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Sources, Fluxes, and Sinks of Nitrogen during Early Reproductive Growth of Maize (*Zea mays* L.)

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ABSTRACT

A study was designed to (a) identify sources and sinks of N in the maize (*Zea mays L.*) shoot, by estimating net N fluxes for each of seven parts of the shoot, (b) determine effects of N entering the plant upon fluxes of N absorbed before reproductive growth, and (c) determine the effects of the *opaque-2* gene on N fluxes in the maize shoot during early reproductive growth. Plants of a maize hybrid (Pioneer 3369A) and its *opaque-2* counterpart (Pioneer L3369) were grown in a greenhouse using nutrient solution/sand culture, with NO_3^- as the N source during the vegetative growth phase. Beginning at the time of pollination, the same nutrient regime was continued, except that some plants received no N, and others received 3.75 millimolar ^{15}N as NO_3^--N.

Stalk and leaves were found to be primary N sources for the grain, while shank, husk, and cob acted first as N sinks, then as N sources during reproductive growth. Net fluxes of N for each plant part were estimated by calculating the first derivatives of regression equations used to fit data for N contents of each plant part as functions of time. All parts of the shoot were sinks for exogenous N (absorbed after pollination). Thirty-six days after pollination, the grain contained 60% endogenous N (absorbed before pollination) when 3.75 millimolar NO_3^--N was supplied after pollination. Rates of total N influx to the grain were identical whether or not N was supplied in the nutrient solution during reproductive growth. At 36 days after pollination, less N had accumulated in the grain of the *opaque-2* genotype, but otherwise there were no differences in N contents or dry weights of the shoots due to the *opaque-2* gene. Absence of N from the rooting medium significantly affected N fluxes throughout the shoot during reproductive growth, but there were no detectable effects of the *opaque-2* gene on N fluxes in parts of the plant other than the grain.

During the reproductive growth phase of maize, some of the N in the vegetative organs of the plant moves into the developing grain where it is stored largely as protein. While N source/sink relationships between the grain or ear and other parts of the maize plant have been described (2, 3, 8, 11, 13), little information is available regarding simultaneous fluxes of N for individual parts of the maize shoot in the context of a whole plant model. For attaining maximum benefit from fertilizer N, considerations should include the efficiency of postanthesis transfer of N from vegetative parts of the plant to the grain. Dalling *et al.* (6) found that correlation between NRA[2] and wheat grain N was improved if account was taken of N translocation efficiency.

The primary purpose of the present study was to determine net N fluxes for various parts of the shoot of maize plants during the reproductive growth phase and the effects on these fluxes of N absorbed through the roots during that growth stage. Calculation of fluxes is based on analysis of the data for N contents of each plant part as functions of time by fitting polynomial equations to the N data and by differentiating the regression equations. The responses of two related maize hybrids, Pioneer 3369A and its *opaque-2* counterpart, L3369, were compared using a sand/nutrient solution culture technique. The maize plant in the present study is considered a system (Fig. 1) composed of parts in the sense that Wiggins (14) defines 'compartments' or 'regions' of a biological system into which and through which particles may move.

Although it is recognized that values calculated for the net changes in the amounts of N per unit time in each plant part represent net results of many dynamic processes, such data can help to elucidate the mechanisms operating in the whole plant during the reproductive growth phase. Nitrogen absorbed by the plant before pollination is designated as endogenous N. The N absorbed by the plant after pollination, as indicated by calculations based on the presence of ^{15}N which had been added to the nutrient solution, is exogenous N. The sum of endogenous N and exogenous N is total N. The use of ^{15}N as a tracer provides a better means than by difference of estimating the portion of grain N provided by postpollination absorption (3).

MATERIALS AND METHODS

In a greenhouse with evaporative cooling, plants of two maize (*Zea mays* L.) hybrid genotypes, Pioneer 3369A (normal) and its *opaque-2* counterpart, L3369, were grown in sand contained in plastic pots with free drainage. One normal and one *opaque-2* plant were grown in each of 28 13-L containers. Each container was irrigated daily with 3.7 L of nutrient solution, the amount of liquid held in the sand after free drainage. During the vegetative phase of growth, all pots were initially irrigated with a Hoagland No. 1 solution (10) at 33.3% strength. Iron and zinc deficiency symptoms appeared during the 2nd week after emergence. To correct the apparent macronutrient deficiencies and to minimize the possibility of macronutrient deficiencies during the vegetative phase of growth, the nutrient solution was changed to 50% strength Hoagland No. 1 for all macronutrients, and micronutrients were supplied at full strength, as specified in a modified Hoagland solution formula (7), except that the iron was added from a $FeSO_4 \cdot 7H_2O$ solution prepared daily. Interveinal chlorosis and white areas along the midribs of plants which had exhibited such symptoms disappeared after the nutrient solution was changed, and the plants were healthy when N treatments were initiated at pollination. Until pollination, all pots were irrigated with the same solution with a pH of 5.0.

