

fication on corn and sugarbeet grown under limited moisture. p. 330. *In* Agronomy abstracts, ASA, Madison, WI.

Fritton, D.D., and G.W. Olson. 1972. Bulk density of a fragipan soil in natural and disturbed profiles. *Soil Sci. Soc. Am. Proc.* 36:686-689.

Parker, C.J., M.K.V. Carr, N.J. Jarvis, M.T.B. Evans, and V.H. Lee. 1989. Effects of subsoil loosening and irrigation on soil physical properties, root distribution and water uptake of potatoes (*Solanum tuberosum*). *Soil Tillage Res.* 13:267-285.

Soane, G.C., R.J. Godwin, and G. Spoor. 1986. Influence of deep loosening techniques and subsequent wheel traffic on soil structure. *Soil Tillage Res.* 8:231-237.

Taylor, H.M., C.E. Van Doren, C.L. Godfrey, and J.R. Coover. 1963. Soils of the Southwestern Great Plains Field Station. Texas Agric. Exp. Stn. Misc. Publ. MP-669, College Station.

Unger, P.W. 1970. Water relations of a profile-modified slowly permeable soil. *Soil Sci. Soc. Am. Proc.* 34:492-495.

Unger, P.W., and F.B. Pringle. 1981. Pullman soils: Distribution, importance, variability and management. Texas Agric. Exp. Stn. Bull. B-1372, College Station.

Van Ouwwerkerk, C., and P.A.C. Raats. 1986. Experiences with deep tillage in the Netherlands. *Soil Tillage Res.* 7:273-283.

Post-Anthesis Nitrogen Loss from Corn

D. D. Francis,* J. S. Schepers, and M. F. Vigil

ABSTRACT

Published research has shown relatively large amounts of NH_3 being lost from aboveground vegetation during grain development for various grain crops. For corn (*Zea mays* L.), maximum net N accumulation usually occurs during early reproductive development (R1-R3) and a subsequent decline is often observed. Two recently completed N fertilizer recovery studies on irrigated corn utilizing isotopic techniques were re-examined to quantify post-anthesis N losses from aboveground biomass of irrigated corn under different N regimes. These studies were conducted at different sites, in different years, with fertilizer rates ranging from 50 to 300 kg N ha^{-1} . Measured losses of labeled N from aboveground plant material ranged from 7 to 34 kg N ha^{-1} . Isotopic dilution suggests that apparent real N losses from aboveground biomass ranged from 45 to 81 kg N ha^{-1} , assuming there is no selectivity for N source (i.e., ^{15}N vs. ^{14}N). Plant N losses accounted for 52 to 73% of the unaccounted-for N in ^{15}N balance calculations. Failure to include direct plant N losses when calculating an N budget leads to overestimation of losses from the soil by denitrification, leaching, and ammonia volatilization. Proper accounting for volatile plant N losses may improve management strategies that affect N fertilizer use efficiencies.

THE TOTAL AMOUNT OF N in aboveground biomass (grain plus stover) of annual grain crops generally reaches a maximum well before maturity, often followed by a subsequent decline (Wetselaar and Farquhar, 1980). Virtually all reported plant N losses occur after anthesis and are generally greater at higher levels of soil N. Exudation of N from living roots has been cited as a possible explanation, although substantial translocation of N to the roots of annuals after anthesis has not been demonstrated. Published research suggests that any post-anthesis N loss from roots would be small (Daigger et al., 1975; Wetselaar and Farquhar, 1980; Martin, 1987). Smith et al. (1983) rejected the hypothesis that N is redistributed to the roots near maturity in winter wheat (*Triticum aestivum* L.). Their data indicated that under N conditions ranging from deficient to excessive, that the reverse was actually true with roots serving as a source of N remobilized to the grain during final maturation processes.

