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Interaction of Carbon and Nitrogen Metabolism in the Productivity of Maize[1]

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ABSTRACT

Five maize (*Zea mays* L.) hybrids, FS854, B73 × Mo17, B84 × Mo17, B73 × B77, and P3382, grown under field conditions, were sampled at intervals during the grain-filling period. Plants were subdivided into stalks (including sheaths), leaves, and kernels. These parts were assayed for dry weight, reduced nitrogen, and extractable nonstructural carbohydrates. The duration and rates of net nitrate reduction and photosynthesis were approximated by the changes over time in the accumulation of reduced nitrogen and dry weight by the plant (total, above ground), respectively.

Data on the accumulation of reduced nitrogen and dry weight by the plant show that decreases in nitrate reduction preceded (in time and extent for four of the hybrids and in extent for FS854) decreases or cessation of photosynthesis. FS854 continued to accumulate reduced nitrogen and dry matter throughout the grain-filling period.

The patterns of change in stalk carbohydrate and reduced nitrogen during the early stages of ear development show the stalk serves as a storage reservoir and that these reserves were remobilized during the final stages of grain development. The marked increase and maintenance of dry weight and carbohydrate content of stalks until 34 days after anthesis, shows the capacity of the leaves to produce photosynthate through the first half of the grain-filling period exceeds the needs of the ear and/or the transport system. In contrast, stalk nitrogen content shows a slight increase up to 12 days after anthesis and decreases continually thereafter. Leaf nitrogen was lost continuously throughout grain development. The potential capacity of the plant to supply newly reduced nitrogen was inadequate to support initiation and early development of the kernels without remobilization of vegetative nitrogen. Of the two hybrids having delayed leaf senescence, FS854 with its initially higher concentration and content of reduced nitrogen in the stalk, initiated and developed a bigger ear than P3382, which had lower levels of stalk nitrogen.

Three of the five hybrids had 'near linear' rates of accumulation of kernel dry weight, whereas none of the hybrids had linear rates of gain in kernel nitrogen. All hybrids had maximum or near maximum rates of gain of kernel nitrogen between 26 and 34 days after anthesis and a marked reduction (41–52%) of rates in the following sampling interval. These decreases are concurrent with decreases in rates of nitrate reduction (nitrogen accumulation) by the whole plant for four of the hybrids and with decreases in remobilization of nitrogen from the vegetation of FS854. Data for the ratio of rates of accumulation of dry weight/reduced nitrogen by the kernels *versus* time after anthesis, show that the accumulation of dry weight and reduced nitrogen are independent of each other. The variations in the ratio values appear best related to variations in the availability of nitrogen from the vegetation.

The high carbohydrate content of maize grain (approximately 80% carbohydrate *versus* 1.5% N) dictates a predominant role for photosynthesis in achieving maximum yields. However, the metabolism of C and N are so closely linked and with the increased use of fertilizer N being closely associated with enhanced maize yields (6) it seems reasonable that both C and N metabolism should be considered when attempting to identify factors that limit productivity. In Evans's book (5) on the physiological basis of yield of nine major food crops, only the chapter on rice accords a major role for N as a yield-limiting factor (14). In the chapter on maize (4) N and N metabolism as factors affecting productivity were not discussed. This preoccupation with photosynthesis as the primary limiting factor of yield is again indicated in Johnson's recent book (8). Shading, defoliation, and canopy studies are usually interpreted with respect to the effect on photosynthesis and little attention given to the effect of such treatments on nitrate assimilation, although it is known that light affects nitrate reduction in leaves.

For rice, high yields are possible only under high levels of N supply and plant characteristics that confer high yielding abilities are often associated with responsiveness to N (14). These authors (14) and Yoshida (21) indicate N has two major roles: the establishment of the yield capacity and the establishment and maintenance of photosynthetic capacity. The work of Morita (13) showed 90% of the N lost from the leaves during normal senescence was from the chloroplasts.

For soybean, Sinclair and deWit (17) suggested it was the loss of N from the vegetation to support grain development that was responsible for 'self-destruction.' Wittenbach *et al.* (20) showed the loss of N from the soybean leaves of field-grown plants was concurrent with changes in chloroplast structure and loss of photosynthetic activity during the grain-filling period.

In certain cereals, Stoy as quoted by Mengel and Kirkby (12) noted that an adequate N supply during early growth stages was important in determining the number of ears per unit area. For tomatoes, a deficiency of N, but not carbohydrate, repressed megaspore development, whereas the reverse was true for microspore development (7). Tollenaar (18) has suggested that sink sizes may frequently limit crop yields.

For maize, little information is available on the physiological processes that determine ear and kernel initiation (4). However, Kranz and Chandler (10) noted that increasing soil N level from deficient to sufficient increased grain weight 3 or 4 times more than stover weight. The occurrence of barren plants is commonly associated with an inadequate N supply. Decrease in leaf N of maize during the grain-filling period was concurrent with the loss of Chl (3).

