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Differential Senescence of Maize Hybrids following Ear Removal[1]

I. WHOLE PLANT

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ABSTRACT

Visual senescence symptoms and associated changes in constituent contents of three field-grown maize (*Zea mays* L.) hybrids (Pioneer brand 3382, B73 × Mo17, and Farm Service brand 854) were compared in response to ear removal. Whole plants were harvested at eight intervals during the grain-filling period, and analyzed for dry matter, total N and nitrate N, phosphorus, sugars, and starch.

Upper leaves of earless P3382 and B73 × Mo17 showed reddish discoloration by 25 days after anthesis (DAA) and all leaves had lost most of their chlorophyll by 40 DAA. In striking contrast, leaves of earless FS854 plants remained green and similar in appearance to eared controls throughout the grain-filling period.

For all hybrids, ear removal led to a decrease in dry weight, reduced N, total N, and phosphorus contents of the total plant, and an increase in carbohydrate content of the leaves and stalks, relative to respective controls. Although changes in carbohydrate and N contents, which previously had been associated with senescence, were observed for all earless hybrids, these changes were followed by accelerated senescence and early death only for P3382 and B73 × Mo17. By 30 DAA, earless P3382 and B73 × Mo17 plants ceased to accumulate dry weight, total N, and phosphorus, indicating a termination of major metabolic activities. In contrast, earless FS854 plants retained a portion of these metabolic activities until 58 DAA, indicating a role for roots in determining rate of senescence development. Thus, the course of senescence was more accurately reflected by measurements of metabolic activities than by measurements of metabolite contents at any given time. These results show that the ear *per se* does not dictate the rate or completion of the senescence process, and implicated an association between the continued accumulation of N and associated root activities with the delayed senescence pattern of the earless FS854 plants. It is evident that studies involving control of senescence among species must also consider genotypic influences within species.

Senescence, the natural deteriorative processes that terminate the functional life of an organism, is important to crop productivity in that leaf area and grain fill duration have been related to yield (9). Thomas and Stoddart (22), in an excellent reivew of the process of leaf senescence, concluded that although correlative factors (competition for space, light, nutrients, and growth regulators) and environmental factors (light, temperature, etc.) are clearly associated with senescence, the actual process of leaf senescence is genetically controlled and programmed. However, genetic control is subject to modification through external influences. Thus, although the symptoms associated with senescence of organs or organisms have been extensively studied, the factor(s) that initiate the senescence process remain elusive.

The delay in development of senescence often associated with the elimination of the reproductive phase (14, 22) provided support for the view that depletion of the nutrients from the vegetation during fruit or ear development was the cause of senescence. However, in other species (*Hordeum*, *Capsicum*), ear or fruit removal hastens rather than delays the development of senescence (11, 13). This divergence in response to ear or fruit removal and other lines of evidence (17, 22) have been interpreted to indicate that competition for nutrients is only a symptom and not the cause of senescence.

Moss (15) reported that barren (natural or induced by bagging or removal of the ear) maize plants developed purple stalks and leaf margins, had higher (60 to 112%) concentration of sugar in the stalks, and senesced later than eared plants. Ear bagging resulted in a rapid initial decrease (up to 65% of control) in photosynthetic activity; however, the leaves of the treated plants, relative to controls, retained a higher level of photosynthetic activity during later stages of grain fill. Similarly, Allison and Weinmann (1) found that bagging or removal of ears from maize resulted in development of red pigmentation, and accumulation of higher concentrations of carbohydrates in the leaf, relative to eared plants; however, the onset of senescence was more rapid. Because the accumulation of photosynthate in the leaf may impair leaf functions, Allison and Weinmann (1) implied that the accumulation of carbohydrates in the leaves was related to the rapid development of senescence. Subsequently, Christensen *et al.* (4) and Thiagarajah *et al.* (20) using different maize cultivars, reconfirmed that bagging or removal of ears accelerated rather than delayed senescence. Using the maize hybrid, B73 × Mo17, Christensen *et al.* (4) confirmed that ear removal resulted in a marked decrease in photosynthetic activity (measured by dry weight accumulation of all above-ground parts). They also found that ear removal resulted in an equally drastic decrease in nitrate uptake and reduction, as measured by accumulation of reduced N. The decreases in reduced N and nitrate N contents, and nitrate reductase activity of the leaves, were consistent with the view that there was less nitrate fluxing into the leaves of the earless than the eared plants. When changes in reduced N and Chl contents of leaves were used as markers, the leaf senescence patterns of earless plants showed similar times of onset, but faster

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rates of development, relative to eared controls. A subsequent study (19) which compared three maize hybrids (P3382, B73 × Mo17, and FS854) showed that FS854 continued to accumulate reduced N and dry matter during the grain-filling period, and exhibited delayed senescence, relative to the other two hybrids.

The objectives of this study were to extend the observations of Christensen *et al.* (4) and Swank *et al.* (19) and to compare and contrast the changes in various physiological parameters of maize hybrids that exhibited either enhanced or no change in the rate of development of the visual symptoms of senescence in response to ear removal.