Substantial post-anthesis N losses for wheat ranging from 25 to 80 kg N ha^{-1} (Daigger et al., 1976), 5.9 to 7.4 kg N ha^{-1} (Harper et al., 1987), and 14.9 to 76.9 kg N ha^{-1} (Papakosta and Gagianas, 1991) were attributed to N volatilization from the aboveground biomass. For soybean [*Glycine max* (L.) Merr.], Stutte et al. (1979) estimated that at least 45 kg N ha^{-1} was lost from the foliage because of N volatilization. Although, both reduced and oxidized forms of volatile N have been shown to be released from plant tissue, the prevalent form of post-anthesis loss is NH_3 (Harper et al., 1980; da Silva and Stutte, 1981; Weiland and Omholt, 1985). Harper et al. (1987) attributed these losses mainly to NH_3 volatilization resulting from inefficient N translocation and reassimilation within the plant during senescence. Volatile N losses from cultivated crops may play a significant role in the systematic spatial and temporal variations noted in atmospheric NH_3 concentrations (Lemon and Van Houtte, 1980; Cadle et al., 1982; ApSimon et al., 1987), especially in areas with little livestock production.

The effects of vegetative N losses on N balance calculations are typically not emphasized. Legg and Meisinger (1982), in a review of ^{15}N balance studies with corn, cited "unaccounted for" fertilizer N losses ranging between 6 and 28%. Most N balance calculations are made at maturity and assume gaseous loss (mainly from denitrification) as the major cause of unaccounted for N losses. However, ignoring volatile N losses from aboveground plant biomass may lead to erroneous conclusions regarding fertilizer N recovery and denitrification.

Accounting for these N losses may play an important role in developing cropping systems to improve N fertilizer use efficiencies and reduce adverse environmental impacts. A better understanding is needed of the magnitude of loss and pathways involved. This is especially true for corn production which relies on high N fertility levels. Unfortunately, little information is available on volatile N losses from field-grown corn plants during maturation. The objective of this study was to quantify, under field conditions, post-anthesis N losses from the aboveground biomass of irrigated corn under different N regimes.

MATERIALS AND METHODS

Data generated from two irrigated corn studies in Nebraska, the first on a Hall silt loam (fine-silty, mixed, mesic Pachic

D.D. Francis and J.S. Schepers, USDA-ARS, 119 Keim Hall, Univ. of Nebraska, Lincoln, NE 68583; M.F. Vigil, USDA-ARS, Akron, CO 80720. Published as Paper no. 9933, J. Series, Nebraska Agric. Res. Div., Lincoln. Received 20 April 1992. *Corresponding author.

Argiustoll) soil and the second on a Wood River silt loam (fine, montmorillonitic, mesic Typic Natrustoll), were evaluated for uptake and subsequent loss of tagged N from the aboveground biomass. The first study was designed to quantify the effect of nitrate in irrigation water on N fertilizer recovery. This experiment contained both enriched and depleted ^{15}N fertilizer components. For N budget analysis of the soil-plant system, microplots treated with enriched ^{15}N were utilized. These microplots were constructed by trenching rectangular blocks of soil (0.76 by 1.2 m) to a depth of 1.2 m. To prevent the lateral movement of ^{15}N -labeled fertilizer out of the plot and to ensure that the plant's nutrient supply was coming from within the plot area, the resulting soil blocks were wrapped to a depth of 1.1 m with polyethylene plastic sheeting. The trenches were backfilled from the outside to keep the plastic in place. Approximately 0.15 m of plastic sheeting was left exposed above the soil surface where it was supported by a wooded frame.

Plant N uptake was monitored during the growing season by destructive whole plant sampling. Depleted ^{15}N fertilizer was used on these plots for economic reasons. Depleted ^{15}N plots were constructed in the same manner as the enriched plots above, but had a larger surface area of 4.65 m². Fertilizer treatments in this experiment (0, 50, 100, and 150 kg N ha⁻¹) were sidedressed as NH_4NO_3 solution at the V3 growth stage (developmental stages according to Ritchie et al., 1986). Soil water status was monitored using a neutron probe and the crop was irrigated as necessary. To reduce the leaching potential of any subsequent rainfall, irrigation amounts were controlled to maintain a soil water deficit of at least 4 cm of water below field capacity for the rooting profile. The goal was also to have a 50% water deficit in the top 1.8 m of soil at the end of the growing season.

