EFFECTS OF ASSIMILATE ENHANCEMENT ON GRAIN FILLING AND CARBOHYDRATE AND NITROGEN PARTITIONING IN MAIZE

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To Manuela

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ABSTRACT

Source-sink relationship is a controversial topic. Some workers assert that grain yield in corn is limited by availability of assimilate during the grain filling period. Others have reported the sink size as the limiting factor. In this research, I studied the effects of assimilate availability on kernel growth rate and final weight by investigating the effects of altered source/sink ratios on soluble sugars, starch and nitrogen content in plant parts of maize. Special attention was given to plant's compensatory response such as soluble carbohydrates and nitrogen redistribution to the grain.

Two genotypes: M14 x W64A and Pioneer-brand '3780,' were grown in field plots at St. Paul, MN in 1982. The treatments were arranged in a split plot manner in a randomized complete block design of four replicates. The alterations of source/sink ratio consisted of partial kernel removal (removing the tip half of the ear), and thinning by a 50% plant population reduction imposed before and after the onset of linear growth (6 days and 24 days after mid-silking, respectively).

M14 x W64A responded to early thinning, as indicated by an extended grain filling period, increased starch content of the kernels and greater final kernel weight. However, kernel growth rate, number of kernels per ear and kernel soluble sugars content were not affected. Thinning and partial kernel removal on both dates increased internode dry weight and soluble sugar content. Kernel removal early enhanced the nitrogen content in the internodes and kernels.

For most of the parameters analyzed Pioneer-brand 3780 was not affected by the treatments. However, treatments did increase nitrogen

content in the internodes and kernels and soluble sugars content of internodes.

Partial kernel removal and thinning treatments were imposed in this study on the premise that they would increase the availability of assimilates for kernel growth. Data reported, which showed increased soluble sugar and nitrogen content of the internode as well as increased nitrogen content of the grain, clearly demonstrated that the treatments were effective. However, the results suggested that the excess assimilate supply that originated from these treatments resulted in a significant increase in dry weight of the grains only in M14 x W64A and when treatments were imposed during the early stages of kernel development. This may imply that in the other genotype and later treatments, endosperm-sink capacity had already reached its maximum. Number and size of endosperm cells and starch granules are factors that mediate kernel size. Sucrose unloading at the pedicel tissue is also a factor to be considered in the utilization of enhanced assimilates, since the efficiency of the enzyme invertase may dictate whether or not the assimilates will be converted to dry matter and starch.

INTRODUCTION AND LITERATURE REVIEW

Final grain yield in maize (Zea mays L.) depends on the availability of assimilates to the grain during the grain filling period and on the capacity of the grain to utilize assimilates. The rate and duration of kernel growth are also relevant and are often positively correlated with corn grain yield (8, 18). Source-sink relationships are directly responsible for the establishment of rate and duration of kernel growth. There is a controversy regarding the source and sink as limiting factors in productivity of maize. Some authors (34) assert that the assimilate supply to the grain is the limiting factor for grain yield. Conversely, others (10, 15, 16, 18) suggest the sink size as the limiting factor provided that sink size is defined as number of kernels per plant times the capacity of these kernels to accommodate assimilates.

Source-sink relationships have most often been studied in wheat and barley. Currently, there is very little information on the effects that enhanced assimilate availability may have on kernel development, nitrogen and carbohydrate partitioning in corn.

Enhanced assimilate availability in corn can be achieved by plant population reduction. The reduced competition among plants results in greater light interception per unit leaf, which results in an increased supply of photoassimilates. Leaf area per plant is one of the major factors which determines source strength. Reduction of ear size also enhances the relative supply of assimilate (23). Because the number of kernels per ear is decreased, the amount of photosynthate potentially available for each individual kernel that remains is increased resulting therefore in a reduction in the competition among kernels for available assimilates. According to TOLLENAAR (30) and GOLDSWORTHY et al., (16), both source and sink limitations occur in maize. They asserted that the combination of genotype and environment determines which limitation predominates.

Corn is one of the least tolerant crops to high plant densities. Grain yield can be positively correlated with crop growth rate only at the optimum population density. Beyond this point, grain yield is negatively correlated with population density, because the percentage of barren stalks increases (38). SCHOPER et al. (26) found that increasing assimilate supply by thinning two and one half weeks before silking can result in an increase in grain yield without an improvement in sink strength or partitioning efficiency. FREY (14), also attempting to increase assimilate supply per plant, thinned corn to fifty percent stand density at mid-silking. He reported an increase in the rate of plant dry matter accumulation. However, the results for kernel growth were not conclusive. Some workers have shown that grain weight/ear can be increased by thinning treatments at 30 and 50 days after emergence and 10 and 20 days after mid-silking (4). On the other hand PONELEIT and EGLI (25) reported that plant density has no effect on the rate of kernel growth, but effective filling period duration was influenced to a limited extent.

WILSON and ALLISON (37), working in a similar fashion, found the greatest increment of dry weight per plant and grain dry weight at harvest for the low populations, followed by medium and high populations, respectively. The considerable decrease in dry weight of the non grain shoot parts reported for the high population implies that dry matter which normally goes to the shoot was diverted to the grain.

These studies for the most part have not presented any results for carbohydrate and nitrogen content from different parts of corn plants. It is important when one is dealing with assimilate enhancement studies to look at the concentration and partitioning of assimilates because they can decisively influence not only the final yield but also the quality of the grain in maize plants. Analysis of carbohydrates and nitrogen in the nodes and in the kernels shows a relationship between translocation and mobilization of these assimilates during the growing season. Furthermore, the concentration of soluble carbohydrates in the stem may furnish information about the relative source limitation in a plant (10). Corn plants normally contain a sizeable reserve of photosynthate in the stalk (9, 30, 33). Mobilization of stalk carbohydrates toward the ear has been observed in studies of assimilate enhancement (7, 13) and assimilate reduction (2, 23, 33). There is evidence that considerable mobilization of photosynthate occurs during the main ear fill period (1, 7, 23). It was further reported that this occurs when the carbohydrate requirements of the grain exceed plant photosynthate production (31). Soluble carbohydrates temporarily stored in the stem, cob, shank and husks serve as a source of grain growth when plant photosynthesis declines at the end of the growing season (30, 33). The stem also serves as an active sink whose relative capacity to attract assimilate declines during the latter part of the grain filling period (30).

JONES and SIMMONS (23) found that in corn enhanced assimilate supply treatment did not significantly effect kernel growth rate, final kernel weight, duration of the effective grain filling period or soluble carbohydrate concentration. However, soluble carbohydrates and nitrogen concentration in the internode above the ear was higher than in control plants. Nitrogen content of the grain was also increased. Similarly, TOLLENAAR and DAYNARD (32), using a method in which the husks were excised at silking time and kernels were removed from the same set of ears at several subsequent sampling dates, reported no increase in dry matter accumulation in the remaining kernels. In contrast, JENNER (21) and SIMMONS et al. (29) reported that kernels of wheat, when assimilate supply was enhanced by removing spikelets, were capable of higher kernel growth rates and greater final weight. These studies may suggest that greater potential for increased kernel weight via increased assimilate supply may exist for wheat than in corn.

ALLISON and WATSON (2) showed that when the grain sink is removed by preventing pollination in corn, the dry matter that would have passed to the grain accumulates in the stover. ALLISON and WEINMANN (3) further showed that prevention of pollination caused premature senescence of the leaves above the ear and the concentration of sugars and starch increased markedly in both upper and lower leaves, the increase being greater in the upper leaves.