The role of N in achieving high productivity of other crops appears similar to the two roles proposed for rice. A third role for N as a factor limiting maize yields can be inferred from the work of Tsai *et al.* (19). They suggested that protein accumulation in the kernel could be a factor in regulating kernel development. With five corn hybrids, Below *et al.* (1) found the capacity of the

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[1] Supported by Allied Chemicals.

plant to supply N to the ear was more limiting than the capacity to provide photosynthate. One of the five hybrids showed a decrease in the rate of accumulation of N by the ear at 30 to 33 d after anthesis. Although this does not prove a need for concurrent accumulation of N and dry weight by the kernels, it may indicate a potential limitation in availability of N. Possible needs for continued N acquisition by the kernel would be to permit adequate and normal embryo development which could affect hormone balance, and to maintain the enzyme and enzyme systems needed for deposition of starches and proteins and for energy generation.

The objective of this work was to investigate the interaction of C and N metabolism in relation to productivity of maize.

MATERIALS AND METHODS

Cultural Procedures. Kernels of five maize (*Zea mays* L.) genotypes (FS854, P3382, B73 × Mo17, B84 × Mo17, B73 × B77) were overplanted on May 25, 1981, and thinned to a final stand of 59,250 plants/ha. The reasons for selecting these hybrids were: FS854, world record yield (213 quintals ha^{-1}, 1975, nonirrigated, H. Warsaw, Saybrook, IL); B73 × Mo17, a widely used hybrid planted on half of the acreage in the central corn belt; B84 × Mo17 and B73 × B77, high yielding hybrids identified under 'nonlimiting' environmental conditions; and P3382, a recently released commercial hybrid. All hybrids were of the same maturity group with grain black layer formation occurring at approximately 57 DAA.[2] FS854 has the potential for development of two ears, however in the current experiment this trait was not expressed. P3382 and FS854 maintain viable appearing green leaves until after grain black layer formation. In contrast, the three open pedigree hybrids, hereafter referred to as the "B" hybrids, senesced earlier as judged visually by leaf yellowing and by Chl content. The decreases in Chl for the first leaf above the ear between anthesis and 46 DAA were 60%, 48%, 46%, 35%, and 32% for B73 × Mo17, B84 × Mo17, B73 × B77, P3382, and FS854, respectively. Soil type was Drummer silt loam with high levels of P and K with a spring application of 200 kg N/ha. The experiment was a 3 × 5 factorial with five replications. The main effects for A consisted of a control and two fertilizer treatments (applied primarily as a supplemental source of N), whereas the five genotypes comprised the B effects. Because the fertilizer treatments had no significant effect on the measured parameters, the effect of genotypes was averaged across fertilizer treatments. The lack of significance in fertilizer treatments was attributed to the small amount of supplemental N applied (12 kg N/ha) or to the excessive (28 cm above average) summer rainfall that directly or indirectly could have nullified the effects of the supplemental N treatments. Each experimental unit consisted of a three-row plot (rows 9.1 m long, spaced 76 cm apart) containing 42 plants per row. Grain yield per plot was determined from the center row and side rows were used for destructive sampling including yield expressed on a per plant basis.

Sampling. Whole plants were harvested on July 21, five DBA, and at 12, 18, 25, 34, 43, 50, and 57 DAA. Plants were harvested between 1400 and 1600 h. Because the hybrids differed in susceptibility to lodging, representative individual plants were selected from row sections having uniform distribution of standing plants. A sample consisted of three plants from within each of the 15 replicate plots. Each data point plotted represents the mean value of 45 individual plants.

The harvested plants were divided into stalks (including sheaths) leaves, and ears and weighed fresh. Husks, cobs, and tassel were discarded. A conscientious effort was made to save all senesced leaves. Leaves and stalks were passed through a mechanical silage chopper. Portions (50 g leaves, 100 g stalks) of the chopped parts were dried at 70°C in a forced draft oven. After 60 h, the dried portions were reweighed. The dried tissue was mechanically ground (20-mesh screen) prior to analysis for NO_3^--N, total N, and extractable nonstructural carbohydrate. The ears were dried to constant weight at 70°C in a forced draft oven. After hand shelling, the kernels were weighed, ground, and stored for subsequent analysis.

Reduced N. A sample (100 mg) of dry, ground tissue was weighed into a Folin-Wu tube and digested in concentrated H_2SO_4 as previously described (3). After digests had been diluted and mixed, aliquots were assayed for NH_4^+ (2). In samples that contained high levels of NO_3^- (stalks), reduced N was determined by substracting NO_3^--N from total N values. In such samples, NO_3^- was converted to reduced N by the predigestion procedure of Nelson and Sommers (15).