Stauffer S7767 hybrid was planted 1 May 1982. Shortly after emergence, plants were thinned to a population of approximately 64 500 plants ha⁻¹. Six plants were collected from each depleted ^{15}N plot at the 12th leaf (V12), tasseling (VT), blister (R2), and physiological maturity (R6) growth stages.

The original objective of the second study being evaluated for N loss from aboveground biomass was to assess N fertilizer recovery and the subsequent uptake of residual N by winter cover crops. Pioneer brand hybrid 3379 was planted 3 May 1990 in 0.76-m spaced rows at an approximate population of 69 000 plants ha⁻¹. The experimental design was a randomized block with four replications. Plots were six rows wide by 18 m in length. The N treatments were applied at the V3 growth stage as depleted $(\text{NH}_4)_2\text{SO}_4$ and ranged from 75 to 300 kg N ha⁻¹. Irrigation was conventional furrow applied to every other row. Irrigation scheduling was by soil-water budgeting procedures, with evapotranspiration values determined by the local county extension office. Total aboveground biomass (six plants each plot) was collected at silking (R1), milk (R3), dent (R5), and physiological maturity (R6) growth stages.

For both studies the plant samples were separated into leaf, stalk, and grain components with the cob and husks being included with the stalk material. The plant material was oven-dried at 65 °C, weighed, ground, and analyzed for total N and N isotope ratio with an automated N analyzer and stable isotope mass spectrometer (ANCA-MS, Carlo Erba Instr., Milan, Italy, and Europa Scientific, Crewe, England) (Schepers et al., 1989).

RESULTS AND DISCUSSION

In the first experiment, no significant differences within N rates were noted in the total amount of N accumulated by corn between R2 and R6, but there was substantially less fertilizer N in the aboveground plant material by R6 as compared to R2 (Table 1). Grain yields for the 0, 50, 100, and 150 kg N ha⁻¹ fertilizer rates averaged 9.3, 10.6, 10.9, and 10.6 Mg ha⁻¹, respectively. Between the blister stage (R2) and physiological maturity (R6),

Table 1. Total plant N, percentage of plant N derived from fertilizer, and percentage of fertilizer N utilized at R2 and R6 growth stages of corn fertilized at 50, 100, and 150 kg N ha⁻¹ with depleted ^{15}N (Exp. 1).

Fertilizer kg N ha ⁻¹	Growth stage	Total N plant tops kg N ha ⁻¹	%Ndff†	% Fert. recovered‡
50	(R2) Blister	152	17.4	52.5
	(R6) Maturity	153	12.4	37.9
	F-test	NS	*	**
	LSD (0.05)	—	3.6	6.4
100	(R2) Blister	160	36.0	56.5
	(R6) Maturity	161	24.7	39.8
	F-test	NS	**	**
	LSD (0.05)	—	7.2	10.7
150	(R2) Blister	211	44.3	62.2
	(R6) Maturity	204	31.4	42.5
	F-test	NS	**	**
	LSD (0.05)	—	4.7	6.5

* ** significant at 0.05 and 0.01 levels of probability, respectively.

† %Ndff = percentage of plant N derived from fertilizer. % Fert. recovered. = percentage of fertilizer N recovered in the aboveground plant material. Data represent means of four replications.

an average of 15, 17, and 20% of the applied fertilizer had been lost from the aboveground biomass for the 50, 100, and 150 kg N ha⁻¹ fertilizer rates, respectively. Harper et al. (1987) reported similar losses with an amount equivalent to 21% of the applied fertilizer being lost as volatile NH_3 from wheat plants during senescence. Working with late season applied ^{15}N and two corn hybrids with differing leaf-canopy senescence, Ta and Weiland (1992) found significant losses in plant ^{15}N content between 104 d after planting and physiological maturity. Their losses when pooled across N fertility levels were equivalent to 10% of the ^{15}N that was applied at the R1 growth stage.