MATERIALS AND METHODS

Cultural Procedures. Kernels of three maize (*Zea mays* L.) hybrids (Pioneer brand 3382, B73 × Mo17, and Farm Service brand 854) were overplanted on April 27, 1982, and thinned to a final stand of 64,578 plants ha^{-1}. Based on visual evaluations, both P3382 and FS854 are classed as 'stay-green' cultivars because leaves remain green until grain maturity. Soil type was a Flannigan silt loam with high levels of P and K, and 150 kg N ha^{-1} was spring applied. Treatments were arranged in a 2 × 3 factorial in a randomized complete block design with five replications. Factor A treatments were plants with and without ears, and factor B treatments were the three hybrids. Each experimental unit consisted of a four-row plot (9 m long, and spaced 76 cm apart; containing 45 plants/row). For ear removal treatments, all ears (including secondary ear shoots) on all plants of the center two rows were shootbagged to prevent pollination. Unpollinated ears were removed as soon as they could be easily excised from stalks.

Sampling. Whole plants were harvested from the center two rows, eight times during the grain-filling period; 8, 15, 23, 30, 37, 44, 50, and 58 DAA.[2] Anthesis occurred at approximately July 12. Physiological maturity (formation of grain black layer) was at approximately 60 DAA for all hybrids. At each sampling date, three representative plants were harvested from each experimental unit. Plants were harvested between 1400 and 1600 h.

Plants were separated into leaves, stalks (including sheaths), and ears when present. Husks and tassels were discarded. Ears were dried to constant weight at 80°C in a forced draft oven. Leaves and stalks (stover) were weighed and passed through a silage chopper, and subsamples (100 g stalks, 50 g leaves) were dried at 80°C in a forced draft oven. After 60 h, dried tissue was weighed, ground in a Wiley mill (20 mesh), and analyzed for total N, nitrate, phosphorus, and total nonstructural carbohydrates.

Analysis. *Total N and Nitrate N.* Total N and nitrate N were determined as described previously (19). Reduced N was determined by subtracting nitrate N from total N.

Total Phosphorus. Two-ml aliquots from reduced N digests were mixed with 1.0 ml of 2.0 N acetic acid and 5.0 ml of 1.0 N NaOH for subsequent phosphorus determinations by the Fiske-SubbaRow method (10).

Carbohydrates. Total extractable nonstructural carbohydrates (starch plus sugars) and total extractable sugars (hydrolyzed sucrose plus reducing sugars) were determined as described (6). Starch was calculated as total nonstructural carbohydrates minus total extractable sugars × 0.9 (1).

Statistical Analysis. Analyses of variance procedures were used. There were significant differences ($P \leq 0.05$) among sampling dates and treatments for all parameters measured, and the respective error terms for sampling dates and treatments were homogeneous as indicated by Bartlett's test. Therefore, pooled error mean squares from the analysis were used to calculate the LSDs ($P \leq 0.05$) shown on the figures (applicable between treatments within time and within treatments across time).

RESULTS

Total Plant. Striking visual differences in senescence patterns were evident among the hybrids. By 25 DAA, the leaves at the top of the canopy of P3382 and B73 × Mo17 earless plants began to turn red (midribs first) followed by yellowing of the laminae as described previously (1, 4, 20). By 40 DAA, all leaves of earless P3382 and B73 × Mo17 plants were brown (essentially devoid of Chl) while most of the leaves of eared P3382 and B73 × Mo17 plants remained green. By 58 DAA, all leaves of eared plants of B73 × Mo17 were brown, or greenish yellow depending on leaf position, while only two or three of the lower leaves of eared plants of P3382 were brown or greenish yellow. One difference in ear removal induced senescence and normal senescence of hybrids P3382 and B73 × Mo17 was that the sequence of visual leaf senescence was from the top down for the earless plants and from the bottom up for the eared plants. In contrast, differences in visual symptoms of senescence were not evident between eared and earless FS854 plants until 45 DAA. By 58 DAA, most of the midribs of the top leaves of earless FS854 plants were red while only two or three of the lower leaves of eared and earless FS854 plants were brown or greenish yellow. The red pigmentation, indicative of carbohydrate accumulation in the midrib of earless FS854 plants, was not a prelude to enhanced leaf yellowing and death as for P3382 and B73 × Mo17. Subsequently, the rate of visual senescence was indistinguishable and most leaves of eared and earless FS854 plants were dead by 2 weeks after grain black layer formation, as was also true for eared P3382 plants. The visual senescence patterns of eared plants of P3382 and FS854 were essentially indistinguishable. Details of changes in constituents (including Chl and moisture) of a selected leaf of eared and earless plants of the three hybrids are given in a companion paper (7).

Ear removal resulted in less total plant dry matter accumulation (net photosynthesis), but more stover (all above ground vegetative material, principally leaves and stalk) dry matter accumulation, than in respective controls of all hybrids (Fig. 1, A–C). Earless P3382 and B73 × Mo17 plants reached maximum dry weight by 30 DAA and lost more than 50 g dry weight $plant^{-1}$ from 30 to 58 DAA. In contrast, earless FS854 plants continued to slowly accumulate dry matter (9 g $plant^{-1}$) from 30 to 58 DAA.

The relative rate of late season (50 to 58 DAA) accumulation of dry matter of the three hybrids (with ears) was consistent with the late season photosynthetic activity of the third leaf above the ear. In a separate 1982 experiment, CO_2 exchange rates for eared plants of P3382, B73 × Mo17, and FS854 at 52 and 64 DAA were, respectively, 21, 16, and 32% and 5, 7, and 36% of the rates at anthesis (unpublished).