As tassels and silks appeared, they were covered with paper bags. For each pot, pollination was begun when the silk of the primary ear of both plants was at least 3 cm long. Pollen was collected and applied to the silk on the same plant. Despite careful

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[2] Abbreviation: NRA, nitrate reductase activity.

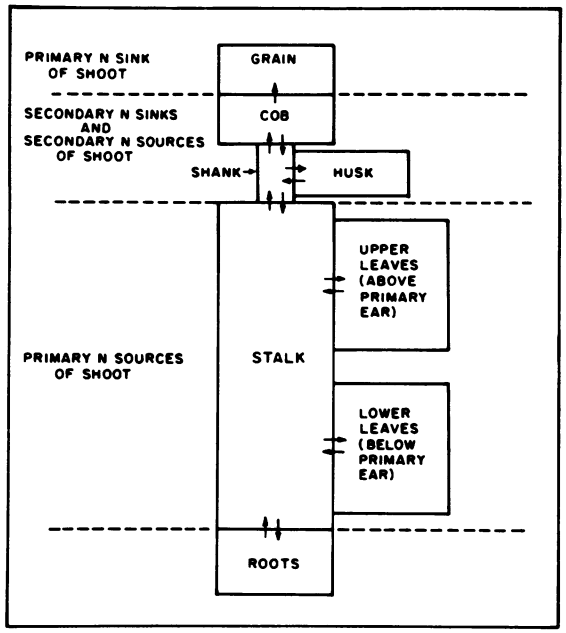

FIG. 1. Conceptual model of maize plant during reproductive growth phase, indicating N sources and sinks of the shoot. Arrows indicate N influx and efflux for all compartments, or regions, of the shoot except the grain for which only influx is assumed.

pollination during the entire period of pollen shed for each plant, incomplete pollination was achieved, probably because of high temperatures in the greenhouse. Air temperatures ranged between a mean maximum of 35°C during the day and a mean minimum of 18°C during the night. Shoots of the maize plants in four pots were harvested when they were ready to be pollinated.

At the time of pollination, the plants were divided into two sets to introduce N treatment variables. Irrigation with nutrient solution was continued, one set receiving solution containing no N, and another set 3.75 mM NO_3^--N enriched with ^{15}N (9.20% ^{15}N excess). At 12, 24, and 36 d after pollination, shoots of plants not receiving N and those receiving 3.75 mM N were harvested, since the focus of the present study is on N sources, fluxes, and sinks in maize during early reproductive growth. Duration to black layer from silking for Pioneer 3369 maize varies from 50 to 60 d, depending upon environmental conditions. Each plant was divided into seven parts: (a) stalk, including stem, tassel and leaf sheaths, (b) leaves below the primary ear, (c) leaves above the primary ear, (d) shank(s), (e) husk(s), (f) cob(s), and (g) grain. For those plants bearing two or more ears, each of the four latter fractions were combined. Samples were immediately placed on Dry Ice and subsequently lyophilized, weighed, and finely ground. Total N was determined by the Kjeldahl method using salicylic acid and Zn dust to reduce oxidized nitrogen (1). Distillates of replicates from the total N determinations were combined, treated, and analyzed by mass spectroscopy to determine ^{15}N contents (15).

Data from the material harvested at pollination and at 12, 24, and 36 d thereafter were tested using analysis of variance, with means being tested by orthogonal comparisons. Analysis of variance showed an effect of the *opaque-2* gene only on total N content of the grain at 36 d after pollination. Therefore, amounts of N per plant, in each plant part and for the shoot, were pooled from the two genotypes to compare effects of the two N treatments (Table I) at the three postpollination samplings. Next, the pooled variates of the normal and *opaque-2* data were used for calculating regression equations for describing effects of the 0 mM N and 3.75 mM N treatments on the amounts of total, endogenous, and exogenous N in each plant part as a function of time for the 36-d experimental period (Table II). In making these calculations, it was assumed that there was no N in the grain at the time of pollination. Differentiation of the regression equations yielded equations describing net fluxes of total, endogenous, and exogenous N for each plant part. Equations describing all curves except those for the grain in the present paper are to be found elsewhere (4).