There is little information about the effect of assimilate supply on kernel growth when altered after the onset of linear kernel dry matter accumulation. Some research has been conducted in which a reduction in assimilate supply was obtained by partial leaf removal (12, 17, 23), and shading (11). Results indicated that there is little effect on kernel growth rate when the treatments are imposed after the final number of kernels per ear has been established but that there is a decrease in kernel weight at maturity due to shorter duration of filling. Studies on the effects of enhancement of assimilate availability to developing kernels at any time during grain development are inconclusive. Additional studies are necessary to identify the potential for enhanced kernel growth rate and final weight. A further point to be explored is how plants compensate in response to assimilate enhancement related to carbohydrate or nitrogen remobilization from vegetative plant parts.

The objective of this study was to identify the effects of assimilate enhancement on kernel growth rate and final weight and on the mobilization of carbohydrate and nitrogen compound in plant parts of maize. Since potential kernel weight is defined as that kernel weight obtained when assimilate supply is unlimiting, I also sought to determine genotypic difference in the expression of this component of grain yield.

MATERIALS AND METHODS

Two genotypes, M14 x W64A and Pioneer-brand '3780' were grown in field plots at St. Paul, MN in 1982. The plots were over planted by hand and later thinned to a uniform density of 50,000 pl/ha. The treatments were arranged in a split plot manner in a randomized complete block design of four replicates, with hybrids as the main plots and assimilate enhancement treatments as sub-plots. Each subplot consisted of four rows 76 cm apart and 9.1 m long. The soil type was a Waukegan silt loam (Typic Hapludoll) and was fertilized according to soil test recommendations for an expected grain yield goal of 10,000 kg ha^{-1}. The mid-silking data were recorded, and plants that were in the same stage of development were tagged.

Treatments were restricted to the center two rows of each plot, and were designed to increase the amount of assimilate available for kernel growth. The treatments were as follows:

1 - Control (nontreated check),

2 - Kernel removal early (KRE), tip one-half of the ear removed, 6 days after mid-silking,

3 - Kernel removal late (KRL), tip one-half of the ear removed, 24 days after mid-silking,

4 - Thinning early (TE), fifty percent stand reduction, 6 days after mid-silking,

5 - Thinning late (TL), fifty percent stand reduction, 24 days after mid-silking.

The kernel removal treatments were imposed by pulling back the husk to expose the tip half of the ear and the apical portion was removed by cutting with a scalpel. Petroleum jelly was applied to the surface to impede growth of fungus and the husks were repositioned over the portion of the ear that remained.

Six days after mid-silking and at four day intervals thereafter, until maturity, 75 kernels were removed from middle portion of two ears per plot by sampling in a radial fashion. Twenty-five kernels were used for dry weight determination by oven drying at 85°C for 48 hours immediately after removal from the ear. The remaining 50 kernels were used to measure soluble sugars and starch content as determined by the technique described by JONES et al. (22) and nitrogen determined by KJELDAHL analysis.

At four day intervals the internode subtending the ear from two plants in each treatment was sampled for dry weight, soluble sugars analysis, and N determination by the procedures mentioned previously (22).

Estimates of kernel growth rates were made from linear regression coefficients calculated over the period from 27 to 54 days after mid-silking. The duration of the effective filling period was calculated as final kernel weight at maturity divided by kernel growth rate.

Other datum collected at harvest was kernels per row. Data were subjected to analysis of variance and means separated by Duncan's multiple range test.

RESULTS AND DISCUSSION

INTERNODE DRY MATTER ACCUMULATION

The profiles for internode dry weight, including stem and leaf sheath, of M14 x W64A and Pioneer 3780 are in Figures 1 and 2, respectively. Both genotypes showed a similar trend between control and treated plants. An initial increase occurred in internode dry weight which decreased slightly by maturity. The magnitude of the response depended upon the time of treatment. Thinning and kernel removal before the onset of linear growth consistently increased internode dry weight of M14 x W64A after 27 days post mid-silking (Fig. 1), whereas the response of Pioneer 3780 was of a smaller magnitude and more variable (Fig. 2). These data suggests that M14 x W64A may be influenced more by assimilate enhancement treatments than Pioneer 3780. The increased internode dry weight of the plants in which half the ear was removed may be due to the increase of assimilates in the internodes which did not translocate to the grains. In other words, when the grain "sink" was partially removed the dry matter that would have moved to the grain accumulated in the stalk (2, 5).

In the treatments involving thinning, the increase of the internode dry weight can also be explained by the accumulation of assimilates which were not translocated to the grain. However, in the present case the increase of assimilates may be attributed to the fact that thinned plants photosynthesized more efficiently due to greater light interception per unit of leaf area. At kernel maturity, sucrose availability of the plant decreases (6). This may be due to decreased photosynthetic capacity since the plant is senescing at this time. Accordingly, remobilization of assimilates occurs from internodes to the grain compensating for the reduced photosynthesis.

INTERNODE CARBOHYDRATE AND NITROGEN CONTENTS

The profiles of internode soluble sugar content for both genotypes (Figs. 3 and 4) were quite similar. In all cases the concentration of soluble sugars in the internode decreased during the linear fill period, but increased subsequently as kernel approached maturity. Treated plants contained a significantly greater percentage of soluble sugars than did the control. In M14 x W64A, no consistent evidence of enhanced sugar content by a particular treatment could be identified. However, at maturity sugar content of the internode was greater for assimilate enhancement treatments imposed 24 days after mid-silking. Pioneer 3780 presented an overall lower soluble sugar content which was also more variable throughout the sampling dates (Fig. 4). KRL treatment for this genotype resulted in the greatest percentage of soluble sugars by the end of the season (Fig. 4). The soluble sugar content present in the internodes indicates the presence of potential translocatable assimilates that could be mobilized to the ear. The apparent decline and subsequent increase in the internode soluble sugar content as kernels approached maturity displayed by most treatments in both hybrids may suggest a resumption of storage of sugar in the internode after demand for carbohydrates by the kernels has been met.

The nitrogen content of internodes of M14 x W64A (Fig. 5) and Pioneer 3780 (Fig. 6) was quite different from that observed for carbohydrate content (Figs. 3 and 4). In the beginning of the grain filling period both genotypes had a low nitrogen content in the internodes. After 45 days after mid-silking thinning and partial ear removal at 6 days post mid-silking caused an abrupt and significant increase in the internode nitrogen content. The increase was greater for M14 x W64A than for Pioneer 3780. Early kernel removal displayed a greater percentage of nitrogen than early thinning whereas the late treatments and control plants remained low throughout the grain filling period (Figs. 5 and 6). JONES and SIMMONS (23) found similar results when they enhanced assimilates by kernel removal at 12 and 24 days after mid-silking. At maturity the grains reach their maximum dry weight. Therefore, translocation to the grain ceases. Additionally, at the end of the filling period leaves senesce and compounds which are mobilized may accumulate in the stalk. This phenomenon may have occurred in all treatments including the control. However, only KRE and TE presented increased nitrogen within the internodes at maturity. As far as KRE is concerned, the increase of nitrogen in the stalk was probably due to the reduction of the "sink" strength by decreasing the number of kernels on the ear. Note that even KRL, especially for the cultivar Pioneer 3780 (Fig. 6), presented a similar trend to KRE, but in this case since the treatments were imposed later (24 days after mid-silking) much of the nitrogen absorbed probably had already been translocated to the grains before they were cut off, therefore resulting in a lower nitrogen content in the internodes. For the TE treatment the greater accumulation of nitrogen can be explained by the greater photosynthetic efficiency. This possibly resulted in a greater availability of sugars which facilitated the assimilation of nitrogen (35). α-ketoglutarate is derived from sucrose (photosynthesis) and it is an important compound in the assimilation of nitrogen. Therefore, more photosynthesis results in more sucrose which increases availability of α-ketoglutarate and accordingly facilitates assimilation of nitrogen that is accumulated in part in the internodes (35).