Extractable Nonstructural Carbohydrate. Tissue samples (100 mg) were weighed into Folin-Wu digestion tubes and autoclaved (20 min, 1.05 kg/cm^2) in a 25-ml solution of 0.25% (w/v) benzoic acid. After cooling, the autoclaving was repeated. The benzoic acid served to hydrolyze the sucrose and also acted as a preservative. Extracts were filtered and appropriate aliquots (50–500 µl) taken. Aliquots were brought to a volume of 750 µl by adding 50 mM potassium acetate (pH 5.0) containing 0.25% (w/v) benzoate. Starch was hydrolyzed by adding 250 µl of a solution containing both alpha-amylase and amyloglucosidase, 1 and 40 mg, respectively, in 50 ml of 50 mM potassium acetate buffer (pH 5.0) and incubating for 15 h at 42°C. The sample was assayed for reducing

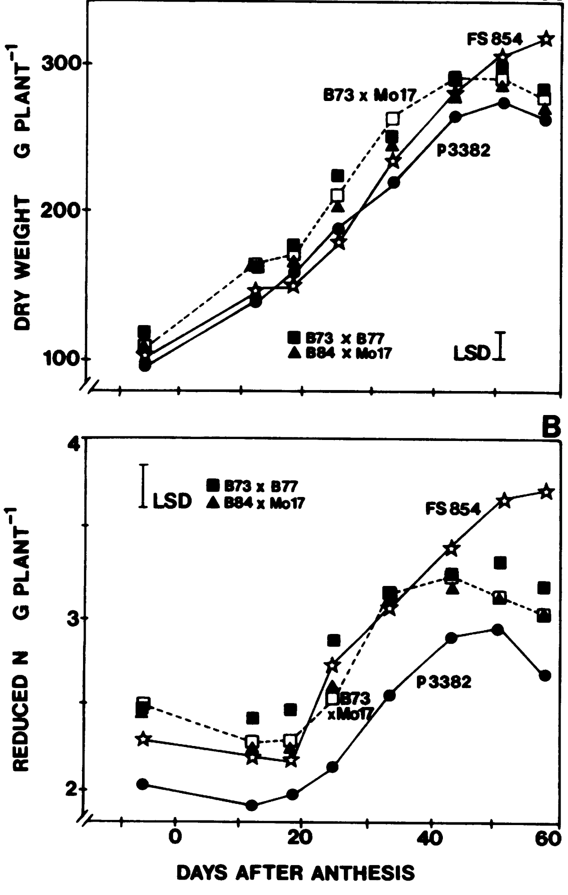

FIG. 1. Accumulative changes in dry weight (A) and reduced N (B) of the total above ground plant during grain development of five maize hybrids. For clarity, points of two of three related B hybrids were not connected. Each plotted point represents mean value of 45 plants.

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[2] Abbreviations: DBA, days before anthesis; DAA, days after anthesis.

sugars (16) in order to determine the total nonstructural carbohydrate content. All carbohydrate values were expressed as glucose equivalents.

Nitrate-N. Extracts assayed for carbohydrates were subsequently analyzed for NO_3^--N by the method of McNamara *et al.* (11).

Metabolite Changes. Changes in dry weight and reduced N of the total plant were used to approximate *in situ* rates and duration of photosynthesis and nitrate reduction.

Statistical Analysis. Data were analyzed by analysis of variance procedures. Significant differences ($P \leq 0.05$) between both genotypes and sampling dates were observed for all the parameters measured. The data for respective genotypes and sampling dates were tested for homogeneity of the error variance by Bartlett's test. Because the data had homogenous error terms, the pooled error mean square from analysis of variance was used to calculate the LSD ($P \leq 0.05$) shown on the figures.

RESULTS AND DISCUSSION

Total Plant. As judged by the continued accumulation of total plant dry weight, photosynthetic activity of FS854 was maintained throughout the grain-filling period (Fig. 1, A). In contrast, dry weight accumulation was terminated by 43 DAA for B73 × Mo17 and 50 DAA for the other three hybrids.

Based on the accumulation of reduced N by the total plant (Fig. 1, B) it can be deduced that the rate of nitrate reduction decreased markedly between 34 and 43 DAA for the three B hybrids, 43 and 50 DAA for P3382, and between 50 to 57 DAA for FS854. These decreases in the accumulation of N preceded (in time and extent for four of the hybrids and in extent for FS854) the decreases in dry weight accumulation.