Coefficients of determination, R^2, were used as the primary criterion of best fit in choosing a linear, quadratic, or cubic regression equation to estimate changes with time in amounts for each category of N in each plant part. Quadratic polynomials were generally most suitable, but cubic polynomials proved superior in some instances. Equations describing the fluxes, or net rates of movement, of N into or out of each plant part were calculated by taking the first derivatives of the polynomials. The days on which a plant part changed from N source to N sink or from N sink to N source were determined by setting the first derivatives of the regression equations equal to zero and solving for x.

RESULTS

For each plant part, and for the shoot as a whole, neither at pollination nor at the three subsequent samplings were there significant ($P = 0.05$) differences in dry weights between Pioneer 3369A (normal) and Pioneer L3369 (*opaque-2*) genotypes. At 36 d after pollination, however, the mean dry weight (23.0 g) of the lower leaves of plants treated with no N was less ($P = 0.05$) than that of plants treated with 3.75 mM N. The lower leaves of all plants which had received no N during reproductive growth were generally chlorotic with some necrosis at the 36-d sampling. In contrast, the lower leaves of the plants which had received 3.75 mM N treatment during the 36 d of reproductive growth were mostly green, except for slight necrosis appearing among the lowermost leaves. Except for the lower leaves, for no other part of the shoot, including the grain, were there any significant ($P = 0.05$) differences in dry weight at any of the four samplings due to either nitrogen treatment or the *opaque-2* gene.

Compared to its normal counterpart, the grain of the *opaque-2* plants showed significantly ($P = 0.05$) less accumulation of N at the final 36-d sampling. In contrast to this effect on N accumulation in the grain, the presence of the *opaque-2* gene had little or no effect on the amounts of total and endogenous N in the other six parts of the maize shoot. There were many significant differences in amounts of total and endogenous N associated with different N treatments in several plant parts (Table I). In the stalk and in both the lower and upper leaves, the amounts of total N were greater with the 3.75 mM N treatment, compared to the no N treatment. Of the N which accumulated in the stalk and lower leaves by the time of pollination, the amount remaining at 12, 24, and 36 d thereafter was markedly higher for plants receiving 3.75 mM N, compared to those receiving no N. The total N in stalk and lower leaves was also higher in plants treated with 3.75 mM N, compared to the plants deprived of N during reproductive growth. Total N in the upper leaves was equal for both N treatments at 12 d, but was significantly ($P = 0.01$) greater at 24 and 36 d after pollination when N was supplied after pollination.

Regardless of N treatment, net loss of endogenous N occurred continuously in the stalk and upper leaves (Table I). Net gain occurred continuously in the grain, and in the grain of plants receiving 3.75 mM N, the proportion of exogenous N/endogenous N increased as reproductive growth progressed. The amounts of endogenous N in the cob and husk increased, becoming greatest at the 12-d sampling, but showed a decline on the 24- and 36-d samplings. At 12 d after pollination, identical quantities of endogenous N had been accumulated by the grain and cob, 274 and 276 mg, respectively, for the 0 mM N treatment, and 208 and 205 mg, respectively, for the 3.75 mM N treatment. By the 24- and 36-d samplings, however, the grain contained much more endogenous

Table I. *Effects by Levels of N in Nutrient Solutions Provided Postpollination on the Amounts of Total and Endogenous N in Various Plant Parts*

Pooled data are shown for Pioneer 3369A and L3369 plants.

Plant Part (N present at pollination)	Time after Pollination	Levels of N in Nutrient Solution[a]		
		0 mM	3.75 mM	
		Total N	Total N	Endogenous N
mg/plant	*d*		*mg/plant*	
Grain (0)	12	274	308	208
	24	1114	1247	758***
	36	1998	2102	1243***
Cob (126)	12	276	270	205**
	24	172	183	136
	36	149	146	104*
Husk (158)	12	291	316	263
	24	200	288	228
	36	129	180**	142
Shank (30)	12	50	48	37
	24	50	63	47
	36	48	64	44
Upper leaves (568)	12	527	638	494
	24	420	516**	449
	36	318	415**	351
Lower leaves (674)	12	654	758**	711
	24	500	680**	573
	36	237	556***	462***
Stalk (1509)	12	1038	1368**	1137
	24	566	1218***	918**
	36	502	1266***	878***
Shoot[b] (3122)	12	3110	3604**	3002
	24	3023	4194***	3108
	36	3380	4730***	3224

[a] Levels of significance for differences between means for amounts of N in plant with 0 N *versus* added N: *, P = 0.05; **, P = 0.01; ***, P = 0.001.

[b] The amount of N in the shoot for each replicate was calculated by summing the amounts of N for each part of the shoot. Analysis of variance was then performed on the sums.

N than did the cob (Table I).