KERNEL DEVELOPMENT AND DRY MATTER ACCUMULATION

The pattern of kernel development for M14 x W64A and Pioneer 3780 are shown in Figures 7 and 8, respectively. The response differed slightly between the two hybrids. Notwithstanding an increase in assimilate supply, kernel development relative to the control for most of the filling period was not affected by the treatments. The KRE treatment imposed on M14 x W64A obtained the greatest dry weight per kernel. The initial increase in kernel dry weight occurred about 9 days after the early treatments were imposed. This implies a rather rapid response to assimilate supply (Fig. 7). This response probably contributed to the greater final weight displayed by KRE at maturity (Table 3). However, JONES and SIMMONS (23) using the same genotype, but imposing KRE 6 days later, reported that kernel dry weight was not enhanced at any point during grain filling. They concluded that substantial increases in carbohydrate availability did not occur early enough to be a consequence to kernel development.

The pattern of kernel development for Pioneer 3780 (Fig. 8) showed no differences between treatments in the first 25 days after mid-silking. After this period, KRL revealed a slight tendency for greater kernel dry weight, but this increase was not always statistically significant and occurred only after half of the filling period had passed. Such a late enhancement was not sufficient to cause differences in the rate of dry matter accumulation (Table 1). This result is consistent with a similar study (23) where the late enhancement did not cause differences in final kernel weight and growth rate relative to the control.

Kernel removal and thinning at both 6 and 24 days after mid-silking did not significantly affect the kernel growth rate (KGR) in either genotype (Table 1). This is similar to that which was reported by JONES and SIMMONS (23).

Thinning at six days after mid-silking significantly prolonged the duration of the effective-filling period for M14 x W64A whereas the other treatments did not affect this parameter (Table 2). This result is in agreement with the work done by PONELEIT and EGLI (25). There were no statistical differences at the 5% level, between treatments in the duration of the effective filling period for the cultivar Pioneer 3780 (Table 2).

The number of kernels per ear for both hybrids was not affected by the treatments (Table 3). SCHOPER et al. (26) also imposed assimilate enhancement by thinning and found no differences in number of kernels per row. However, they reported an increase in the number of kernels per ear.

The final kernel weight for the genotype M14 x W64A was substantially increased by KRE and KRL (Table 3) whereas Pioneer 3780 was unaffected. The increase in kernel weight of M14 x W64A supports the initial hypothesis that decreasing the number of kernels per ear should decrease competition for assimilates. SIMMONS et al. (29) and JENNER (21) made similar findings in wheat when they enhanced assimilates by decreasing the number of kernels per spike at anthesis. In contrast JONES and SIMMONS (23) did not observe a significant effect of kernel removal on final kernel weight in their two year study using the genotype M14 x W64A. This lead them to surmise that final kernel weight was already approaching the upper limits of its genetic potential in this hybrid. Differences between the results obtained for M14 x W64A in the current study and those reported by JONES and SIMMONS (23) may suggest that the expression of genetic potential for final kernel weight can be mediated by the environment.

Assimilate enhancement by fifty percent thinning did not result in a significantly greater final kernel weight for both hybrids (Table 3). This effect is partially supported by other researchers (14, 37). WILLEY and HOLLIDAY (36) showed that thinning at anthesis in wheat did not increase grain yield per ear because the limited ear capacity at that time was already determined. In addition they asserted that thinning before anthesis did increase grain yield. In corn increases in yield by thinning have been obtained by augmenting the number of kernels per ear rather than the final weight of the kernels (14, 26).

KERNEL CARBOHYDRATE AND NITROGEN PARTITIONING

Table 4 shows the percentage of soluble sugars present in the kernels for both genotypes at maturity. Except for the KRE treatment in Pioneer 3780 which showed an unexpected lower percentage of soluble sugar, no differences were detected in the amount of soluble sugars in the kernels for M14 x W64A or Pioneer 3780. This finding is consistent with the results reported by JONES and SIMMONS (23) and is probably due to limited capacity of the sink to accommodate assimilates or approachment of its genetic potential. JENNER and RATHJEN (19, 20) working with wheat also found similar results, where the provision of greater amounts of sucrose than normal did not induce increase in the level of sucrose in the grain or enhance deposition of starch. They asserted that the level of sucrose in the grain is not limited by the production of assimilates.

In the present study sugar analysis measured only total soluble sugar. A better way to assess the effect of treatments that result in assimilate enhancement would be to examine invertase activity and the compartmentalization of specific carbohydrates within the kernel after imposing treatments.

The starch content in the kernels at maturity (Table 5) was significantly affected by thinning early in M14 x W64A only. All other treatments imposed on the two genotypes showed no significant differences in kernel starch content. Despite the increase in kernel starch content at maturity for M14 x W64A, thinning early did not result in a greater weight per kernel as mentioned previously. This suggests that kernel weight is not exclusively associated with storage of starch but with other factors as well, such as: kernel size and protein storage.

There are many physiological processes which can limit the accumulation of dry matter in the grain. For instance, a limitation in the invertase activity could be a critical point resulting in no increase of kernel dry weight or starch content, even with enhancement of assimilates. SHANNON (27) showed that sucrose is split by acid invertase to glucose and fructose before it enters the endosperm of maize kernels. Even with a greater availability of sucrose, there may not be an increase in kernel dry weight if sucrose is not utilized with greater efficiency via increased invertase activity. A study of the invertase activity associated with assimilate enhancement treatments might reveal the origin of the limitation to the process of dry matter accumulation. In other words, if increasing the supply of assimilates does not result in an increase in the invertase activity, then this enzyme may be limiting the process of starch synthesis or at least limiting the maximum utilization of available sugars. Conversely, if a greater activity of the invertase associated with assimilate enhancement treatments does not lead to an increase in dry matter, it can be concluded that other physiological process may be influencing the potential of the kernel to accumulate assimilates. Such influence may be attributed to enzymes involved in the synthesis of starch or physical limitations like kernel size.

The kernel nitrogen content for both hybrids (Figs. 9 and 10) showed a similar pattern, however Pioneer 3780 had overall greater nitrogen content in the grain. Initially, nitrogen was higher in all treatments, but decreased rapidly between 15 and 25 days after mid-silking, and did not change appreciably thereafter. From 20 days after mid-silking until the end of season KRE resulted in the greatest percentage of nitrogen. In contrast, the kernel N content of control plants was always lower. It seems that early treatments resulted in a greater content of nitrogen than did late treatments. The above was more evident for Pioneer 3780 than M14 x W64A (Figs. 9 and 10).