Although our enriched ^{15}N microplots did not provide information for growth stage N uptake comparisons, they did permit completion of an N balance budget (Table 2). By comparison, the amount of fertilizer N lost from the aboveground plant material in the adjacent depleted ^{15}N plots between growth stages R2 and R6 (Table 1) represents 52 to 73% of the total unaccounted for fertilizer N in the enriched ^{15}N microplot budgets (Table 2). Previously, soil N loss processes were assumed to be primarily responsible for the unaccounted for N, even though care was taken to avoid conditions favorable to denitrification and leaching. Considering the conditions maintained in this study, it appears more likely that post-anthesis volatile N losses from the aboveground biomass may represent a major mechanism for the N loss and

Table 2. Nitrogen balance for microplots treated with ^{15}N enriched fertilizer in Exp. 1.

Fertilizer kg N ha ⁻¹	Crop uptake	Soil 0-2.4 m	Unaccounted for fertilizer
	% of initial N applied†		
50	48.0 ± 1.1 (5.0)‡	23.7 ± 7.5	28.3 ± 7.4
100	49.8 ± 3.1 (5.7)	20.0 ± 5.0	30.2 ± 7.0
150	53.1 ± 2.9 (5.9)	19.8 ± 8.1	27.1 ± 6.5

† Mean ± the standard deviation.

‡ Values in parentheses are included in the total and represent an estimate of the contribution of roots to total removed by plants based on roots comprising 15% of total plant dry weight at physiological maturity.

could account for a large portion of the unaccounted for ^{15}N , although no direct measurements of plant volatile N losses were made.

A fraction of the unaccounted for N may also be related to volatile N loss occurring earlier from younger plants (pre-anthesis). Hooker et al. (1980) and Morgan and Parton (1989) reported NH_3 volatilization from wheat shoots during vegetative growth, although at rates much lower than in post-anthesis emissions. Conceivably, some volatile N losses from corn plants may occur continuously over the full growing season and only become detectable from aboveground plant tissue when the rates of loss exceed the rates of uptake by the roots. This problem of detection represents a major weakness in calculating N loss as the difference between the maximum N content of the crop at some intermediate growth stage and that found at physiological maturity.

Implicating plant volatilization as a means by which substantial amounts of N may be lost from the soil-plant system for many grain crops does not imply that total N losses from the soil-plant system are greater than current estimates indicate, but rather that a greater proportion of the loss is in the NH_3 form and coming from the plant rather than the soil. However, this information has major implications in the development and interpretations of strategies to improve N fertilizer use efficiencies.

In the second experiment, maximum N accumulation occurred at the R3 growth stage (Table 3). Significant decreases in the total amount of N accumulated in the corn plants occurred between growth stages R3 and R5 for all but the lowest fertilizer rate. In addition, the greatest decline in fertilizer N recovery by aboveground plant

material occurred between growth stages R3 and R5. Working with four corn genotypes, Reed et al. (1980) found that kernel N accumulation was linked more with leaf protease activity than with leaf nitrate reductase activity. For spring wheat, Morgan and Parton (1989) attributed the increased potential for NH_3 volatilization during maturation to changes in the balance between NH_4^+ releasing reactions (deamination reactions, nitrate reduction, senescence-induced proteolysis) and NH_4^+ uptake reactions (N transport and NH_4^+ assimilation via glutamine synthetase) that shifts in favor of NH_4^+ release, resulting in the establishment of new, higher steady-state tissue $[\text{NH}_4^+]$. Plant N losses noted during this time would be in agreement with the concept that N losses are associated with inefficient redistribution of N within the plant. Wetselaar and Farquhar (1980) propose that losses will be largest when stomatal conductance is greatest, as occurs with high light intensities, ample moisture, high temperatures, and high levels of nutrition, particularly N. All these conditions are usually present during the reproductive growth phase for corn.