The reason for the low rate or lack of dry weight accumulation between 12 and 18 DAA for four of the hybrids is not clear (Fig. 1, A). Examination of environmental records implicated neither light or temperature as the causal factor. The effect of discarding tassel, husk, and cob should have decreased the rate of accumulation between 5 DBA and 12 DAA rather than between 12 and 18 DAA. Seasonal canopy photosynthesis profiles of maize are bell shaped with maxima just prior to anthesis (D. B. Peters, personal communication). In contrast, the negative rates of N accumulation between 5 DBA and 12 DAA and the low rates or lack of accumulation between 12 and 18 DAA (Fig. 1, B) are attributed to the discarding of tassels, husks, and cobs and a quiescent period of nitrate reduction. Pollen shed of maize can account for a loss of 0.1 to 0.2 g N per plant (9).

The late season losses in dry weight and N of four of the five hybrids could be due to continued respiratory activity by the plant or invading organisms, remobilization to the root, or volatilization of N to the atmosphere. Rain can leach components from the plant, however rainfall between 50 and 57 DAA was low.

Plants Parts and Components.

Leaves. All hybrids had attained maximum leaf dry weight by 5 DBA and retained most of this weight until 50 DAA (Fig. 2, A). The weight loss over this interval, ranged from 28% for B73 × Mo17 to 9% for FS854. Between 50 and 57 DAA, there was a marked loss of leaf dry weight, especially for the earliest senescing hybrid, B73 × Mo17. Of all hybrids, P3382 developed the smallest amount of leaf mass per plant. At anthesis, the leaf areas for the first leaf above the ear were 750, 726, 703, 689, and 610 cm^2 for B84 × Mo17, B73 × Mo17, B73 × B77, FS854, and P3382, respectively. Canopy leaf area was not measured.

For all hybrids, the patterns of nonstructural carbohydrate content were similar with the exception of B73 × Mo17 (Fig. 2, B). Although there were marked fluctuations in carbohydrate

