of stalk reduced-N is thought to involve proteolysis (9, 20), although sufficient stalk protease activity was not detected by Reed *et al.* (20). Although it appears that remobilization of stalk and root reduced-N was stimulated by a factor associated with prolificacy,

Table VI. Total P in Each Plant Part at Silk Emergence and Change in P Content between Silk Emergence and Physiological Maturity

N Source	Ears Plant <sup>-1</sup>	Leaves	Stalk	Roots	Top Ear		Bottom Ear		Total
					Grain	Cob + husk	Grain	Cob + husk	
Silk emergence									
<i>g P part<sup>-1</sup></i>									
		0.17	0.23	0.09		0.04 <sup>a</sup>			0.53
$\Delta = (\text{maturity} - \text{silk emergence})$									
$\Delta g P \text{ part}^{-1}$									
Ammonium	1	-0.03	+0.11	+0.02	+0.54	+0.04			+0.68
	2	-0.04	-0.09	-0.03	+0.53	+0.01	+0.50	+0.03	+0.91
Nitrate	1	-0.06	+0.08	+0.01	+0.51	+0.02			+0.56
	2	-0.06	-0.12	-0.03	+0.48	+0.00	+0.44	+0.02	+0.73
N source		NS <sup>b</sup>	NS	NS	NS	NS	NS	NS	—
Ear No.		NS	— <sup>c</sup>	—	NS	—			—
N source × Ear No.		NS	NS	NS	NS	NS			NS

<sup>a</sup> Sample comprises entire earshoot, husk, and silks. <sup>b</sup> Not significant. <sup>c</sup> — = Significant F test at the 0.05 level.

Table VII. Total K<sup>+</sup> in Each Plant Part at Silk Emergence and Change in K<sup>+</sup> Content between Silk Emergence and Physiological Maturity

N Source	Ears Plant <sup>-1</sup>	Leaves	Stalk	Roots	Top Ear		Bottom Ear		Total
					Grain	Cob + husk	Grain	Cob + husk	
Silk emergence									
<i>g K<sup>+</sup> part<sup>-1</sup></i>									
		1.30	2.44	0.53		0.21 <sup>a</sup>			4.48
$\Delta = (\text{maturity} - \text{silk emergence})$									
$\Delta g K^+ \text{ part}^{-1}$									
Ammonium	1	-0.01	-0.61	+0.12	+0.59	+0.09			+0.18
	2	+0.00	-0.72	-0.10	+0.60	+0.16	+0.55	+0.21	+0.70
Nitrate	1	-0.07	-0.42	+0.09	+0.56	+0.09			+0.25
	2	+0.07	-0.62	-0.10	+0.57	+0.13	+0.52	+0.20	+0.77
N source		NS <sup>b</sup>	NS	NS	—	NS	NS	NS	NS
Ear No.		NS	NS	— <sup>c</sup>	NS	NS			—
N source × Ear No.		NS	NS	NS	NS	NS			NS

<sup>a</sup> Sample comprises entire earshoot, husk, and silks. <sup>b</sup> Not significant. <sup>c</sup> — = Significant F test at the 0.05 level.

Table VIII. Equivalent Uptake Values of Anions and Cations during Vegetative and Reproductive Growth

N Source	Ears Plant <sup>-1</sup>	NO <sub>3</sub> <sup>-</sup>	P	NH <sub>4</sub> <sup>+</sup>	K <sup>+</sup>	Ca <sup>2+</sup>	Mg <sup>2+</sup>	Anions	Cations	Ratio Cations/Anions
		Vegetative								
<i>equivalents plant<sup>-1</sup></i>										
		0.32	0.019	0	0.11	0.052	0.070	0.339	0.232	0.68
Reproductive										
<i>equivalent plant<sup>-1</sup></i>										
Ammonium	1	0.044	0.022	0.176	0.005	0.026	0.030	0.066	0.237	3.59
	2	0.067	0.029	0.183	0.019	0.066	0.038	0.096	0.306	3.19
Nitrate	1	0.22	0.018	0.000	0.007	0.038	0.036	0.238	0.081	0.34
	2	0.22	0.024	0.000	0.021	0.042	0.044	0.244	0.107	0.44

Table IX. Gains (+) and Losses (-) of Stalk  $\text{NO}_3^-$ -N and Reduced-N Fractions and Their Contributions to Grain-N during Reproductive Growth

$N_a$  refers to N accumulated in the stalk during reproductive growth;  $N_v$  refers to N accumulated prior to silk emergence. At silking stalks containing 0.67, 1.18, and 1.85 g N plant<sup>-1</sup> of  $\text{NO}_3^-$ -N, reduced-N, and total N, respectively.