Farquhar et al. (1983) noted that because NH_3 can be both absorbed and released, a plant grown with labeled N fertilizer will tend to lose labeled N and gain unlabeled N even if the net flux is zero. This may happen, but it would not explain why the greatest loss of labeled N generally occurs late in the growth cycle. Parton et al. (1988) suggested that the rate and direction of plant NH_3 fluxes may vary according to a number of factors, including plant species, nutritional regime, plant phenology, microclimate, and atmospheric NH_3 level. Morgan and Parton (1989) reported that NH_3 compensation points (the ambient NH_3 concentrations at which no net exchange of NH_3 between plant and atmosphere occurs) rose as plants approached maturity and were unable to find any atmospheric NH_3 taken up by wheat plants as they approached maturity, despite increases in ambient $[\text{N}-\text{NH}_3]$ up to $25 \mu\text{g N}-\text{NH}_3 \text{ m}^{-3}$. They also noted that under conditions of a continuous supply of nutrients to the roots, that N in the form of NH_3 /amines was lost from wheat shoots at ambient $[\text{N}-\text{NH}_3]$ throughout their ontogeny. These growth chamber findings are in agreement with field plot results of Harper et al. (1987) that N was lost as volatile NH_3 from plants after fertilizer application and during the senescence period. Results from the above studies suggest that NH_3 losses from plants may be due to high internal NH_4^+ concentrations which apparently saturate the N transport system. Because NH_4^+ is toxic to tissue and not stored as such by plants, it appears that these losses may be the result of inefficient NH_4^+ assimilation.

Nitrogen in grain can come from remobilization from leaves, stems, and roots, or from post-anthesis soil N uptake and assimilation. Pearson and Jacobs (1987) note that the majority of experiments with corn show approximately 40 to 50% of grain N is taken up from the soil after anthesis. For winter wheat, Harper et al. (1987) found similar results with roughly half the grain N coming from redistribution within the plant, with the balance assimilated directly from the soil after anthesis. They also reported that as this assimilation occurred in the wheat kernel, approximately 11% of the potential N available for redistribution from stems and leaves was lost as volatile NH_3 . Based on results from Exp. 2 (data

Table 3. Total plant N, percentage of plant N derived from fertilizer, and percentage of fertilizer N recovered by corn at four reproductive growth stages under four fertilizer regimes (Exp. 2).

Fertilizer	Growth stage	Total N plant tops	%Ndff†	% Fert. recovered†
kg N ha ⁻¹		kg N ha ⁻¹		
75	R1 (Silking)	65.8	33.7	30.0
	R3 (Milk)	95.0	31.7	40.3
	R5 (Dent)	90.3	24.4	29.8
	R6 (Maturity)	87.4	21.2	24.4
	F-test	*	**	*
	LSD(0.05)	17.4	6.7	12.0
150	R1	121	51.5	41.6
	R3	149	48.5	48.4
	R5	122	42.9	35.0
	R6	122	35.0	28.5
	F-test	*	**	**
	LSD(0.05)	20.6	5.1	6.8
225	R1	135	59.9	36.1
	R3	174	57.1	44.1
	R5	134	54.1	32.1
	R6	164	39.8	28.9
	F-test	**	**	*
	LSD(0.05)	19.2	7.7	8.0
300	R1	157	65.3	34.2
	R3	213	63.3	45.0
	R5	189	61.3	38.7
	R6	194	54.5	35.3
	F-test	**	*	**
	LSD(0.05)	17.3	7.3	5.5

*,** significant at 0.05 and 0.01 levels of probability, respectively.

† %Ndff = percentage of plant N derived from fertilizer. % Fert. recovered = percentage of fertilizer N recovered in the aboveground plant material. Data represents means of four replications.