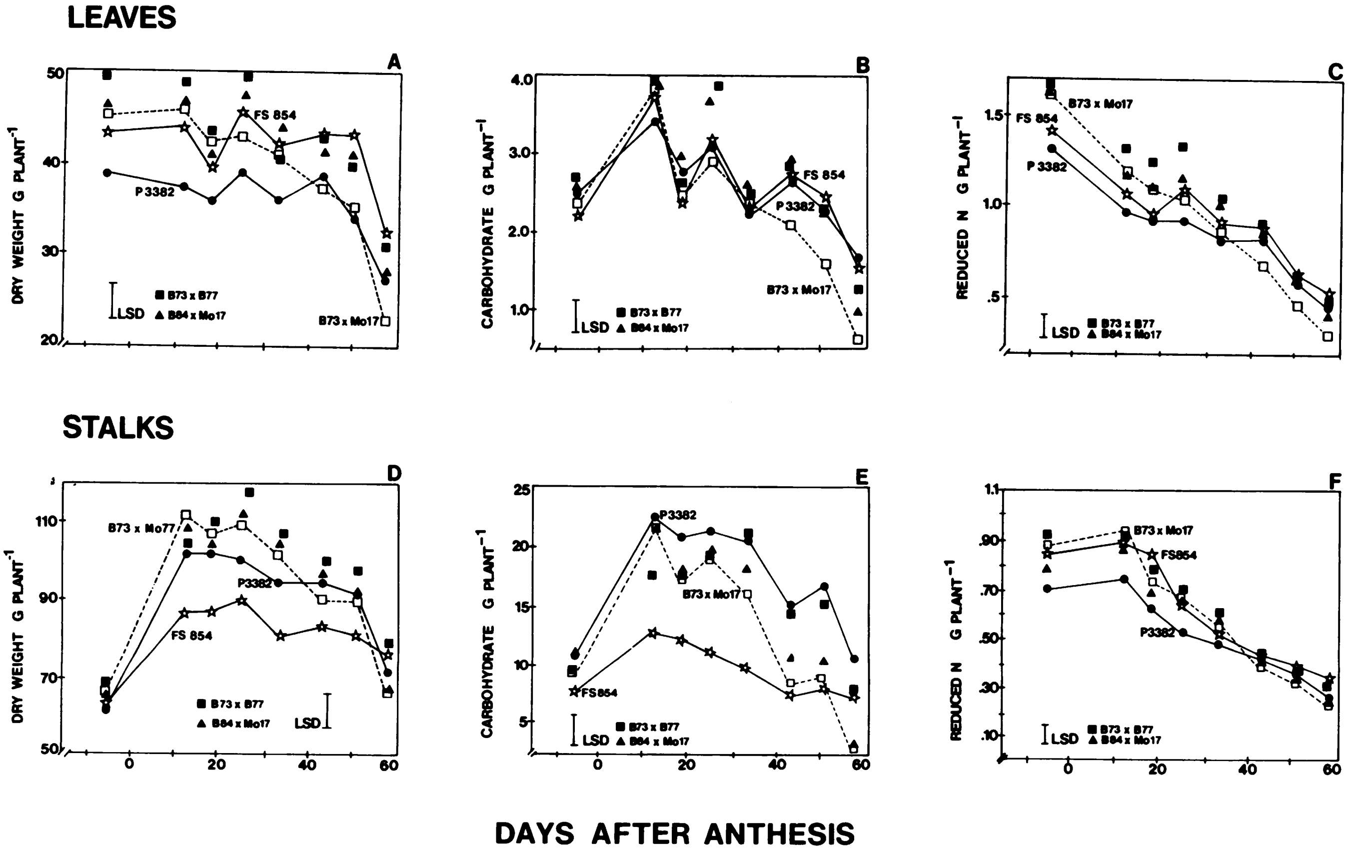

FIG. 2. Changes in dry weight, nonstructural carbohydrate, and reduced N content of leaves and stalks during grain development of five maize hybrids. Other details as given in Figure 1.

content during the grain-filling period, with the exception of B73 × Mo17, the values never decreased below the initial level until the last week of grain development. At grain maturation, the two stay-green hybrids (P3382 and FS854) had higher leaf carbohydrate contents than the three B hybrids.

In contrast to leaf carbohydrate content, there was a marked decrease in leaf reduced N content, between 5 DBA and 12 DAA for all hybrids (Fig. 2, C). With minor exceptions, this loss of N from the leaves continued throughout grain fill. The three B hybrids lost more N (1.6–1.7 g plant^{-1}) and a greater percentage of their initial N (71–75%) than did the two stay-green hybrids (1.3–1.4 and 62–64%, respectively) during the grain-filling period.

Stalks. For all hybrids, stalk dry weight increased markedly between 5 DBA and 12 DAA (Fig. 2, D). Based on the corresponding change in carbohydrate content (Fig. 2, E), much (70–77%) of the increase in weight can be attributed to growth. Stalk dry weight remained relatively constant between 12 and 25 DAA, decreased gradually between 25 and 50 DAA, and declined rapidly thereafter. For four of the hybrids the loss of stalk dry weight between 50 and 57 DAA exceeded (average of 50%) the gain in grain dry weight and also exceeded (average of 64%) the loss of nonstructural carbohydrates and reduced N from the stalk. Some of the dry weight loss could be due to breakdown of structural components by invading organisms. Changes in stalk dry weight of FS854 were uniquely different in two respects: (a) the initial increase in dry weight between 5 DBA and 12 DAA was approximately half that of the other four hybrids, and (b) the decrease in dry weight between 50 and 57 DAA was minimal. Dry weight patterns of the whole plant (Fig. 1, A) show FS854 maintained photosynthetic activity up to 57 DAA.

Each hybrid had a marked increase in stalk nonstructural carbohydrate content between 5 DBA and 12 DAA (Fig. 2, E). Except for B73 × B77, the greatest amount of carbohydrate was accumulated by 12 DAA. Stalks of four of the hybrids maintained large amounts of carbohydrate relative to the initial level, until 34 DAA. Between 34 and 57 DAA, the remobilization of this stored reserve was extensive and the patterns of loss varied among the genotypes, with the two earlier senescing hybrids showing the greatest loss. FS854 differed from the other hybrids in that the initial increase in stalk carbohydrate was smaller, the pattern of loss was more gradual, and there was no rapid depletion between 50 and 57 DAA. From the stalk weights and carbohydrate contents, (Fig. 2, D and E), it is evident that P3382 maintained the highest concentration of stalk carbohydrate throughout grain fill. Although photosynthesis was drastically reduced or terminated by 43 DAA for B73 × B77, B73 × Mo17, B84 × Mo17, and P3382 (Fig. 1, A), their stalks retained 159%, 99%, 98%, and 144% of the initial carbohydrate content, respectively. By this same date, the leaves of the respective hybrids had lost 47%, 57%, 46%, and 36% of their initial reduced N content (Fig. 2, C).

Although P3382 had a lower reduced N content in the stalk during the first half of the grain-filling period, its pattern of change in N content was similar to the other hybrids (Fig. 2, F). For all hybrids, the maintenance or increase in stalk N content between 5 DBA and 12 DAA was followed by a gradual decrease during the remainder of the grain-filling period. These initial plateaus in stalk N contents are attributed to remobilization of leaf N (Fig. 2, C). Although this temporary storage of N in the stalk would indicate the supply of N was in excess of ear needs or transport capabilities for delivery to the ear, the excess was not achieved without cannibalization of leaf N.