Translocation and redistribution of the N (Table I) to and from the different plant parts depicted in Figure 1 is complex and dynamic, inasmuch as all the fluxes changed as time progressed during the 36-d experimental period. Estimates of the simultaneous fluxes of total, endogenous, and exogenous N for these parts of the maize shoot are based on the data for the 0 and 3.75 mM N treatments, combining data of the two genotypes (Fig. 2). It is assumed that N moved only into the grain during the first 36 d of reproductive growth, since intense anabolic activity is known to occur in that organ during reproductive growth. For the other parts of the shoot, however, simultaneous influx and efflux of N were most likely, as indicated in Figure 1. Since the fluxes of Figure 2 are based on data for amounts of N in the plant parts from sequential samplings, they are estimates of net fluxes for each plant part. For plants provided no N after pollination, total N and endogenous N fluxes were identical, and for the 3.75 mM N treatment, total N fluxes are sums of the component endogenous and exogenous N fluxes.

Negative fluxes of total and endogenous N for the stalk (Fig. 2) indicate net efflux and identify the stalk as a source of both endogenous N and total N during most of the 36-d experimental period. At 29 and 33 d after pollination, the total N and endogenous N curves for the 3.75 mM N treatment cross the x axis, denoting changes from net efflux to net influx and indicating, approximately, the time after pollination at which the stalk began to be a sink with respect to both total N and endogenous N. Endogenous N fluxes for the stalks of plants receiving no N after pollination were always negative and throughout the 36-d experimental period were more negative than were the corresponding fluxes for the 3.75 mM N treatment. This indicates that the N which was accumulated in the stalk prior to pollination was always lost at a greater rate when no N entered the plant after pollination than when N was supplied in the nutrient solution. For the 3.75 mM N treatment, the stalk acted as a sink for exogenous N throughout the 36-d experimental period, but the rate of accumulation decreased as time progressed. The efflux of total N and endogenous N from the stalk was initially great, diminished in magnitude as time passed, and neared zero between 30 and 36 d after pollination.

The other two primary N sources of the shoot during reproductive growth are the lower leaves and upper leaves. Net efflux of

Table II. *Regression Equations and Coefficients of Determination (R^2) for Estimating Amounts (mg N plant^{-1}) of Total, Endogenous, and Exogenous N as Functions of Time (Days after Pollination)*

Amounts are shown for various parts of maize plants treated with 0 or 3.75 mM N from pollination to 36 d thereafter (pooled data from Pioneer 3369A and L3369 plants; y = mg N plant^{-1}, x = days after pollination).

Plant Part	N Treatment	N Fraction	Regression Equation	R^2
	mM			
Grain	0	Total	$y = 2.5509x^2 - 0.279x^3$	0.94
	3.75	Total	$y = 3.0671x^2 - 0.0399x^3$	0.95
	3.75	Endog.[a]	$y = 1.9542x^2 - 0.0275x^3$	0.95
	3.75	Exog.	$y = 1.1128x^2 - 0.0124x^3$	0.94
Cob	0	Total	$y = 125.6250 + 32.5885x - 2.0598x^2 + 0.0326x^3$	0.69
	3.75	Total	$y = 125.6250 + 29.3785x - 1.7721x^2 + 0.0270x^3$	0.70
	3.75	Endog.	$y = 125.6250 + 18.0336x - 1.1661x^2 + 0.0180x^3$	0.61
	3.75	Exog.	$y = 11.3495x - 0.6066x^2 + 0.0090x^3$	0.90
Husk	0	Total	$y = 157.6250 + 27.3108x - 1.6315x^2 + 0.0236x^3$	0.68
	3.75	Total	$y = 162.8094 + 17.0127x - 0.4645x^2$	0.36
	3.75	Endog.	$y = 161.9856 + 11.3389x - 0.3351x^2$	0.29
	3.75	Exog.	$y = 5.7694x - 0.1315x^2$	0.67
Shank	0	Total	$y = 31.2717 + 1.8335x - 0.0388x^2$	0.18
	3.75	Total	$y = 30.1188 + 1.9473x - 0.0276x^2$	0.40
	3.75	Endog.	$y = 29.9283 + 1.0017x - 0.0164x^2$	0.18
	3.75	Exog.	$y = 0.9584x - 0.0116x^2$	0.77
Upper leaves	0	Total	$y = 570.7228 - 3.0583x - 0.1124x^2$	0.69
	3.75	Total	$y = 563.6660 + 0.3859x - 0.1210x^2$	0.35
	3.75	Endog.	$y = 563.7746 - 4.2893x - 0.0408x^2$	0.54
	3.75	Exog.	$y = 4.6738x - 0.0802x^2$	0.95
Lower leaves	0	Total	$y = 730.7826 - 2.2376x - 0.3179x^2$	0.90
	3.75	Total	$y = 734.8709 + 4.3520x - 0.2619x^2$	0.46
	3.75	Endog.	$y = 734.9344 - 3.8362x - 0.1073x^2$	0.69
	3.75	Exog.	$y = 8.1737x - 0.1542x^2$	0.92
Stalk	0	Total	$y = 1526.3315 - 53.1722x + 0.6727x^2$	0.88
	3.75	Total	$y = 1518.7316 - 19.0435x + 0.3236x^2$	0.24
	3.75	Endog.	$y = 1509.9303 - 38.3384x + 0.5761x^2$	0.71
	3.75	Exog.	$y = 20.0893x - 0.2680x^2$	0.89