SUMMARY AND CONCLUSIONS

M14 x W64A and Pioneer 3780 responded differently to assimilate enhancement treatments. M14 x W64A was affected by thinning early which increased the grain filling period and starch content of the kernels. Thinning and kernel removal on both dates increased internode dry weight and internode soluble sugar content. Kernel removal early enhanced the nitrogen content in the internodes and kernels. This hybrid also responded positively to kernel removal before and after the onset of linear growth by increasing final kernel weight.

Pioneer 3780 was not affected by the treatments for most of the parameters analyzed. However, the enhanced treatments did affect nitrogen content in the internodes and kernels and soluble sugar content within internodes.

Partial ear removal and thinning treatments were imposed in this study on the premise that they would increase the availability of assimilates for kernel growth. Data reported showing increased soluble sugar and nitrogen content of the internode as well as increased dry weight clearly demonstrates that the treatments were effective. However, the results suggest that the excess of assimilates originated from treatments did not always lead to a significative increasing in dry weight of the grain. This probably occurred due to the fact that grains had already reached their maximum potential to accumulate dry weight. These data suggest that assimilate supply is not a major limitation to grain yield in maize. Therefore, limitation to increase kernel mass appears to be controlled by intrinsic factors of the seed itself. Factors such as number and volume of cells in the endosperm could be limiting the size of the kernels, therefore impeding the utilization of further amounts of assimilates (24). Another factor that can limit the utilization of enhanced assimilates could be sucrose unloading in the pedicel (28), where the efficiency of invertase activity is fundamental for the conversion of assimilates to dry matter and starch. Answers to these and related questions await further investigations.

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LIST OF TABLES

Table 1. Effect of assimilate enhancement on kernel growth rate for two hybrids of maize.

	Kernel Growth Rate[†]	
Treatment	M14 x W64A	Pioneer 3780
	--- mg $kernel^{-1}$ day^{-1} --	
Control	5.65	5.97
Kernel Removal Early	5.66	5.85
Kernel Removal Late	5.43	6.14
Thinning Early	5.09	5.55
Thinning Late	5.33	5.50

[†] No significant differences between means.

Table 2. Effect of assimilate enhancement on effective grain filling period of two hybrids of maize.

	Effective Filling Period	
Treatment	M14 x W64A	Pioneer 3780
	------------ Days ------------	
Control	46.64	50.54
Kernel Removal Early	50.21	49.88
Kernel Removal Late	51.37	50.41
Thinning Early	53.18*	53.45
Thinning Late	51.18	56.25

*Significantly different from control at $P \leq 0.05$.

Table 3. Effect of assimilate enhancement on number of kernels per row (K/R)[†] and final weight (mg)[††] per kernel for two hybrids of maize.

Treatment	M14 x W64A		Pioneer 3780	
	K/R	KDWt (mg)	K/R	KDWt (mg)
Control	42.25	263.10	43.75	299.25
Kernel Removal Early	-	283.22*	-	295.80
Kernel Removal Late	-	279.04*	-	313.76
Thinning Early	45.50	268.69	44.50	288.61
Thinning Late	41.00	271.68	44.75	296.56

*Significantly different from control at $P \leq 0.05$.

[†] Values are the mean of four replications.

[††] Values are the mean of three sampling dates taken after physiological maturity.

Table 4. Effect of assimilate enhancement on kernel soluble sugar content at maturity** for two hybrids of maize.

	Soluble Sugar	
Treatment	M14 x W64A	Pioneer 3780
	%	%
Control	5.41	7.06
Kernel Removal Early	5.64	5.53*
Kernel Removal Late	5.95	6.59
Thinning Early	5.69	6.99
Thinning Late	5.25	7.21

*Significantly different from the control at $P \leq 0.05$.

**Values are the mean of four sampling dates taken after physiological maturity.

Table 5. Effect of assimilate enhancement on kernel starch content at maturity** for two hybrids of maize.

	Starch	
Treatment	M14 x W64A	Pioneer 3780
	%	%
Control	75.14	76.78
Kernel Removal Early	74.04	73.77
Kernel Removal Late	72.89	72.25
Thinning Early	77.72*	76.50
Thinning Late	76.05	75.19

*Significantly different from the control at $P \leq 0.05$.

**Values are the mean of four sampling dates taken after physiological maturity.

LIST OF FIGURES

Figure 1. Effect of kernel removal and thinning on internode dry weight during grain filling period. (M14 x W64A.) Arrows indicate times of treatment application.

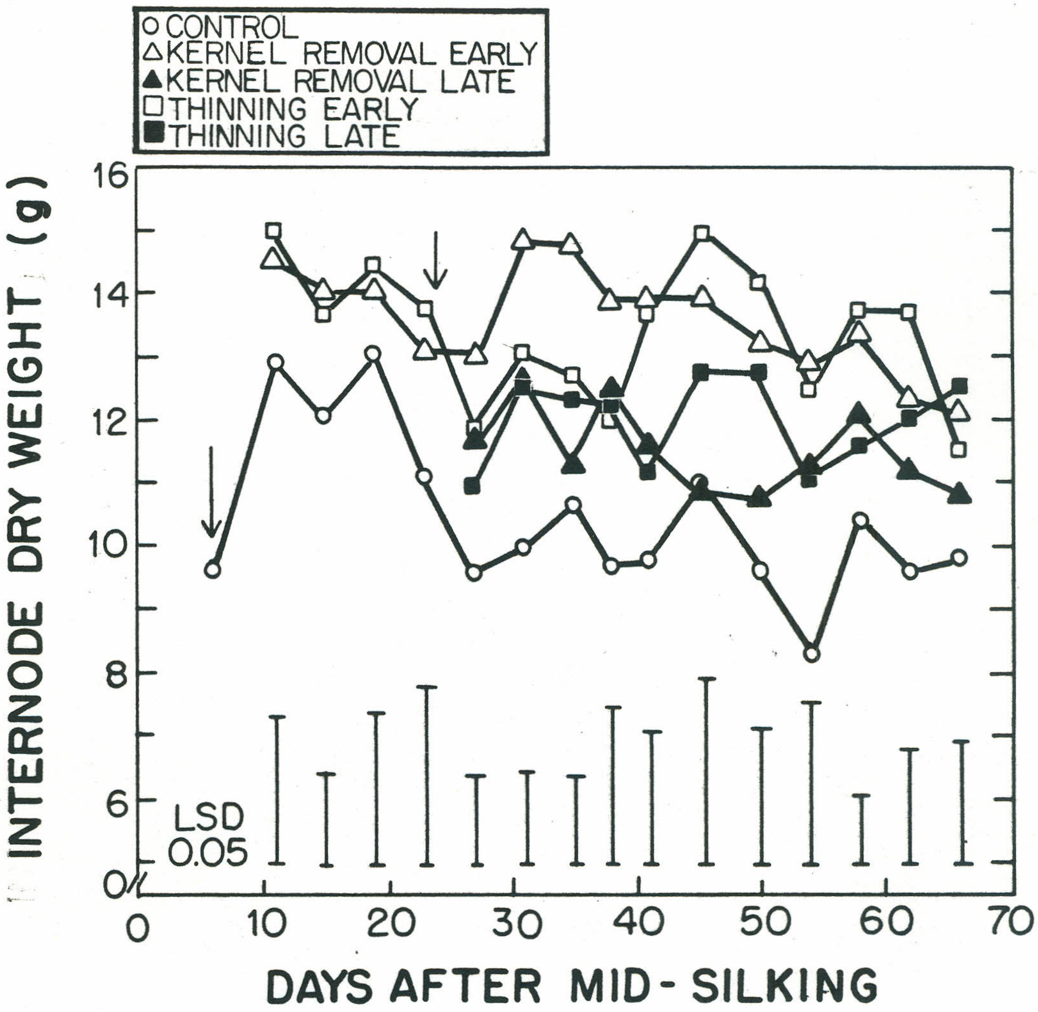

○ CONTROL
△ KERNEL REMOVAL EARLY
▲ KERNEL REMOVAL LATE
□ THINNING EARLY
■ THINNING LATE
INTERNODE DRY WEIGHT (g)
16
14
12
10
8
6
0
LSD
0.05
0
10
20
30
40
50
60
70
DAYS AFTER MID-SILKING

Figure 2. Effect of kernel removal and thinning on internode dry weight during grain filling period. (Cultivar Pioneer 3780.) Arrows indicate times of treatment application.