For the eared plants, hybrid FS854 continued to accumulate total plant dry matter throughout the grain-filling period, while P3382 and B73 × Mo17 plants reached maximum stover + ear dry weight by 50 DAA (Fig. 1, A–C), as previously reported (19). Because dry matter accumulation following anthesis was confined primarily to the grain, as indicated by minimal changes in stover dry weight, calculations showed that >90% of grain dry weight was derived from current photosynthesis for all hybrids.

For all hybrids, the profiles of reduced N accumulation were similar to those observed for dry weight (Fig. 1, D–E and A–C). Earless P3382 and B73 × Mo17 plants reached maximum reduced N content by 30 DAA and lost reduced N slowly (0.3 and 0.4 g $plant^{-1}$, respectively) between 30 and 58 DAA. In contrast, earless FS854 plants continued to accumulate reduced N (0.3 g $plant^{-1}$) between 30 and 58 DAA.

For the eared plants, FS854 continued to accumulate reduced

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[2] Abbreviation: DAA, days after anthesis.

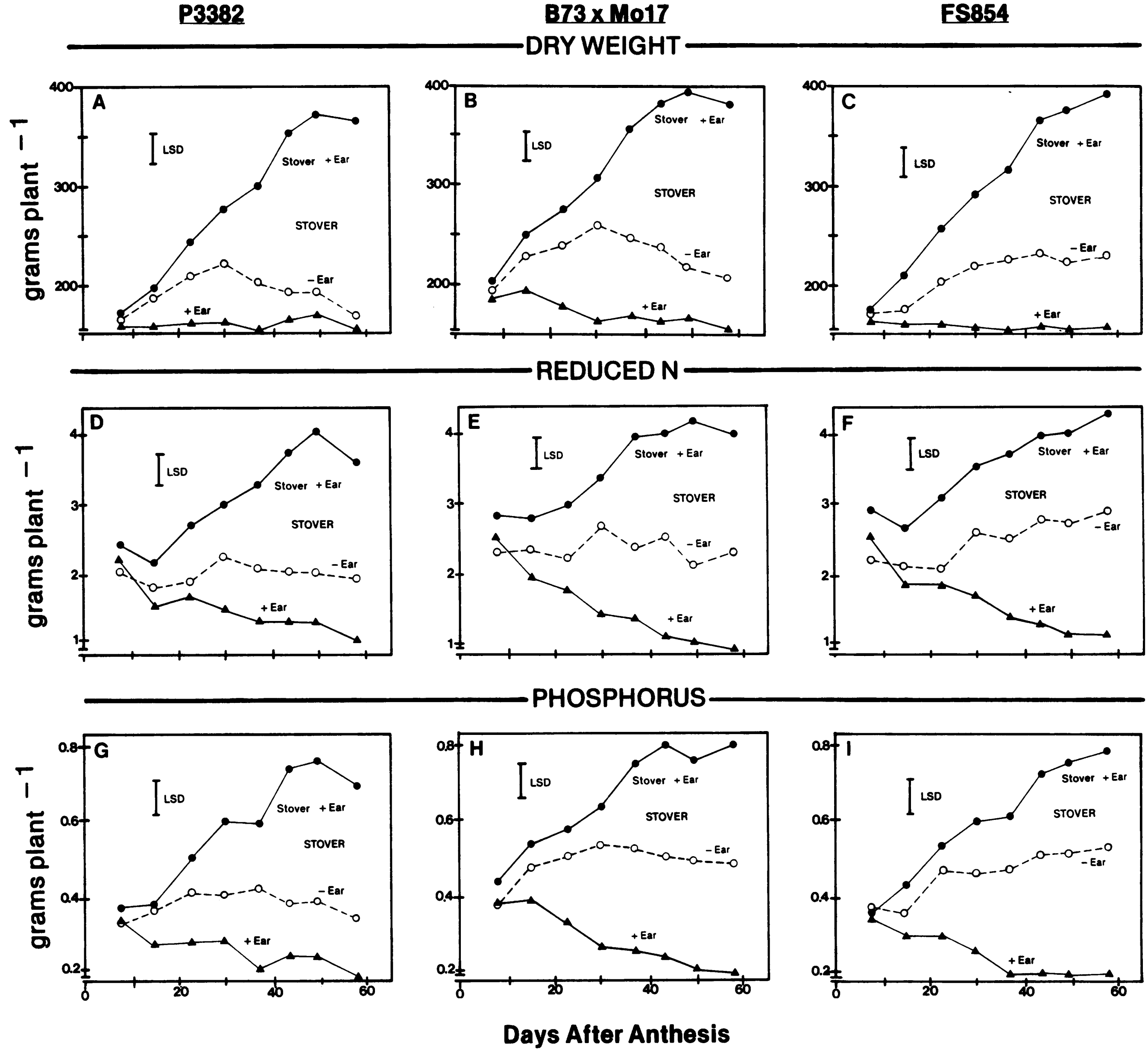

FIG. 1. Effect of ear removal on dry weight and constituent content of whole plants (above ground portion) of three maize hybrids. Treatments involved bagging and excising the primary ear shoot and any secondary ear shoots (−ear) compared with controls (+ear) which were intact plants including all above-ground parts except husk and tassle. The curves designated stover + ear represent data for stover + grain of the control treatment. Curves under the subheading STOVER represent data for the stover fraction only of earless (−ear) and control (+ear) treatments. The LSDs shown are applicable between treatments within time, and within treatments across time. Grain yield at maturity was 185, 208, and 199 g plant^{-1} for P3382, B73 × Mo17, and FS854, respectively.