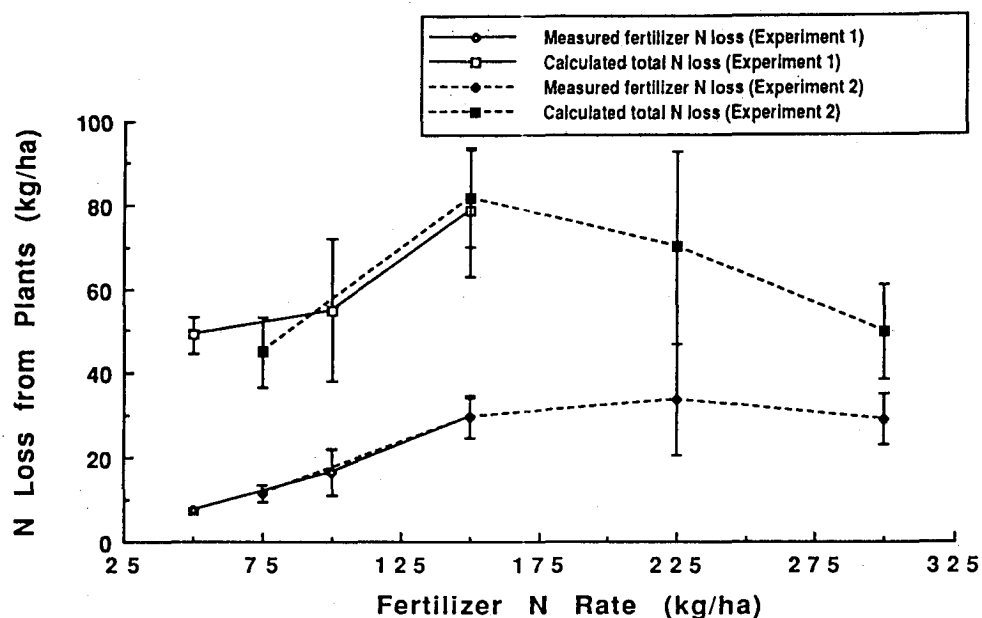


Fig. 1. Measured post-anthesis fertilizer N losses from aboveground biomass of corn and the calculated total N losses for two studies using ^{15}N depleted fertilizer. Bars denote standard errors of the means.

not shown), it also appears that about half the corn grain N came directly from the soil; however, translocation losses were greater than the 11% found for wheat with this particular corn hybrid, and perhaps larger losses may occur for corn in general. Average grain yields were 3.6, 6.8, 9.3, 10.3, and 10.3 Mg ha^{-1} for the 0, 75, 150, 225, 300 kg N ha^{-1} fertilizer rates, respectively. The amount of tagged fertilizer N accumulated in the corn grain between growth stages R3 and R6 accounts for only 20 to 50% of the labeled fertilizer N removed from leaves and stalks during this period (Table 4).

For these two studies, measured fertilizer N losses from the aboveground plant material ranged from 7 to 34 kg N ha^{-1} . Total N losses from the aboveground biomass would be greater if we consider nonfertilizer N. Tagged and apparent non-tagged N losses should be proportionate to their ration in the plant, assuming there is no selectivity for N source (i.e., ^{15}N vs. ^{14}N) as N is volatilized from the plant. Additionally, if the direction of plant NH_3 fluxes is affected by the nutritional regime, soil inorganic N concentrations in these two studies (data

not shown) increased during the reproductive growth phase, indicating a continuous supply of N to the roots. After adjusting labeled N losses for isotope dilution, the calculated N losses from the aboveground plant material ranged from 49 to 78 kg N ha^{-1} in Exp. 1, and 45 to 81 kg N ha^{-1} in Exp. 2 (Fig. 1).

Isotope dilution calculations will underestimate total N losses if fertilizer N is being taken up at the same time it is being lost from plants. This situation may explain the lower losses noted at the 225 and 300 kg N ha^{-1} fertilizer rates. High N fertilizer rates would increase the probability that some plant available fertilizer N would be in the soil inorganic N pool late in the season. An ample supply of N typically increases N turnover rate, thus increased availability of fertilizer N late in the growing season under high N application rates is often associated with mineralization of earlier immobilized fertilizer N.

The hypothesis that the apparent decrease in plant N losses at the 225 and 300 kg N ha^{-1} fertilizer rates is related to late season uptake of tagged N fertilizer may be supported by results relating N loss to leaf area. Parton et al. (1988) reported that NH_3 loss rates from wheat on a leaf area basis were similar for both low-N and high-N plants despite higher tissue N concentrations in high-N plants. They concluded that differences in amount of NH_3 loss was related to low-N plants having a much smaller leaf area during maturation because of earlier senescence of lower leaves. Considering the senescence process, the leaf area explanation would be in agreement with most studies which show greater volatile N loss as fertilizer rates increase. High N fertility levels often increase leaf area indices, but the greatest difference during maturation is the ability to maintain a larger number of green leaves late in the season as compared with low N fertility levels.