[a] Endog., endogenous; exog., exogenous.

total N for all the leaves was of greater magnitude in plants receiving no N, compared with those treated with 3.75 mM N (Fig. 2). In plants receiving the 3.75 mM N treatment, the lower leaves acted as a sink for total N until about 8 d after pollination, while the upper leaves did also until 2 d after pollination. Thereafter, the leaves acted as sources of total N. Both the lower and upper leaves of plants receiving no N during reproductive growth acted only as sources of total N. The magnitude of net efflux of endogenous N in both lower and upper leaves increased as time progressed and the plants deprived of N lost endogenous N from the leaves more rapidly than did those supplied with N after pollination (Fig. 2). Both the lower and upper leaves acted as sinks for exogenous N until 26 and 29 d after pollination, respectively. Then they began to show slight net efflux of exogenous N.

Unlike the stalk and the leaves, the shank tended to accumulate total N during the 36-d experimental period. The amounts and net fluxes of N in the shank are small in comparison to other parts of the plant (Fig. 2), and there were no significant ($P = 0.05$) differences due to N treatment or genotype (Table I). With the 3.75 mM N treatment, the shank acted as a sink for exogenous N during the entire 36-d period and was a sink for total N and endogenous N until 35 and 30 d after pollination, respectively, after which the shank acted as a source of endogenous and total N. When N was not supplied after pollination, the shank was a sink of endogenous N for the first 24 d of reproductive growth, after which net efflux of N occurred.

Estimates of N flux indicate that when N did not enter the plant after pollination, the husk (Fig. 2) initially accumulated endogenous N and total N at greater rates and acted as an endogenous N sink for a shorter time, compared to the 3.75 mM N treatment. Moreover, with the no N treatment, the magnitude of the net efflux of N was greatest about 2 weeks earlier when compared to the net efflux of total and endogenous N for the 3.75 mM N treatment. At 35 d after pollination, the husk had ceased to be a source of N for the grain in the no N treatment, but when N was supplied in the nutrient solution, the husk lost N more and more rapidly from about 17 d to the end of the experimental period. At the 36-d sampling, the tips of the husk leaves of all plants, regardless of N treatment, were brown, while the rest of the husk leaves ranged in color from yellow to light green.

For the cob, total and endogenous net N fluxes were of the same pattern, regardless of N treatment (Fig. 2). With the 3.75 mM N treatment, exogenous N was accumulated by the cob at decreasing rates for 13 d after pollination, and net loss began, continuing for the next 19 d. A striking aspect of the net flux curves for the cob is that they indicate the cob became a sink for