N throughout the grain-filling period while P3382 and B73 × Mo17 plants reached maximum content of reduced N in the stover + ear by 50 DAA, confirming a previous study with these hybrids (19). Relative to dry weight, the stover of all eared hybrids lost a greater proportion of their reduced N content between 8 and 50 DAA. Estimates made from changes in stover and grain reduced N contents between 8 and 58 DAA, showed that 57, 62, and 54% of the grain N for hybrids P3382, B73 × Mo17, and FS854, respectively, were remobilized from the stover. These results indicated that current nitrate assimilation played a major role in providing N for the grain.

For all hybrids, the profiles of phosphorus accumulation were similar to those observed for dry weight and reduced N (Fig. 1, A–F and G–I). Earless P3382 and B73 × Mo17 plants reached maximum phosphorus content by 38 and 30 DAA, respectively, and lost phosphorus slowly (77 and 43 mg phosphorus plant^{-1}, respectively) thereafter. In contrast, earless FS854 plants continued to accumulate phosphorus (64 mg plant^{-1}) between 30 and 58 DAA.

For the eared plants, FS854 continued to accumulate phosphorus throughout the grain-filling period while P3382 and B73 × Mo17 reached maximum content of phosphorus in the stover + ear by about 44 DAA. Estimates made from changes in stover and grain phosphorus contents between 8 and 58 DAA showed that approximately 30% of the grain phosphorus was remobilized from the stover of all hybrids.

Profiles of phosphorus accumulation by the whole plant (with or without ears) were used as an approximation of intensity and duration of root uptake and/or translocation capabilities. In this vein, the continued accumulation of phosphorus (and also NO_3^- as judged by total N and reduced N) by FS854, implied that some root uptake capabilities were retained until grain maturity. Root uptake capabilities apparently decreased or ceased some 10 to 14 (eared plants) and 22 to 30 d (earless plants) before the time of grain maturity for P3382 and B73 × Mo17, respectively.

Leaves. Dry weight and all constituent contents, except starch, of leaves of all eared hybrids declined during the grain-filling period (Fig. 2, A–O). For all parameters measured, the hybrid by treatment interactions were significant ($P \leq 0.01$) due to the differing response to removal of ear from FS854 than from B73 × Mo17 and P3382 plants (statistical analysis not shown).

Ear removal resulted in initial increases in leaf dry weights, relative to eared plants of all hybrids (Fig. 2, A–C). The intersection of the leaf dry weight curves of eared and earless P3382 and B73 × Mo17 plants between 37 and 44 DAA was indicative of accelerated senescence of leaves of the earless P3382 and B73 × Mo17 plants. In contrast, leaf dry weight of earless FS854 plants remained greater than leaf dry weight of eared controls throughout. However, the overall patterns of leaf dry weight change over time were similar for eared and earless plants.

For all hybrids, the initial (8 DAA) effect of ear removal was to decrease leaf reduced N content (Fig. 2, D–F). Because the leaf is a major site for nitrate reduction, the decreases in reduced N in the leaf, as well as the whole plant (Figs. 1 and 2, D–F), indicated that nitrate assimilation was adversely affected soon after ear removal. The initial rate of reduced N loss from the leaves was not sustained; between 8 and 58 DAA the average rate of loss of reduced N from eared and earless P3382 and B73 × Mo17 plants was similar while the average rate of loss was greater for eared than for earless FS854 plants. Significant amounts of reduced N (0.81, 1.09, and 0.93 g N $plant^{-1}$) were remobilized from the leaves of eared P3382, B73 × Mo17, and FS854 hybrids, accounting for 36, 40, and 35% of the grain N, respectively.

In contrast to the initial decrease in leaf reduced N content of all hybrids, there was no immediate (8 DAA) effect of ear removal on phosphorus content of the leaves (Fig. 2, G–I). However, between 8 and 23 DAA, the phosphorus content of leaves of all earless hybrids, especially FS854, increased relative to respective eared controls. Presumably, this increase resulted from continued uptake from the root medium (also see Fig. 1, G–I) and lack of phosphorus demand for ear development. Regardless of treatment, all leaves of all hybrids lost phosphorus between 23 and 58 DAA, although the patterns of loss differed (Fig. 2, G–I). The phosphorus curves of the earless P3382 and B73 × Mo17 plants intersected the curves of the eared plants between 23 and 30 DAA, showing an accelerated loss of phosphorus from the leaves of the earless plants. In contrast, the phosphorus content of the leaves of the earless FS854 plant was greater than for the eared plants between 8 and 58 DAA.

Ear removal resulted in small initial increases in sugar content of the leave of all hybrids by 8 DAA and marked increases by 15 DAA (Fig. 2, J–L). Between 15 and 37 DAA, the sugar content of the leaves had increased to a maximum level (FS854) or were maintained at high levels (P3382 and B73 × Mo17). Between 37 and 50 DAA, the sugar content of leaves of earless P3382 and B73 × Mo17 plants decreased to the level of respective eared controls while the earless FS854 plants maintained a higher content of sugar than did its control. The patterns of sugar contents of the leaves of all eared hybrids were similar (Fig. 2, J–L).