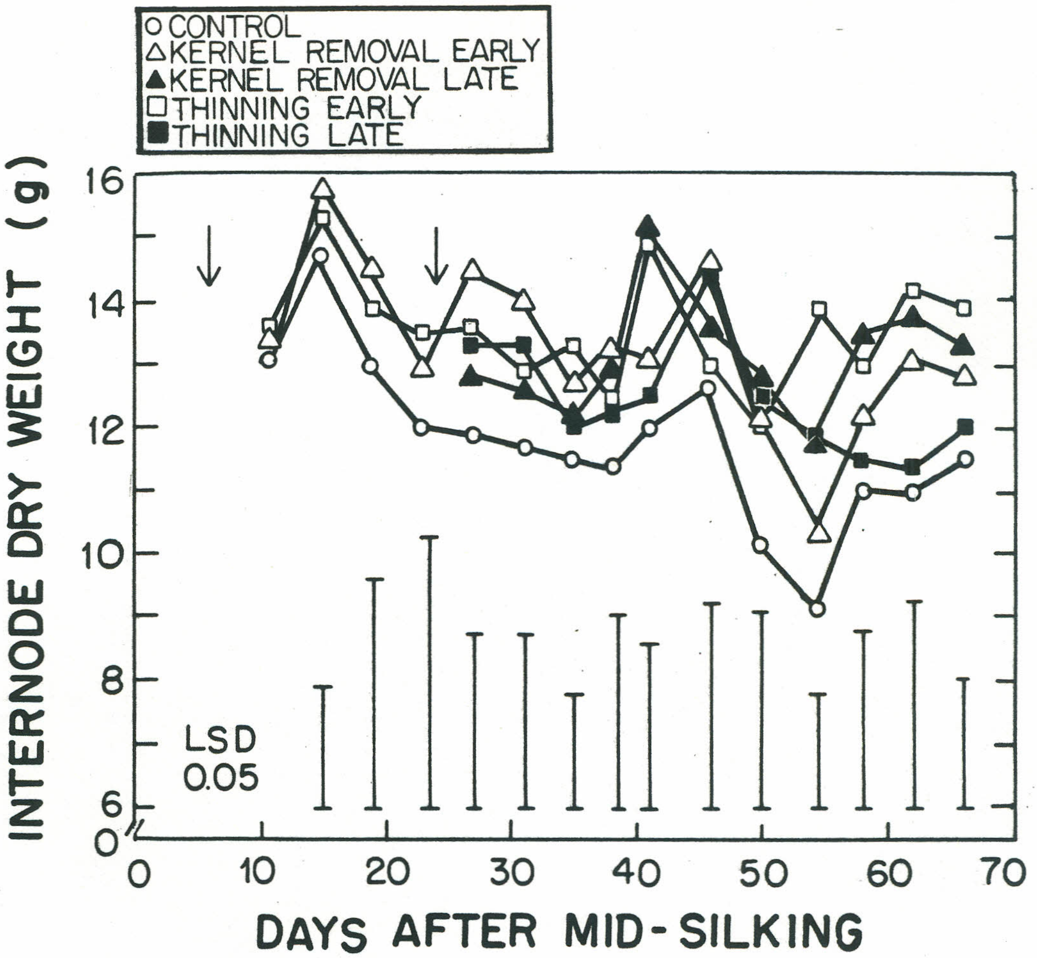

○ CONTROL
△ KERNEL REMOVAL EARLY
▲ KERNEL REMOVAL LATE
□ THINNING EARLY
■ THINNING LATE
INTERNODE DRY WEIGHT (g)
16
14
12
10
8
6
0
LSD
0.05
0
10
20
30
40
50
60
70
DAYS AFTER MID-SILKING

Figure 3. Effect of kernel removal and thinning on internode soluble sugar content. (M14 x W64A.) Arrows indicate times of treatment application.