Stalk-N Fractions	Ammonium		Nitrate	
	1-Ear	2-Ear	1-Ear	2-Ear
	$\Delta \text{ g N plant}^{-1}$			
1. $\Delta$ Total N	+0.05	-0.95	+0.21	-0.81
As $N_a$	+0.77	+0.25	+0.80	+0.33
As $N_v$	-0.72	-1.20	-0.59	-1.14
2. $\Delta \text{NO}_3^-$ -N	-0.58	-0.57	-0.36	-0.32
As $N_a^a$	+0.09	+0.10	+0.31	+0.35
As $N_v^a$	-0.67	-0.67	-0.67	-0.67
As $N_a^b$	0.0	0.0	0.0	0.0
As $N_v^b$	-0.58	-0.57	-0.36	-0.32
3. $\Delta$ Reduced-N	+0.63	-0.38	+0.57	-0.49
As $N_a^a$	+0.68	+0.15	+0.49	-0.02
As $N_v^a$	-0.05	-0.53	+0.08	-0.47
As $N_a^b$	+0.77	+0.25	+0.80	+0.33
As $N_v^b$	-0.14	-0.63	-0.23	-0.82
4. % Loss of stalk $N_v$				
As Total-N	39	65	32	62
As $\text{NO}_3^-$ -N <sup>a</sup>	100	100	100	100
As $\text{NO}_3^-$ -N <sup>b</sup>	87	85	54	48
As reduced-N <sup>a</sup>	4	45	(+7)	40
As reduced-N <sup>b</sup>	12	53	19	69
5. Grain-N from $N_v$	1.87	2.50	1.81	2.54
% Derived from stalk <sup>a</sup>				
$\text{NO}_3^-$ - $N_v$	36	27	37	26
% Derived from stalk <sup>a</sup>				
Reduced-N <sub>v</sub>	3	21	(-4)	19
% Derived from stalk <sup>b</sup>				
$\text{NO}_3^-$ - $N_v$	31	23	20	13
% Derived from stalk <sup>b</sup>				
Reduced-N <sub>v</sub>	7	25	13	32

<sup>a</sup> Assumes that all  $\text{NO}_3^-$ -N absorbed prior to silk emergence ( $\text{NO}_3^-$ - $N_v$ ) was lost (0.67 g plant<sup>-1</sup>), i.e. that  $\text{NO}_3^-$  present at maturity accumulated during ear development. <sup>b</sup> Assumes that no  $\text{NO}_3^-$ -N accumulated during reproductive growth ( $\text{NO}_3^-$ - $N_a$ ), i.e. that  $\text{NO}_3^-$ -N present at maturity was accumulated by silk emergence.

the nature of the signal and mechanism responsible for this stimulation remain unknown.

Phosphorus uptake, in contrast to N uptake, was increased during reproductive growth by the formation of a second ear, from 0.62 g P plant<sup>-1</sup> for one-eared plants to 0.82 g P plant<sup>-1</sup> for two-eared plants (Table VI). Nevertheless, the increase in uptake was not sufficient to fulfill the 0.47 g P plant<sup>-1</sup> accumulated by the second ear. It is unclear why P uptake was stimulated by second ear formation (in spite of a decrease in root mass, Table I), yet N uptake was not, especially as second ear formation required extensive remobilization of stalk- and root-N. Remobilization of P also increased with the formation of the second ear although not as dramatically as N remobilization.

A small percentage of total  $\text{K}^+$  uptake occurred during grain fill (Table VII). By virtue of this low  $\text{K}^+$  uptake, the cation/anion ratio for the  $\text{Ca}(\text{NO}_3)_2$  treatment decreased during reproductive growth compared to that during vegetative growth (Table VIII).

Significantly more net  $\text{OH}^-$  efflux (10) during reproductive growth is indicated. It seems likely that  $\text{K}^+$  recirculation between

root and shoot (11) must play a role in the co-transport of  $\text{NO}_3^-$  to sites of storage and reduction in the stalk and leaves during this period. When N was supplied to the plant as  $\text{NH}_4^+$ , the cation/anion uptake ratio increased appreciably and, to maintain charge balance,  $\text{H}^+$  would have been released into the rhizosphere. The extent of pH changes occurring in the rhizosphere will depend on the buffering capacity of the soil (17), but the present data suggest the effects would be appreciable. Nevertheless, the metabolic adjustments within the root tissue required to bring about these changes in ion balance during exposure to the two N forms (10) did not have any influence on total dry matter (Table I) or N accumulation (Table II).

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