Ear removal resulted in increased starch content of the leaves of all hybrids; however, the patterns were different for each hybrid (Fig. 2, M–O). In leaves of P3382, starch accumulated rapidly between 15 and 30 DAA and decreased just as rapidly between 30 and 58 DAA to a level similar to that of eared control. The reasons for the uniquely high accumulation of starch in the leaves of the earless P3382 plant and for the divergence in patterns among the hybrids is not clear. In leaves of B73 × Mo17 starch accumulated slowly between 15 and 37 DAA and decreased rapidly between 37 and 44 DAA to levels found in the eared controls. For FS854, starch content of the leaves was generally higher in the earless than eared plant, between 30 and 58 DAA. Relative to the other hybrids, the maintenance of higher levels of sugar and starch in the leaves of eared and earless FS854 plants prior to grain maturity was consistent with the maintenance of higher photosynthetic activity, as observed with eared FS854 plants in other experiments (unpublished). The general trends indicated that starch content of the leaves of all hybrids increased slowly throughout grain fill, and constituted about 15% of the total nonstructural carbohydrates.

The leaves of earless FS854 plants maintained greater leaf weight and retained more of their constituents during the last half of the grain-filling period than did the other hybrids. These results implied that, during this time period, the slower senescence of the leaves of the earless FS854 plants was associated with retention of metabolic activities, as documented later (7).

Stalks. Dry weights and constituent contents of the stalks of eared and earless hybrids diverged during the grain-filling period (Fig. 3, A–O). The marked increase in dry weight and all constituent contents of the stalks of all earless hybrids, relative to respective controls, showed that the stalk served as a substitute for the ear sink. Except for starch, there were significant hybrid-treatment interactions for all stalk parameters, due to the contrasting effects of ear removal on FS854 *versus* P3382 and B73 × Mo17 plants (statistical analysis not shown).

Stalk dry weight profiles (Fig. 3, A–C) of eared plants were similar to the leaf profiles (Fig. 2, A–C), in that stalk weights of P3382 and FS854 remained relatively constant while stalks of B73 × Mo17 lost weight (26 g $plant^{-1}$ between 8 and 58 DAA). For earless plants, stalk dry weight increased 53, 67, and 47 g $plant^{-1}$ from 8 to 30 DAA for P3382, B73 × Mo17, and FS854, respectively. Stalks were alternate sinks in the absence of the ears. For P3382 and B73 × Mo17, the stalks of earless plants ceased to gain dry weight by 30 DAA, indicating diminishing metabolic activities and the advanced senescence of these plants. Increased respiration resulting from ear removal (21) and/or invasion of the stalk by microorganisms (8) are possible reasons for the loss of stalk weight. For FS854, the earless stalk continued to gain dry weight (24 g $plant^{-1}$) between 30 and 58 DAA, of which 62% could be accounted for by remobilization from the leaves with the rest, presumably due to current photosynthesis.

Reduced N was depleted from the stalks of all eared hybrids during grain fill, but not to the extent of depletion from the leaves (Figs. 2 and 3, D–F). Ear removal led to increased stalk reduced N in all earless hybrids, relative to respective controls, between 8 and 30 DAA. During this period, remobilization of leaf reduced N could account for 64, 52, and 2% of the increase in stalk reduced N of the earless P3382, B73 × Mo17, and FS854 plants, respectively. Stalks of earless P3382 and B73 × Mo17 plants ceased to accumulate reduced N by 30 DAA. In contrast, stalks of earless FS854 plants continued to accumulate reduced N throughout the sampling period and between 30 and 58 DAA gained 0.9 g $plant^{-1}$ of reduced N, 64% of which could be accounted for by loss from leaves.

For all hybrids, the eared and earless plants exhibited divergent patterns of phosphorus content of stalks (Fig. 3, G–I). All eared hybrids lost phosphorus from their stalks between 8 and 58 DAA, while similar to the earless whole plants (Fig. 1, G–I), the phosphorus content of the stalks of earless plants increased until 37 and 30 DAA for the P3382 and B73 × Mo17 plants, respectively, and until 58 DAA for the FS854 plants. The increased