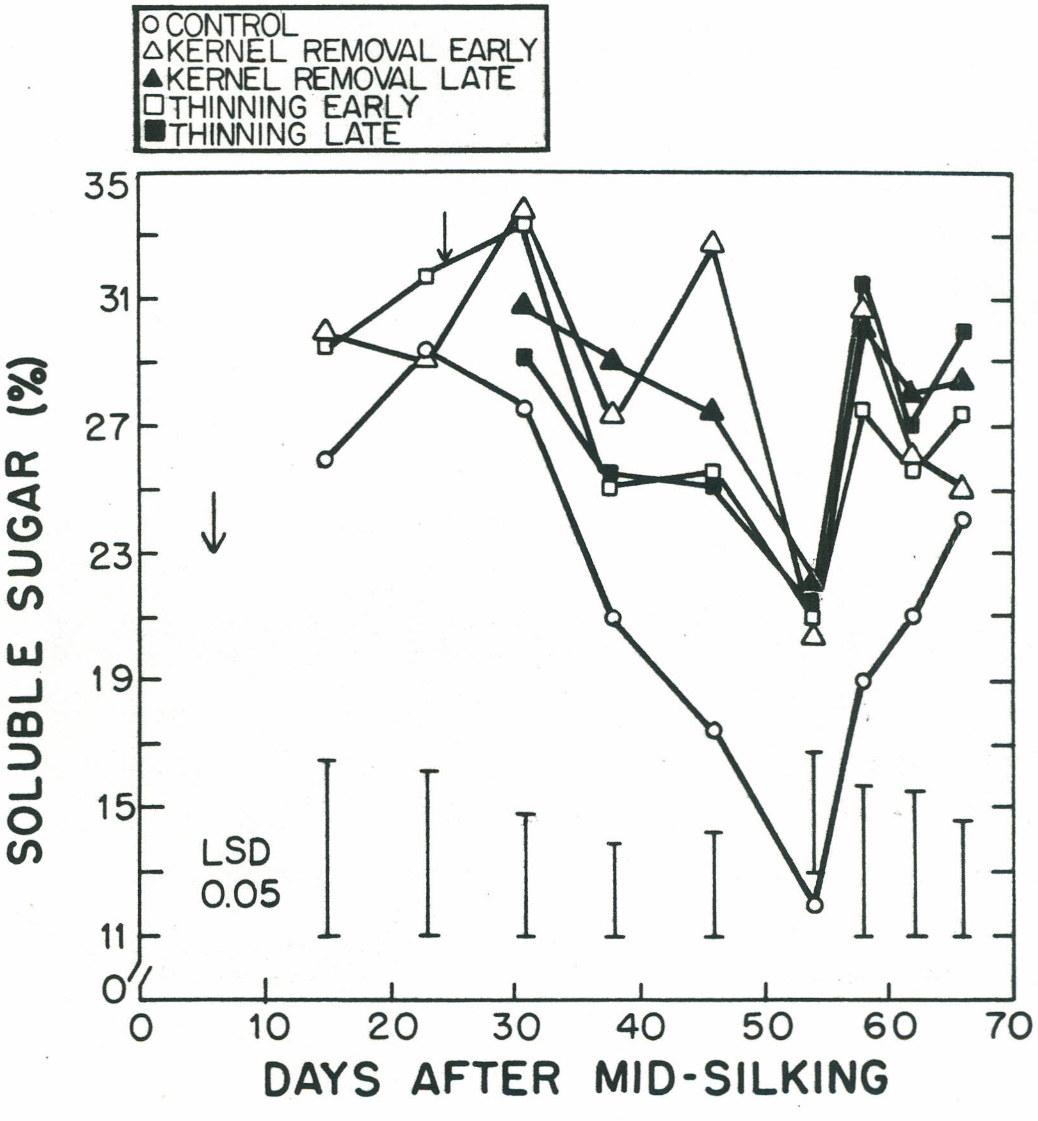

○ CONTROL
△ KERNEL REMOVAL EARLY
▲ KERNEL REMOVAL LATE
□ THINNING EARLY
■ THINNING LATE
SOLUBLE SUGAR (%)
35
31
27
23
19
15
11
0
LSD
0.05
0
10
20
30
40
50
60
70
DAYS AFTER MID-SILKING

Figure 4. Effect of kernel removal and thinning on internode soluble sugar content. (Cultivar Pioneer 3780.) Arrows indicate times of treatment application.

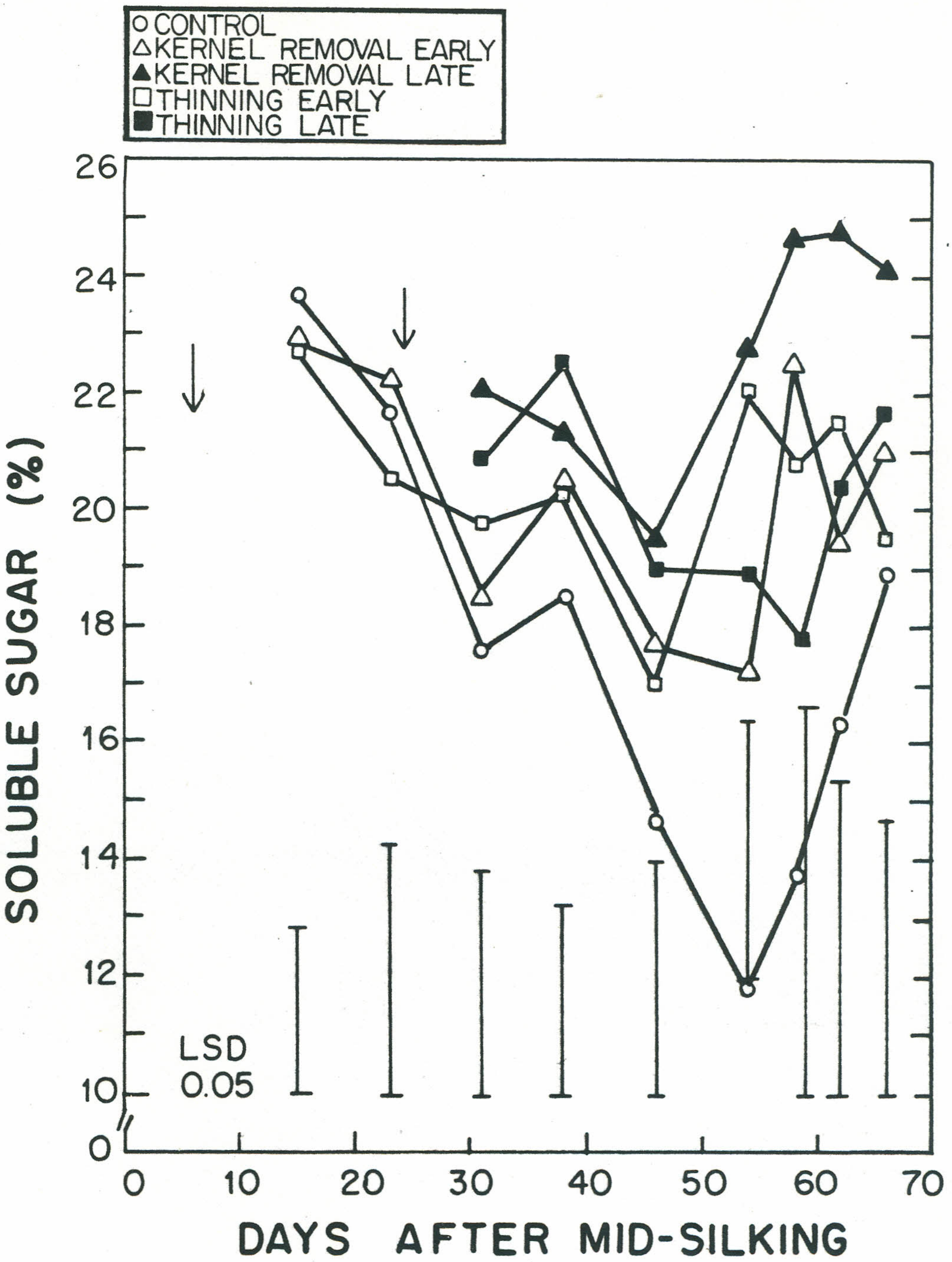

○ CONTROL
△ KERNEL REMOVAL EARLY
▲ KERNEL REMOVAL LATE
□ THINNING EARLY
■ THINNING LATE
SOLUBLE SUGAR (%)
26
24
22
20
18
16
14
12
10
0
LSD
0.05
0
10
20
30
40
50
60
70
DAYS AFTER MID-SILKING

Figure 5. Effect of kernel removal and thinning on internode nitrogen content. (M14 x W64A.) Arrows indicate times of treatment application.