Volatile N losses based on leaf area suggests that N losses would plateau once leaf area was maximized. Arnon (1975) reported that the size of individual corn

Table 4. Fertilizer N in different plant parts of corn at the R3 (milk) and R6 (physiological maturity) growth stages (Exp. 2).

Fertilizer kg N ha^{-1}	Growth stage	Fertilizer N in plant parts		
		Leaves	Stalks	Grain
		kg N ha^{-1}		
75	R3 (Milk)	16.0 \pm 2.4†	4.9 \pm 0.9	9.3 \pm 2.4
	R6 (Maturity)	3.2 \pm 0.5	2.8 \pm 1.1	12.3 \pm 2.4
150	R3	39.1 \pm 5.1	13.9 \pm 2.9	23.7 \pm 4.9
	R6	6.4 \pm 1.1	5.5 \pm 0.7	30.9 \pm 4.8
225	R3	43.6 \pm 6.2	23.8 \pm 5.9	28.9 \pm 5.8
	R6	9.2 \pm 2.9	11.0 \pm 1.9	44.8 \pm 1.8
300	R3	58.5 \pm 5.7	37.0 \pm 3.2	39.5 \pm 3.3
	R6	14.2 \pm 1.4	19.6 \pm 4.8	72.0 \pm 3.3

† Mean \pm the standard deviation.

leaves cannot be influenced after the time when the twelfth leaf is completely unfolded. If leaf area was maximized at the 150 kg N ha⁻¹, volatile plant N losses should also be maximized and decreases from maximum rates would only occur from premature death of leaves caused by nutrient deficiencies. Assuming similar leaf senescence at the three highest N fertilizer rates in Exp. 2, any uptake and assimilation of tagged N from the soil during grain fill would be reflected as an apparent decrease in calculated plant N loss. The decreasing trend in plant N loss at the two highest fertilizer rates fit this N loss concept.

CONCLUSIONS

Post-anthesis fertilizer N losses from the aboveground biomass of corn plants ranged from 10 to 20% of the fertilizer applied. Isotope dilution (assuming no isotope discrimination during volatilization) suggests that apparent total N losses from the aboveground plant material ranged from 49 to 78 kg N ha⁻¹ and 45 to 81 kg N ha⁻¹ for the two corn hybrids studied under different N fertilizer regimes. Although not measured directly, volatile NH₃ losses from the aboveground plant material appears to be the most plausible explanation for the lost fertilizer N. Support for this hypothesis comes from other crop species where gaseous NH₃ losses have been shown to be the prevalent form of volatile N loss.

Volatile NH₃ losses from aboveground plant material could account for much of the unaccounted for N losses found in soil N balance studies. Nitrogen balance calculations showed that apparent post-anthesis N losses from aboveground plant biomass accounted for 52 to 73% of our total unaccounted for fertilizer N in one study. It is possible that some of the labeled N losses may have resulted from gaseous isotopic exchange. Nevertheless, failure to include labeled N losses from aboveground plant biomass in N balance studies will lead to overestimation of N losses from soil by denitrification and leaching. Implicating plant N volatilization does not require an increase in the current estimates of total N loss from soil-plant systems, but it does imply that a greater proportion than currently thought may be coming directly from the plants. Understanding the magnitude and mode of N loss from the soil-plant system will be of practical significance in the development of strategies to improve N fertilizer use efficiencies.