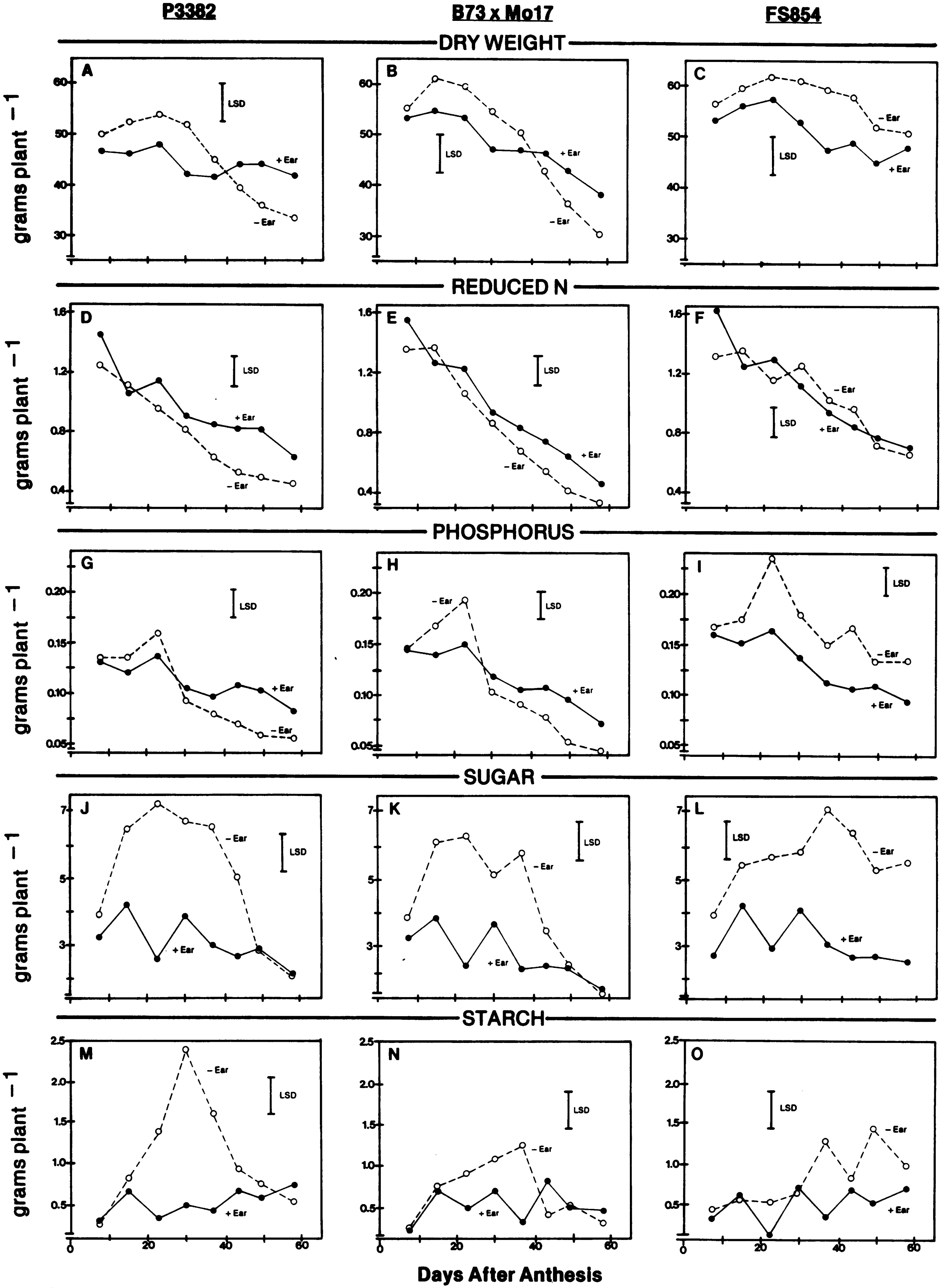

FIG. 2. Effect of ear removal on dry matter and constituent content of leaves of three maize hybrids. The leaf fraction consisted of lamina and midribs (including fallen leaves where retrievable). Treatments involved ear removal (−ear) and intact control plants (+ear). Statistical analysis was as indicated in Figure 1 legend.