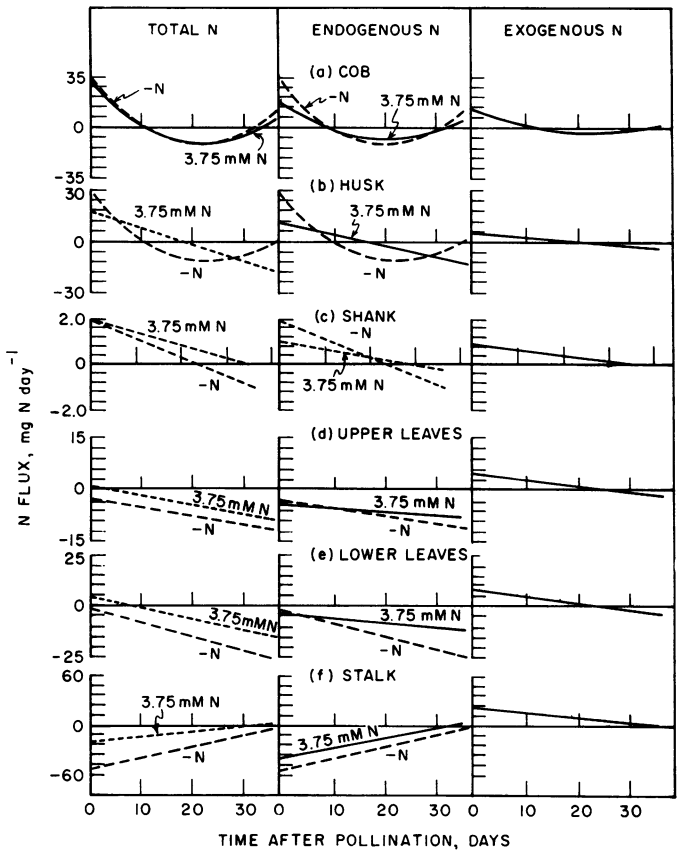

FIG. 2. Fluxes of total, endogenous, and exogenous N for (a) cob, (b) husk, (c) shank, (d) upper leaves, (e) lower leaves, and (f) stalk per maize plant during the first 36 d of reproductive growth when no N (— —) or 3.75 mM N (——) was supplied in the nutrient solution. Flux curves derived from regression equations with $R^2 < 0.60$ are drawn as (- - -), and N treatments are indicated. Data of Pioneer 3369A and L3369 hybrids are pooled.

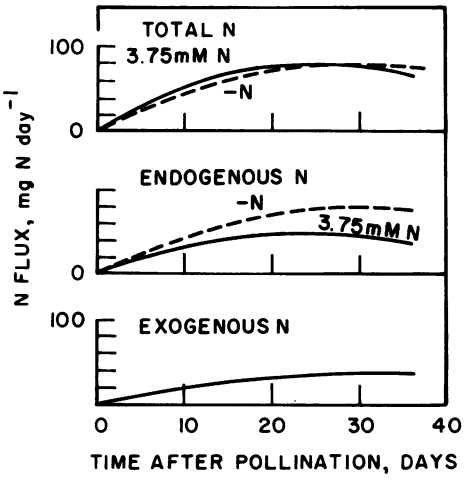

FIG. 3. Fluxes of total, endogenous, and exogenous N for grain per maize plant during the postpollination period with no N (- - -) or 3.75 mM N (——) in the nutrient solutions. Data of Pioneer 3369A and L3369 hybrids are pooled.

N at about 32 to 33 d after pollination. This pattern is very similar to that of total, endogenous N flux for the husk of plants receiving the 0 mM N treatment.

The rates of total N accumulation in the grain (Fig. 3) increased from a rate assumed to be zero at the time of pollination to a maximum of 78 mg N day^{-1} for both the 3.75 mM N treatment at 25 d after pollination and for the 0 N treatment at 30 d after pollination, after which the rate declined, as estimated using the first and second derivatives of the regression equations. For both the 0 N and the 3.75 mM N treatments, the total N fluxes for the grain on any particular day during the experimental period were almost identical. At 24 and 36 d after pollination, the amounts of endogenous N in the grain were significantly greater ($P = 0.001$) in plants receiving no N (Table I), compared to the plants receiving 3.75 mM N, even though the amount of total N in the grain of plants receiving the two N treatments did not differ significantly ($P = 0.05$). Estimates of fluxes of total, endogenous, and exogenous N for the grain of plants receiving no N or 3.75 mM N during the experimental period show (Fig. 3) that, when exogenous N entered the developing grain, the influx of endogenous N was less than in the case of no N entering the plant.

Considering the cob and the grain, we found that total N fluxes for each of these two plant parts were unaffected by lack of N in the rooting medium during reproductive growth. Ear (cob plus grain) net N accumulation rates ranging from 36 to 93 mg day^{-1} $plant^{-1}$ were recently reported by Below *et al.* (3) for four maize hybrids sampled over three (7–21, 21–31, 31–42 d) harvest periods following anthesis. In the present study, the net fluxes for the ear for the 0 N treatment were 46, 64, and 86 mg N day^{-1} $plant^{-1}$ at 12, 24, and 36 d after pollination, respectively. For the 3.75 mM N treatment, the corresponding fluxes were 55, 69, and 72 mg N day^{-1} $plant^{-1}$.

DISCUSSION

One of the features of the postpollination period of development of the maize plant is the development of a relatively large sink for N in the grain. Hanway (9) observed little remobilization of N from one part of the maize plant to another before silking. In his experiments with maize grown in the field, Hanway (9) estimated that about one-half of the N found in the grain at maturity had been remobilized from other parts of the shoot. Our results show that maize plants accumulated the same ($P = 0.05$) amounts of dry matter and N in the grain at 36 d after pollination, whether 100% of the grain N (0 N treatment) or only 60% of the grain N (3.75 mM N treatment) was remobilized from sources of N absorbed prior to pollination.