Kernels. Over the intervals sampled, kernels of B73 × Mo17 and B84 × Mo17 did not exhibit a linear phase of grain dry weight accumulation (Table I and Fig. 3, A). Between 26 and 34 DAA these two hybrids had maximal filling rates that substantially exceeded the rates of the preceding and following intervals. P3382, B73 × B77, and FS854 had 'near linear' rates of filling of 28, 32, and 32 d duration, respectively (Table I). During the 35 to 43 d sampling interval, all hybrids had lower (15–42%) rates of fill relative to the preceding period. For B73 × Mo17, the slow rate of kernel filling between 44 and 50 DAA is consistent with the concurrent cessation of photosynthesis (Fig. 1, A). The final gain in dry weight by the kernels can be attributed to remobilization of vegetative metabolites for all hybrids except FS854. For FS854, the terminal increase in kernel weight could be due to either current photosynthesis or remobilized reserves.

Genotypic ranking for kernel dry weight at maturity (Fig. 3, A) was similar to the ranking for dry weight ($r = +0.92$) and reduced N content ($r = +0.97$) of the total plant (Fig. 1, A and B). The harvest indices for dry weight were; 0.65, 0.67, 0.65, 0.62, and 0.62 and for reduced N, 0.76, 0.81, 0.77, 0.74, and 0.72 for FS854, B73 × Mo17, B84 × Mo17, B73 × B77, and P3382, respectively.

With respect to grain N content (g N plant $^{-1}$) at the time of grain black layer formation, the ranking of the hybrids was FS854 > the three B hybrids > P3382 (Fig. 3, B). A similar order of ranking was noted for per cent grain crude protein (6.25 conversion factor), 8.6, 8.3, 8.2, 8.2, and 7.1 for FS854, B73 × Mo17, B84 × Mo17, B73 × B77, and P3382, respectively.

There was more variability (*i.e.* less linearity) in the daily rates of gain in kernel reduced N at the various intervals than for dry weight (Table I). Maximum rates of acquisition of N by the kernels occurred between 26 and 34 DAA for all hybrids which is consistent with the high rates of nitrate reduction by the plants between 18 and 34 DAA (Fig. 1, B). Between 35 and 43 DAA each hybrid had a marked decrease (41–59%) in the rate of accumulation of kernel N (Table I, Fig. 3, B). These decreases were greater (% basis) than the decreases in rates of dry matter accumulation during the same interval. Except for FS854, the amount of decrease in kernel N accumulation for each hybrid is consistent with the amount of decrease in nitrate reduction by the plant (Fig. 1, B), indicating a relationship between current nitrate reduction and accumulation of kernel N. However, the capacity of current nitrate reduction appears inadequate to meet the N requirement by the kernels because there was a continual depletion of N from leaves and stalks between 12 and 57 DAA (Fig. 2, C and F). Decreases in the rate of loss of N from the leaves of FS854 and P3382, and stalks of FS854 between 35 and 43 DAA could have contributed to the decreases in accumulation of kernel N of these two hybrids.

In contrast, the current photosynthetic rates, as measured by

Table I. *Daily Rates of Accumulation of Dry Weight and Reduced N by the Kernels at Intervals during the Grain-Filling Period for Five Maize Hybrids*

Hybrid	Dry Wt at Following Days after Anthesis						Reduced N at Following Days after Anthesis					
	12–18	19–25	26–34	35–43	44–50	51–57	12–18	19–25	26–34	35–43	44–50	51–57
			g/d						*mg/d*			
B73 × B77	1.7	5.5	5.3	4.1	4.7	0.4	46.7	54.3	77.5	44.0	78.6	0.0
B73 × Mo17	2.3	5.1	7.4	4.3	0.4	2.8	61.7	50.0	108.8	45.0	15.7	24.2
B84 × Mo17	1.4	4.7	6.5	4.1	2.6	1.9	38.3	58.6	92.5	41.0	22.8	20.0
FS854	1.6	5.5	5.3	4.5	4.5	3.2	48.3	68.5	82.5	49.0	80.0	22.9
P3382	2.1	4.0	5.4	4.4	2.8	1.6	43.3	35.7	71.3	42.0	50.0	0.0