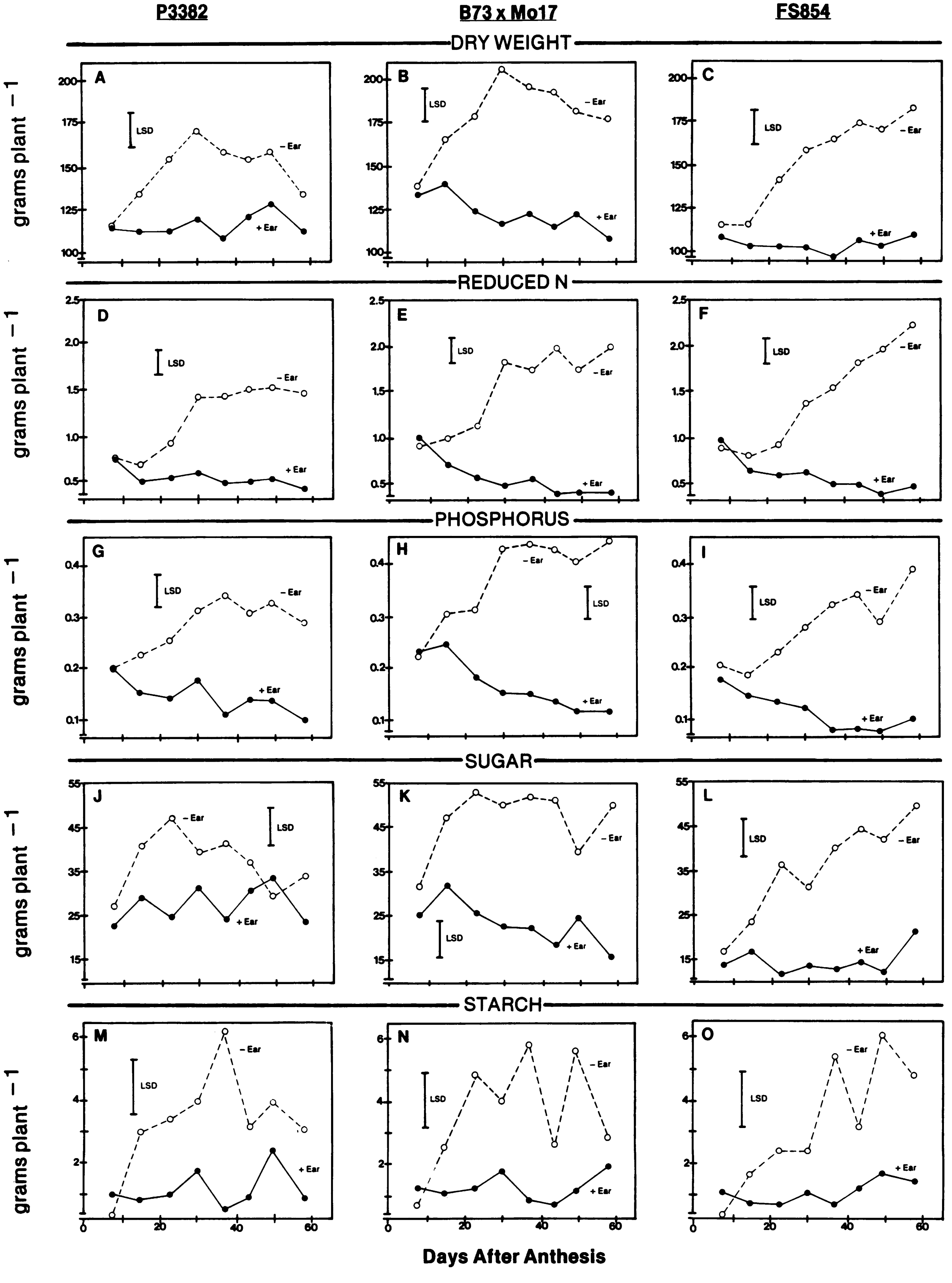

FIG. 3. Effect of ear removal on dry matter and constituent content of stalks of three maize hybrids. The stalk fraction includes leaf sheaths. Treatments and other conditions were as indicated in Figure 2 legend.

phosphorus content of the stalks of all earless plants between 8 and 23 DAA was due to phosphate uptake, as phosphorus content of the leaves increased concurrently (Fig. 2, G–I). However, between 23 and 37 DAA (P3382), 23 and 30 DAA (B73 × Mo17), and 23 and 58 DAA (FS854), the increased phosphorus content of the stalks was derived via phosphate uptake and remobilization of phosphorus from the leaves for earless plants (Figs. 1, 2, and 3, G–I).

Based upon the loss of phosphorus from the leaves and stalks of the eared plants between 8 and 58 DAA, more phosphorus was remobilized to the grain from the stalks than from the leaves (22, 19, and 15% and 10, 13, and 11% of the grain phosphorus was supplied by the stalks and leaves for P3382, B73 × Mo17, and FS854 plants, respectively).

Ear removal resulted in rapid increases in sugar content of the stalk for all hybrids between 8 and 23 DAA. However, between 23 and 58 DAA, the pattern of sugar content of the stalks differed for the three hybrids as follows: decreased for P3382, remained constant for B73 × Mo17, and increased for FS854 plants. The sugar content of the stalks of eared plants remained relatively constant for P3382 and FS854, and decreased gradually for B73 × Mo17, between 8 and 58 DAA.

Ear removal resulted in increased (4- to 5-fold higher than eared controls) starch accumulation in the stalks for all hybrids (Fig. 3, M–O). The patterns of starch accumulation by the earless plants differed for the three hybrids, as follows: for P3382, increased to a maximum at 37 DAA and then decreased; for B73 × Mo17, increased rapidly until 23 DAA and maintained a high but variable level thereafter; and for FS854, increased slowly until 30 DAA and erratically, but more rapidly, between 30 and 58 DAA.

For the eared hybrids, there were no consistent trends or changes in the starch content of the stalk and the patterns were similar for all hybrids.

Total nonstructural carbohydrates (starch plus sugar) of the stalks, increased by 23, 26, and 22 g plant^{-1} (Fig. 3, J–O) and accounted for 60, 63, and 82% of the concurrent increase in dry weights of the stalks between 8 and 23 DAA for P3382, B73 × Mo17, and FS854, respectively. The sugar fraction (predominantly sucrose) constituted the bulk of the nonstructural carbohydrates of the stalks of all hybrids.

Percentage Change in Whole Plant Constituents. The interpretations of the data of Table I were based on the concept that accumulation of dry weight, the three N fractions, and phosphorus, approximates net photosynthesis, nitrate uptake and assimilation, and phosphate uptake, respectively. It was assumed that nitrate was the principal form of N available to the plants. Nitrate constituted only a small (6 to 15%) portion of the total N (per plant basis) throughout the experimental period and regardless of treatment.

By 8 DAA, ear removal resulted in a slight decrease in net photosynthesis as judged by per cent dry weight of earless relative to the eared plant (Table I). Such decreases might be expected from removal of the bulk of the meristematic cells and the magnitude of the decrease reflects the size of the ear at this stage and the rate of photosynthetic and respiratory activities in the earless plant (15, 20, 21). With decreased meristematic activity, all earless plants of all hybrids accumulated carbohydrates (Table I). As judged by reduced N and total N values, nitrate uptake and assimilation were depressed for all earless plants, especially FS854. Phosphate uptake of all hybrids was also decreased by ear removal. By 30 DAA, the adverse effects of ear removal on net photosynthesis (dry weight) and nitrate uptake and assimilation (total N) are of similar magnitude and the response of all hybrids was roughly similar. By 58 DAA, the values of all parameters (Table I) indicated that the FS854 plant had maintained a higher level of metabolic activities relative to control (eared) plant than had P3382 and B73 × Mo17. Data of Figure 1 also support this statement. These data (Table I, Fig. 1) provide a base for the following speculative discussion of factors that affect senescence of the whole plant.