The significantly lower dry weights of the lower leaves for plants receiving no N for 36 d after pollination are indirect effects resulting from N remobilization to satisfy demands for protein synthesis in the grain of both genotypes. Translocation of sucrose from vegetative organs to the grain of maize has been shown to be linked to the accumulation of N in proteins of the grain (13). By comparing nitrogen concentration of the lower leaves at pollination with corresponding values found in earlier studies with the same genotypes of maize, the plants of both genotypes in the present study were found to contain sufficient endogenous N to attain maximum grain yields at maturity (5).

Using half-strength Hoagland solution and maintaining the concentration of NO_3^--N between 4 and 7.5 mM, Friedrich and Schrader (8) estimated by regression analysis that, 35 d after pollination, about 300 mg of exogenous N and about 1300 mg of endogenous N per plant were present in the ear (cob plus grain); thus, about 81% of the N in the ear was endogenous, remobilized N. After the first 35 d of reproductive growth, the proportion of exogenous N in the ear (cob plus grain) was twice as much in the Pioneer 3369A and L3369 hybrids (40% *versus* 19%), compared to the 'W64A × W182E' hybrid used by Friedrich and Schrader. Studies by Reed *et al.* (11) with maize plants of genotypes differing in NRA have shown that N remobilization after pollination can be affected by the balance between protease activity and NRA in various plant tissues.

Considering the amounts of total N and endogenous N lost by

each of the primary N sources of the maize shoot during the first 36 d of reproductive growth, the stalk, followed by the lower and upper leaves, was the prime source of remobilized, endogenous N in the shoot for the grain. The rates of loss of total and endogenous N from the stalk were large at first, lessening as time progressed. In a complementary way, the lower and upper leaves lost total N and endogenous N slowly at first, then more rapidly during the first 36 d after pollination. The maize plant has apparently evolved in such a way as to delay, as long as possible, net loss of N from the most photosynthetically productive organs of the plant, the leaves, whether the environment surrounding the roots is either N-rich or N-poor during the reproductive phase of growth. The presence of N in the rooting medium decreased rates of loss of both total N and endogenous N from the stalk and lower and upper leaves.

Those plant parts closely associated with the grain—the husk, cob, and shank (Fig. 1)—acted first as sinks and then as sources of total N and endogenous N. Apparently, one of the functions performed by these three plant parts is to accumulate N in the early stages of reproductive growth when the total flux of N from the stalk exceeds the total N flux into the grain. As total N flux into the grain increased, the shank, husk, and cob began to act as sources of N, since total N flux from the stalk was no longer sufficient to supply the grain where amino acids (5) and proteins (4) were accumulating at various rates strongly influenced by the *opaque-2* gene. The *opaque-2* gene had significant effects on the amounts of N accumulated in various amino acid fractions of the grain, as indicated for the 24- and 36-d samplings, for the plants of the present experiment which received 0 or 3.75 mM N after pollination (5). Decreased N accumulation in maize grain due to the *opaque-2* gene has been described for other maize genotypes (12, 13) and for the 3369A and L3369 genotypes used in this study (5).

Unlike the stalk and the leaves, the shank accumulated N during the 36-d experimental period. The amounts and net fluxes of N in the shank are small in comparison to other parts of the plant and there were no significant ($P = 0.05$) differences due to N treatment or to the *opaque-2* gene. The fact that the grain accumulated approximately 2000 mg of N and about 115 g of dry matter while the shank accumulated no more than 40 mg of N and about 4 g of dry matter during the first 36 d after pollination is evidence of the efficiency of the shank as a conduit for nitrogen and other elements during the growth of the grain. Because of incomplete pollination in the present experiment, it is expected that, under conditions more favorable for pollination and seed set, the amounts of both dry matter and N accumulated in the grain would be higher than those we report. Amounts and fluxes of N for the components of the shoot would also be expected to differ from those of the present study, under conditions of more favorable pollination, where the primary N sink, the grain, would be larger. The different patterns of net N fluxes for the husk with N-poor and N-rich media surrounding the roots illustrate a range of responsiveness of the husk as it functions as N sink and N source.

The influence of the *opaque-2* gene on translocation of N, in the context of the whole plant model, is localized in the primary sink, the grain. In the maize plants of our studies, amounts of N in individual amino acid fractions of the grain, which may be considered subsinks for N within the primary sink, were in some cases influenced by the *opaque-2* gene (5). In the *opaque-2* grain, greater rates of accumulation of lysine were accompanied by lesser rates of accumulation of methionine, tyrosine, isoleucine, phenylalanine, serine, proline, alanine, and leucine, in comparison to the normal grain (5).