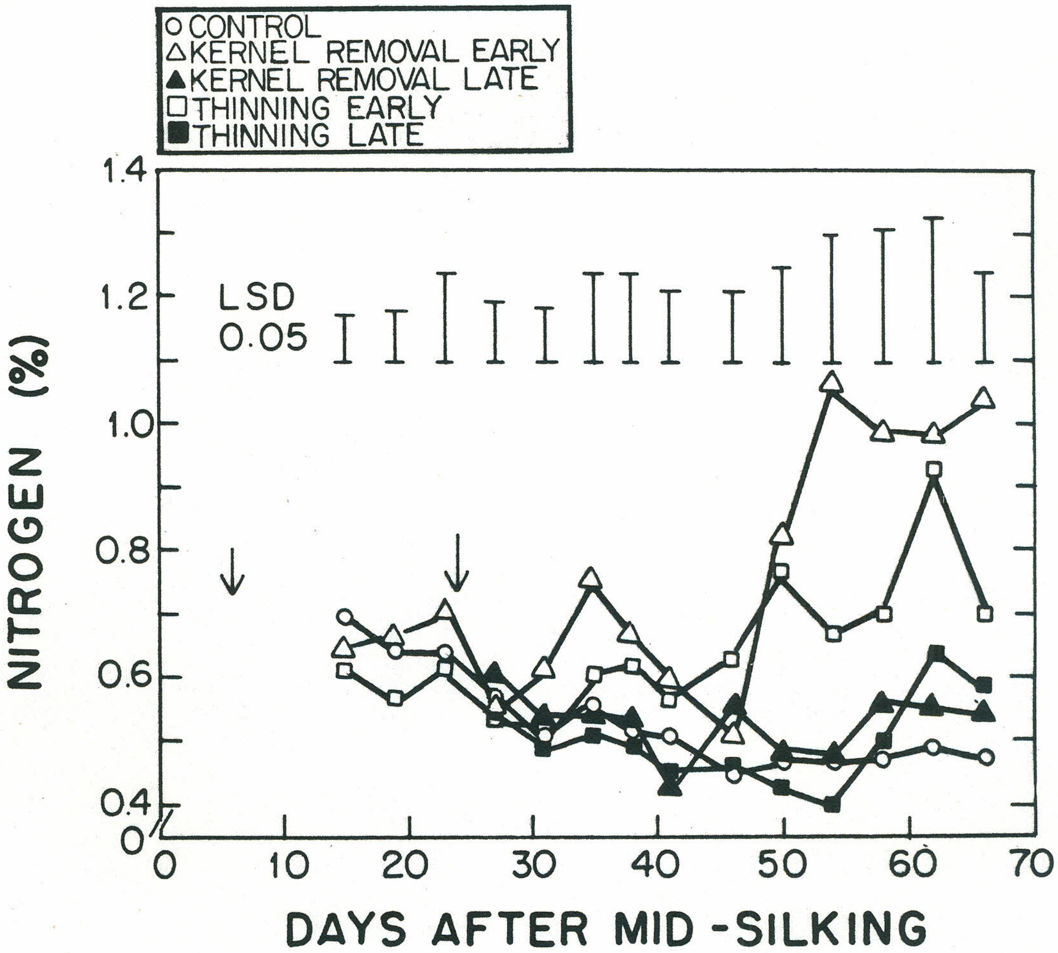

○ CONTROL
△ KERNEL REMOVAL EARLY
▲ KERNEL REMOVAL LATE
□ THINNING EARLY
■ THINNING LATE
LSD
0.05
NITROGEN (%)
1.4
1.2
1.0
0.8
0.6
0.4
0
0
10
20
30
40
50
60
70
DAYS AFTER MID-SILKING

Figure 6. Effect of kernel removal and thinning on internode nitrogen content. (Cultivar Pioneer 3780.) Arrows indicate times of treatment application.

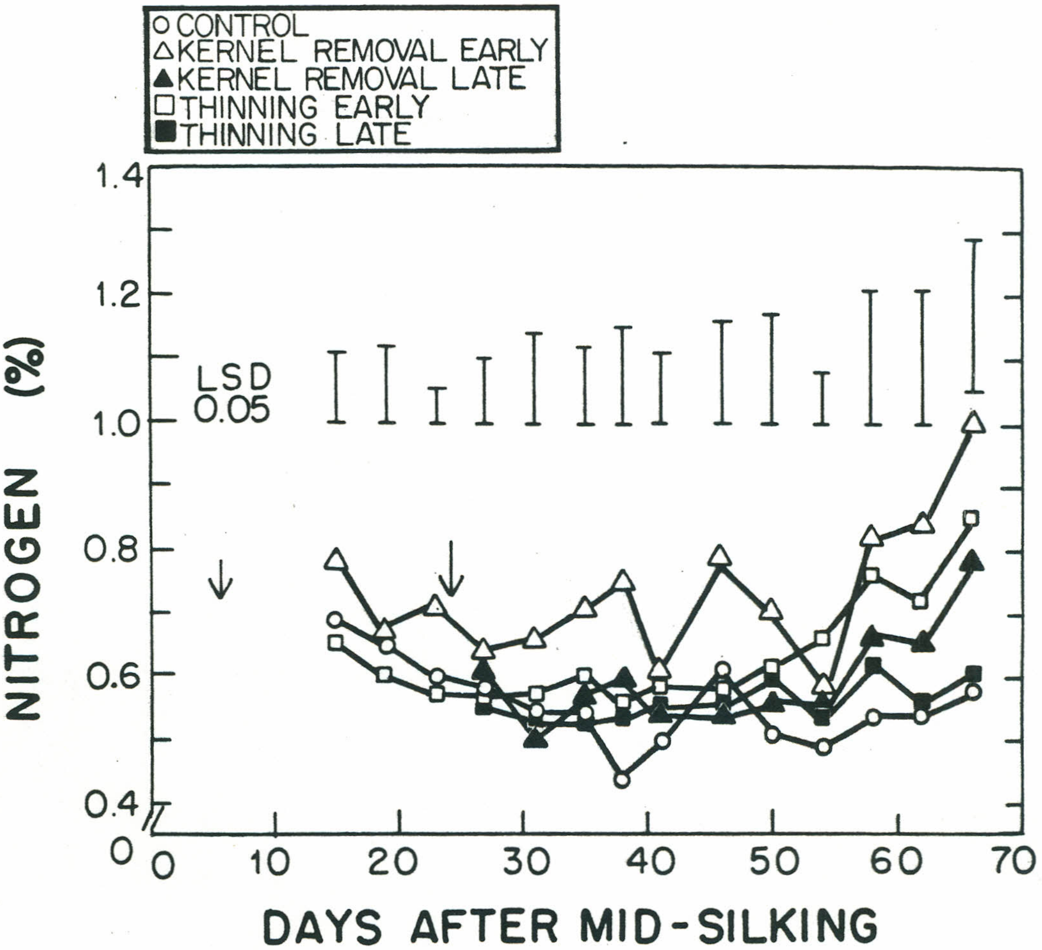

○ CONTROL
△ KERNEL REMOVAL EARLY
▲ KERNEL REMOVAL LATE
□ THINNING EARLY
■ THINNING LATE
1.4
1.2
1.0
0.8
0.6
0.4
0
LSD
0.05
NITROGEN (%)
0
10
20
30
40
50
60
70
DAYS AFTER MID-SILKING

Figure 7. Effect of kernel removal and thinning on the course of dry matter accumulation during grain filling. (M14 x W64A.) Arrows indicate times of treatment application.