DISCUSSION

Removal of ears led to an accelerated development of visual symptoms of senescence for P3382 and B73 × Mo17, but not FS854 plants. The accumulation of carbohydrates by leaves (1, 3) and the loss of N from the leaves and the cessation of nitrate uptake (4) have been suggested as causal factors or factors that are closely associated with senescence of plants. In the present study, the data obtained by 8 DAA showed that ear removal led to accumulation of carbohydrates, decreased nitrate uptake and assimilation, and decreased phosphate uptake for all hybrids. These changes preceded the visual symptoms of senescence. However, there was no direct evidence that these metabolic changes were the cause of senescence or that the changes in carbohydrate contents or nitrate uptake and assimilation are causally related. It seems reasonable that plants having high levels of carbohydrates in the shoots would partition more carbohydrates to the roots, thus sustaining root activities (uptake). This assumes that roots of earless plants at this stage of development are capable of utilizing more photosynthate. Higher levels of sugars in the plant should enhance nitrate reduction. Our data indicate neither nitrate uptake nor reduction was enhanced over time by the accumulation of carbohydrates by the earless, relative to the eared plants.

If carbohydrate accumulation and decreased uptake and metabolism of N are symptoms of senescence, then data of Table I show that senescence was initiated (8 DAA) and developed (30 DAA) at roughly similar rates for all hybrids. However, neither the accumulation of carbohydrates nor the decreased N contents are in full accord with the visual symptoms of senescence by 30 DAA. The loss by earless P3382 and B73 × Mo17 plants and partial retention by earless FS854 plants of metabolic activities (accumulation of dry weight, reduced N, and phosphorus; Fig. 1, Table I) showed that the rate of senescence by the three hybrids was altered before or by 30 DAA. Although senescence patterns and time of plant death varied among the three hybrids in response to ear removal, the ear *per se* does not dictate the rate or completion of senescence, as judged by visual and metabolic symptoms.

The greater relative decrease in reduced N than dry weight of stover, observed in this and other studies with maize (2, 12, 19), indicated that ear development required extensive remobilization of vegetative N. These observations and the senescence pattern of FS854 are not consistent with the effects of sink removal on induction of senescence of nonleguminous species proposed by Thomas and Stoddart (22). They suggest that removal of sinks that have a high demand for current photosynthate and a relatively low requirement for minerals causes carbohydrates to accumulate in the leaves, decreases photosynthesis, and induces senescence.

Although we have no observations or measurements of growth regulator levels in our plants, it is conceivable that removal of such a metabolically active organ as the ear would cause changes in growth regulator levels or balance. From the review by Thomas and Stoddart (22), one can deduce that changes that occur in the leaf at the completion of expansion predispose the leaf for subsequent senescence. Although growth regulators have been implicated, there is no convincing evidence that they are the senescence signal (22). Regardless of the initial senescence signal, and possible secondary signals, it was evident from the hybrids evaluated in this study that the final course of senescence was under genetic control.

The continued accumulation of total N and phosphorus by

Table I. *The Effect of Ear Removal on the Dry Weight and Constituent Contents of the Whole Plant (Above Ground Portion) for Three Maize Hybrids at Three Intervals during the Grain-Filling Period*

For each parameter, the effect was expressed as the percentage of the earless relative to the respective eared (including grain) plant.

Hybrid	Days after Anthesis	Dry Weight	Nonstructural Carbohydrate		Nitrogen Fraction			Phosphorus
			Sugars	Total	Reduced	NO_3^-	Total	
				%				
P3382	8	97	111	103	83	126	86	90
B73 × Mo17		96	117	109	79	90	80	85
FS854		97	110	105	75	64	74	94
P3382	30	79	100	50	75	206	80	56
B73 × Mo17		85	150	54	70	137	83	73
FS854		76	123	42	78	64	73	68
P3382	58	46	100	27	54	133	58	49
B73 × Mo17		54	182	35	58	142	60	59
FS854		59	160	41	68	68	68	67

earless FS854 plants implied that the roots were viable enough to retain some anion uptake capability by 58 DAA. The role of NH_4NO_3 in regreening of tobacco leaves in advanced stages of senescence (16) and the rate of loss of reduced N from the leaves of eared or earless maize plants argues for a role of N in regulating the course of senescence. Other workers (5, 14, 18) have found that cytokinins synthesized in newly formed roots were translocated to the shoot to effectively delay senescence. It is not known whether the roots of FS854 were capable of synthesizing and/or translocating cytokinins between 30 and 58 DAA.

Our data indicate that measurements which reflect metabolic activities more accurately reflect the course of senescence than the measurement of metabolite level. It is our opinion that accumulation of carbohydrates and the depletion of N from the leaves are symptoms rather than the cause of senescence. Senescence of the whole plant is a complex process involving regulatory and metabolic interactions among the various tissues and organs. Until knowledge is obtained about the factors that regulate the metabolic systems, our understanding of the senescence process will remain restricted. It is evident that studies involving control of senescence among species must also consider genotypic influence within species.

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