For the cob and the grain, total N fluxes differ between the two plant parts, but unexpectedly, the total N fluxes for each of these two plant parts were unaffected by either presence or absence of N in the nutrient solution. The maize plant has apparently evolved with a system to translocate N to the developing grain, resulting in strict regulation of the flow of the element as it moves through the cob and into zones of intense anabolic activity in the kernels.

There was no difference ($P = 0.05$) in the amounts of endogenous N in the whole shoots of plants receiving the 0 and 3.75 mM N treatments, comparing treatment means from the samples taken at 12, 24, or 36 d after pollination (Table I). The slight increase in endogenous N in the shoots of plants of both treatments suggests that, under the conditions of this experiment, there may have been slight net loss of about 200 mg of endogenous N from the roots during the first 36 d of reproductive growth. Data of Friedrich and Schrader (8) indicate that, for maize plants of another genotype ('W64A × W182E') grown in a greenhouse with nutrient solution, about 160 mg of endogenous N were lost from the roots during the first 36 d of reproductive growth when no N was supplied in nutrient solution during reproductive growth. They found, however, that a very small net accumulation of endogenous N (25 mg N $plant^{-1}$) appeared to have accumulated during the first 36 d of reproductive growth when N was supplied at concentrations between 4.0 and 7.5 mM N in the nutrient solution. Because the roots were not recovered from the sand in the present study, it was not possible to estimate net fluxes of total, endogenous, and exogenous N. Questions needing to be answered through future research include: (a) under what conditions do the roots of maize act as a net sink or net source of N during vegetative and reproductive growth, and (b) at what net rates is N gained and lost from the roots during the life of the plant?

Changes in N content of the leaves, stalk, or shoot of six maize hybrids were shown to differ among genotypes after the first 24 d of reproductive growth (2), demonstrating that genetic factors influence the movement of N within the shoot of maize plants after silking. Some of the findings of Friedrich and Schrader (8) which are confirmed by the present research show that an environmental factor, the presence of N in the rooting system, influences the amounts of endogenous and total N in various parts of the maize plant during reproductive growth. Therefore, the N flux data of the present experiment, while presenting general trends for maize during the first 36 d of reproductive growth, should be understood to be affected by both genetic and environmental factors. The present research describes fluxes of only total N and the endogenous and exogenous components of total N during the early period of reproductive growth of maize.

On the basis of N flux data from the present experiment, perturbations in the N flux to the grain of maize plants appear to have been minimized in several ways.

(a) The primary sources of N in the shoot—the stalk and the leaves—lost N at greater rates when the influx of N to the roots from the environment was nonexistent. (b) A buffer zone of secondary sinks and sources—the shank, husk, and cob—accumulated N moving toward the developing grain and later released the element as N influx to the grain increased. (c) The cob and husk appear to have been able to accumulate N toward the latter stages of reproductive growth when the influx of N from the other organs of the plant may have exceeded the influx of N to the grain. (d) A fourth, conservative aspect of the system of N translocation to the developing grain entailed initially rapid loss of N from the stalk which became slower with time, complemented by the increasing net efflux of N from the leaves. The benefit of this sequence of remobilization is that carbon is fixed for a longer period of time than would have been possible if catabolic processes were to have predominated in the leaves during the early stages of reproductive growth.

The conclusions of this study are based on measurements covering only a portion of the entire life cycle of two maize genotypes. The percentage grain set was lower than desired. To use the equations developed in this study to estimate N fluxes for maize plants whether before pollination or from 36 d after polli-

nation to physiological maturity would be a misuse of the data. Moreover, since the grain as N sink did not reach its full potential because of incomplete pollination, it is expected that all N fluxes described for the period from pollination to 36 d thereafter in the present study would differ to varying degrees in Pioneer 3369 maize under conditions of 100% pollination. Because both genetic and environmental factors can influence plant metabolism, including N fluxes, it would be inappropriate to use the flux data of the present experiment to model N fluxes of maize grown under field conditions.

Future research is needed to estimate fluxes of total N for the components of the system of the maize plant described in Figure 1, during both the vegetative and reproductive growth phases. Research is also needed to estimate net fluxes of various chemical species containing N—such as nitrate, asparagine, and glutamine—for the various compartments, or parts, of the plant during the entire life cycle of maize. Considering the whole plant as a system composed of contiguous compartments, differential equations derived from regression equations can be used to estimate net fluxes of any element or chemical species which can be measured after periodic sampling.

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