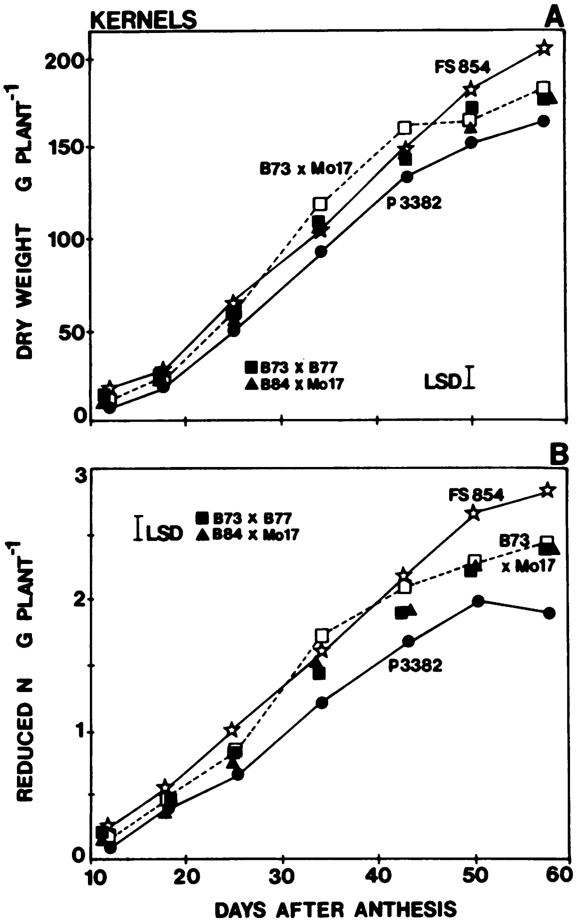

FIG. 3. Accumulative changes in dry weight (A) and reduced N (B) of kernels during development for five maize hybrids. Other details as given in Figure 1.

increases in total plant dry weight, increased for B73 × B77 and P3382 during the 35 to 43 d interval when rates of kernel dry weight accumulation decreased (Fig. 1, A and Table I). During this same interval these hybrids remobilized less than one-third (6–8 g) of the carbohydrate reserves from their stalks (Fig. 2, E). It seems unlikely that it was the unavailability of photosynthate and/or carbohydrate that caused the reduction in rates of kernel dry matter accumulation between 35 and 43 DAA for these two hybrids. For B73 × Mo17 and B84 × Mo17, the decrease in rate of kernel dry matter accumulation between 35 and 43 DAA can be attributed to their decreased photosynthetic activity during the same interval. For FS854, there was little change in rate of photosynthesis (Fig. 1, A) or loss of carbohydrate from the stalks (Fig. 2, E) between 35 and 43 DAA. However, FS854 as well as three other hybrids (the exception being the earlier senescing B73 × Mo17) showed small increases in leaf carbohydrate between 35 and 43 DAA. Could this accumulation of carbohydrates represent a change in rate of transport from the leaves? What factors could trigger such a change? The cause for the decreased accumulation of kernel dry weight between 35 and 43 DAA is not clear.

Relative to the other two B hybrids, B73 × B77 had increased rates of accumulation of both dry weight and N for the 44 to 50 DAA sampling period (Table I). These increases are consistent with the higher rates of nitrate reduction and photosynthesis during this same interval (Fig. 1, A and B).

The ratio values of daily rates of accumulation of dry weight to daily rates of accumulation of N as a function of the sampling interval gave a family of curves for the five hybrids (Fig. 4). A similar sawtoothed plot (not shown) was obtained with data for the ear (kernel plus cob) of B73 × Mo17 grown in 1980 (1). In 1980, the highest ratio value was 90 between 18 and 21 DAA and never exceeded 60 after 26 DAA. Grain yields per plant and grain per cent protein were higher in 1980.

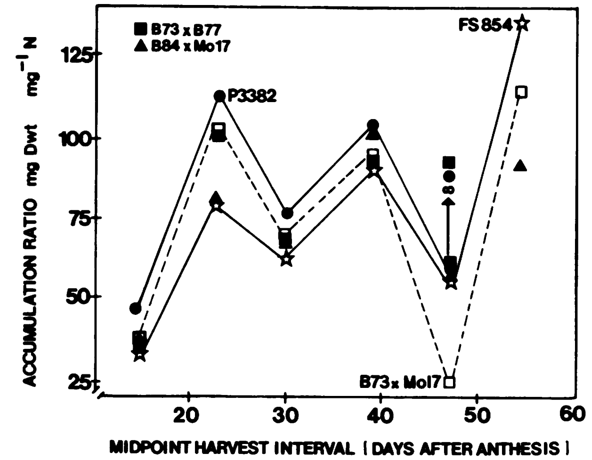

FIG. 4. Changes in the ratio of rates of accumulation of dry weight/reduced N by kernels during grain development for five maize hybrids. Data taken from Table I. ∞ shows that there was no net increase in N of kernels of B73 × B77 and P3382 between 46 and 57 d after anthesis. Other details as given in Figure 1.

Table II. *Estimated Percentages of Dry Weight and Reduced N of the Ear Derived from Current Photosynthesis and Newly Reduced N, Respectively, during the Reproductive Period (5 d before to 57 d after anthesis)*

The current photosynthetic input was calculated by three separate procedures: A, dry weight loss from the vegetation; B, dry weight loss corrected for remobilized N; and C, nonstructural carbohydrate loss from the vegetation. The amount of dry weight loss attributed to remobilization of N was computed by multiplying the value for reduced N lost from the vegetation less the current NO_3^- reduction value (column D) times 8.57 (N to dry wt. conversion factor).