REFERENCES

- ApSimon, H.M., M. Kruse, and J.N.B. Bell. 1987. Ammonia emissions and their role in acid deposition. *Atmos. Environ.* 21:1939-1946.
- Arnon, I. 1975. Mineral nutrition of maize. International Potash Inst. Bern, Switzerland.
- Cadle, S.H., R.J. Countess, and N.A. Kelly. 1982. Nitric acid and ammonia in urban and rural locations. *Atmos. Environ.* 16:2501-2506.
- Daigger, L.A., D.H. Sander, and G.A. Peterson. 1976. Nitrogen content of winter wheat during growth and maturation. *Agron. J.* 68:815-818.
- da Silva, P.R.F. and C.A. Stutte. 1981. Nitrogen volatilization from rice leaves. II. Effects of source and applied nitrogen in nutrient culture solution. *Crop Sci.* 21:913-916.
- Farquhar, G.D., R. Wetselaar, and B. Weir. 1983. Gaseous nitrogen losses from plants. pp. 159-180. *In* J.R. Freney and J.R. Simpson (ed.) Gaseous loss of nitrogen from plant-soil systems. Martinus Nijhoff/Dr. W. Junk, The Hague Netherlands.
- Harper, L.A., R.R. Sharpe, G.W. Langdale, and J.E. Giddens. 1987. Nitrogen cycling in a wheat crop: Soil, plant and aerial nitrogen transport. *Agron. J.* 79:965-973.
- Hooker, M.L., D.H. Sander, G.A. Peterson, and L.A. Daigger. 1980. Gaseous N losses from winter wheat. *Agron. J.* 72:789-792.
- Legg, J.O. and J.J. Meisinger. 1982. Soil nitrogen budgets. p. 503-566. *In* F.J. Stevenson (ed.) Nitrogen in Agricultural Soils. Agron. Monogr. 22. ASA, CSSA, and SSSA, Madison, WI.
- Lemon, E. and R. Van Houtte. 1980. Ammonia exchange at the land surface. *Agron. J.* 72:876-883.
- Martin, J.K. 1987. Carbon flow through the rhizosphere of cereal crops—a review. *INTECOL Bull.* 15:17-23.
- Morgan, J.A. and W.J. Parton. 1989. Characteristics of ammonia volatilization from spring wheat. *Crop Sci.* 29:726-731.
- Papakosta, D.K. and A.A. Gagianas. 1991. Nitrogen and dry matter accumulation, remobilization, and losses for Mediterranean wheat during grain filling. *Agron. J.* 83:864-870.
- Parton, W.J., J.A. Morgan, J.M. Altenhofen, and L.A. Harper. 1988. Ammonia volatilization from spring wheat plants. *Agron. J.* 80:419-425.
- Pearson, C.J. and B.C. Jacobs. 1987. Yield components and nitrogen partitioning of maize in response to nitrogen before and after anthesis. *Aust. J. Agric. Res.* 38:1001-1009.
- Reed, A.J., F.E. Below, and R.H. Hageman. 1980. Grain protein accumulation and the relationship between leaf nitrate reductase and protease activities during grain development in maize (*Zea mays* L.). *Plant Physiol.* 66:164-170.
- Ritchie, S.W., J.J. Hanway, and G.O. Benson. 1986. How a corn plant develops. Iowa State Univ. Coop. Ext. Serv. Spec. Rep. 48.
- Schepers, J.S., D.D. Francis, and M.T. Thompson. 1989. Simultaneous determination of total C, total N, and ¹⁵N on soil and plant material. *Commun. Soil. Sci. Plant Anal.* 20:949-959.
- Smith, T.L., G.A. Peterson, and D.H. Sander. 1983. Nitrogen distribution in roots and tops of winter wheat. *Agron. J.* 75:1031-1036.
- Stutte, C.A., R.T. Weiland, and A.R. Blem. 1979. Gaseous nitrogen loss from soybean foliage. *Agron. J.* 71:95-97.
- Ta, C.T. and R.T. Weiland. 1992. Nitrogen partitioning in maize during ear development. *Crop Sci.* 32:443-451.
- Weiland, R.T. and T.E. Omholt. 1985. Methods for monitoring nitrogen gas exchange from plant foliage. *Crop Sci.* 25:359-361.
- Wetselaar, R. and G.D. Farquhar. 1980. Nitrogen losses from tops of plants. *Adv. Agron.* 33:263-302.