Hybrid	Current Photosynthesis			Current NO_3^- Reduction
	A	B	C	D
			%	
B73 × B77	95	102	98	22
B73 × Mo17	88	96	95	26
B84 × Mo17	90	96	95	28
FS854	101	104	100	51
P3382	99	103	100	30

These plots show that over the grain-filling period, the accumulation of dry weight is independent of the accumulation of N for the five hybrids. The reasons for these variations and why all hybrids gave similar patterns is not clear. Because there is more variability in the rates of accumulation of N than for dry weight, it can be suggested the availability of N (reduction of nitrate and remobilization) appears to be more closely associated with the variability in ratio values.

Grain samples from the yield row were used to determine per cent oil (Dicky John analysis). At maturity the per cent oil was; 5.2, 4.3, 3.8, 3.8, and 3.6 for P3382, B73 × B77, FS854, B73 × Mo17, and B84 × Mo17, respectively. These data are included for possible use in computer modeling.

Sources of Supply. Using data presented in Figures 2 and 3, estimates were made of the percentages of dry weight and reduced N of the grain derived from current photosynthesis and newly reduced NO_3^- during the grain development period (Table II). For all hybrids, these data show the bulk of the ear dry weight was derived from current photosynthesis and that remobilization of metabolites from the vegetation played a minor role. In contrast, more than two-thirds of the ear N was derived from remobilization of vegetative N for four of the hybrids. For FS854, which continued to reduce NO_3^- throughout the grain-filling period (Fig. 1, B), half of the ear N was derived from current nitrate reduction.

The proportions of ear N derived from current nitrate reduction and remobilization of vegetative N for B73 × Mo17 (Table II) are the reverse of the results obtained with this hybrid in 1980 (*i.e.* 72% derived from current NO_3^- reduction). This divergence is attributed to the differences in environmental conditions and cultural practices. In 1980, the plants were subjected to a severe drought just prior to anthesis followed by timely and moderate rainfall over the filling period. In 1981, excessive rainfall (28 cm above average) occurred throughout the reproductive phase. The plant density was 40,700 plants ha^{-1} in 1980 and 59,250 plants ha^{-1} in 1981. These results indicate the extreme flexibility of the maize plant to adjust to environment and cultural practices.

Characteristics Associated with High Yields. The hybrid FS854, that has an established productivity potential (world record yield, nonirrigated), differs in the following physiological traits from the other four hybrids, especially P3382. (a) The accumulation of reduced N by the above ground parts was maintained at relatively high amounts and rates throughout the grain-filling period, thus demonstrating a continued input of newly reduced NO_3^- (Fig. 1, B). (b) The accumulation of dry weight by the above ground plant parts also continued at relatively high rates during the final stages of grain fill, thus demonstrating that photosynthetic activity was maintained (Fig. 1, A). (c) The accumulation of dry weight and reduced N by the kernels was maintained at relatively high rates during the final stages of grain development (Table I, Fig. 3). (d) The stalks, which serve as a storage reservoir, had the lowest concentration of carbohydrates through the first 44 d of grain development and the highest concentration of amino N and reduced N throughout the period relative to the other hybrids (data not shown).

Based on data presented and other observations, FS854 can be classified as a high N-low carbohydrate, P3382 as a low N-high carbohydrate, and the B hybrids as intermediate types.

For FS854, we suggest it is the continued input of N into the plant that is responsible for the maintenance of leaf duration and continued photosynthetic activity. This view is also supported by the relationship between accumulation of N and dry weights for the other hybrids (Fig. 1). The availability of current photosynthate and reduced N ensures the longer duration of grain fill. The end result was a higher yield per plant.

FS854 has two deficiencies that have kept it from being widely used by farmers. First, the record yield has been obtained by specialized cultural procedures as practiced by Herman Warsaw, Saybrook, IL. Second, this hybrid is highly susceptible to lodging (*i.e.* it has poor stalk quality). The effect of plant lodging on yield was shown in the current experiment. The yields per plant (Fig. 3, A) are the mean values of 45 standing plants harvested as described previously. The mean yields, expressed as q ha^{-1}, obtained from harvesting the entire center row of plants, were 83, 96, 86, 91, and 105 for B73 × B77, B73 × Mo17, B84 × Mo17, FS854, and P3382, respectively. Lodging scores (percentage of plants lodged) at the time of grain black layer formation were 12, 9, 8, 36, and 1 for B73 × B77, B73 × Mo17, B84 × Mo17, FS854, and P3382, respectively. A forthcoming paper will describe the relationship between the ratio of the concentration of reduced N and carbohydrates in the stalk and susceptibility to lodging.

This work raises the following questions. Are high nitrogen and high carbohydrate traits mutually exclusive, at least to a certain extent? What is the best approach to use to develop a high N-high C type plant that will incorporate the high production potential and good plant standability into the same genotype?

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