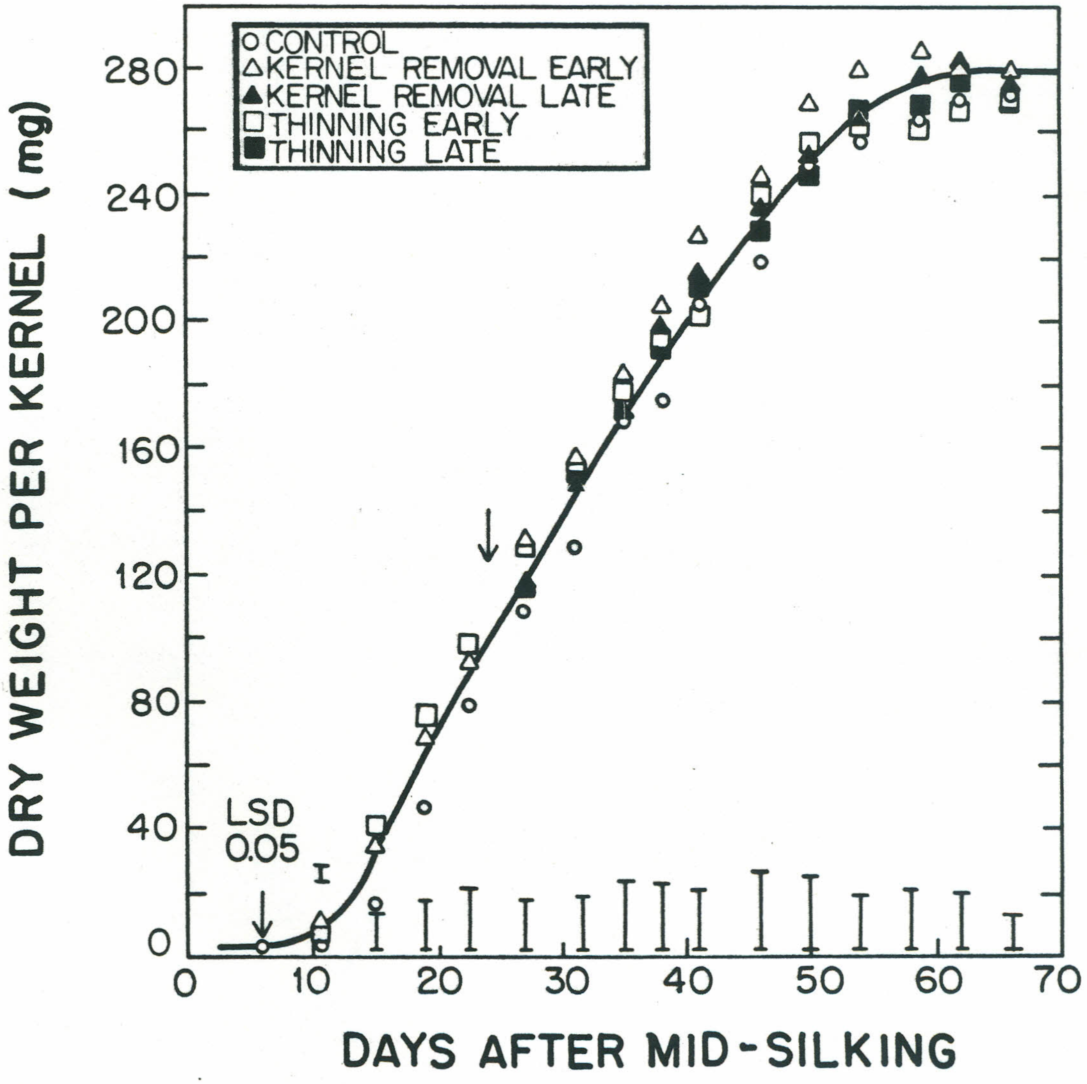

○ CONTROL
△ KERNEL REMOVAL EARLY
▲ KERNEL REMOVAL LATE
□ THINNING EARLY
■ THINNING LATE
LSD 0.05
DRY WEIGHT PER KERNEL (mg)
0
40
80
120
160
200
240
280
0
10
20
30
40
50
60
70
DAYS AFTER MID-SILKING

Figure 8. Effect of kernel removal and thinning on the course of dry matter accumulation during grain filling. (Cultivar Pioneer 3780.) Arrows indicate times of treatment application.

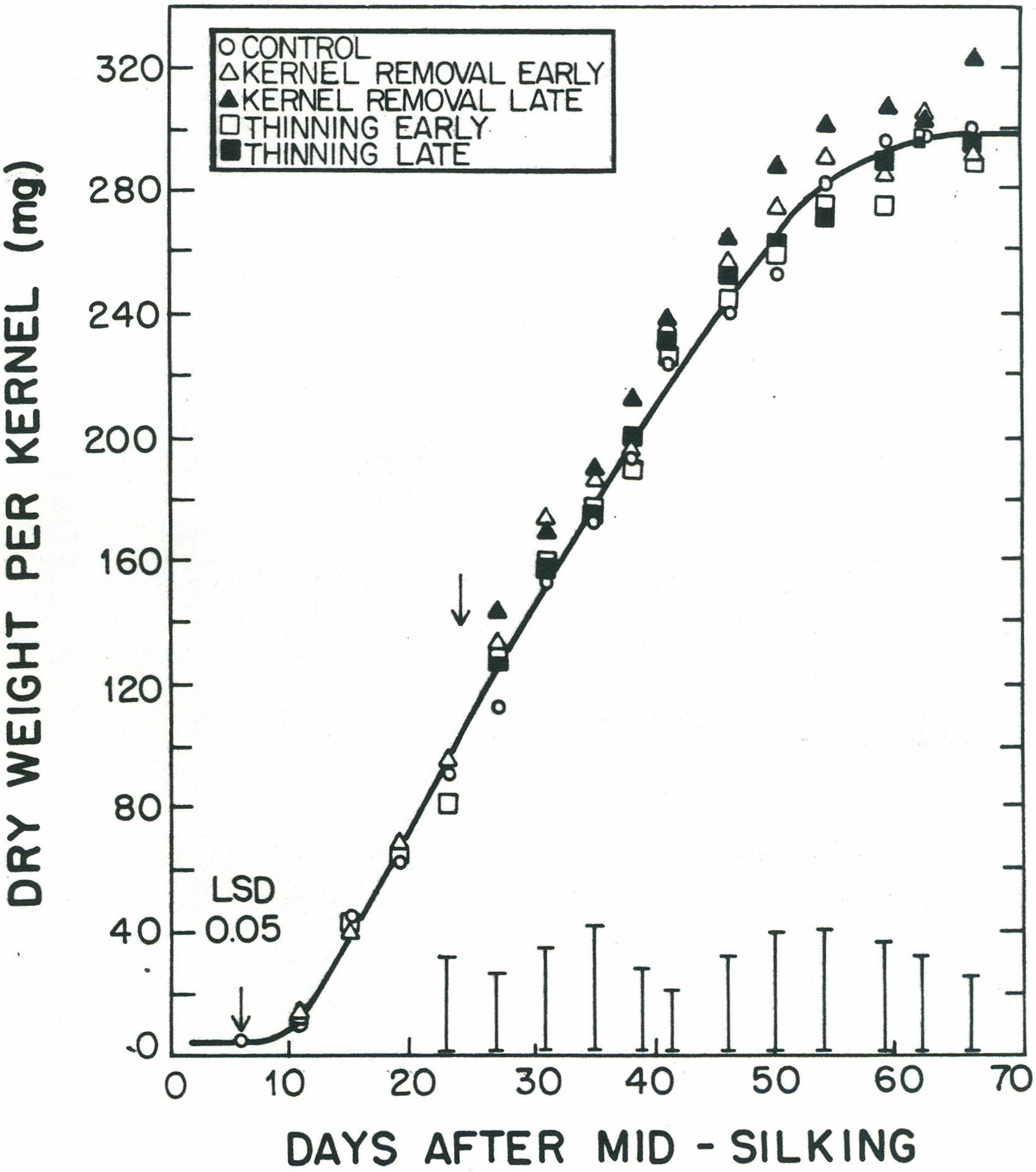

○ CONTROL
△ KERNEL REMOVAL EARLY
▲ KERNEL REMOVAL LATE
□ THINNING EARLY
■ THINNING LATE
DRY WEIGHT PER KERNEL (mg)
320
280
240
200
160
120
80
40
0
LSD
0.05
0
10
20
30
40
50
60
70
DAYS AFTER MID - SILKING

Figure 9. Effect of kernel removal and thinning on kernel nitrogen content. (M14 x W64A.) Arrows indicate times of treatment application.

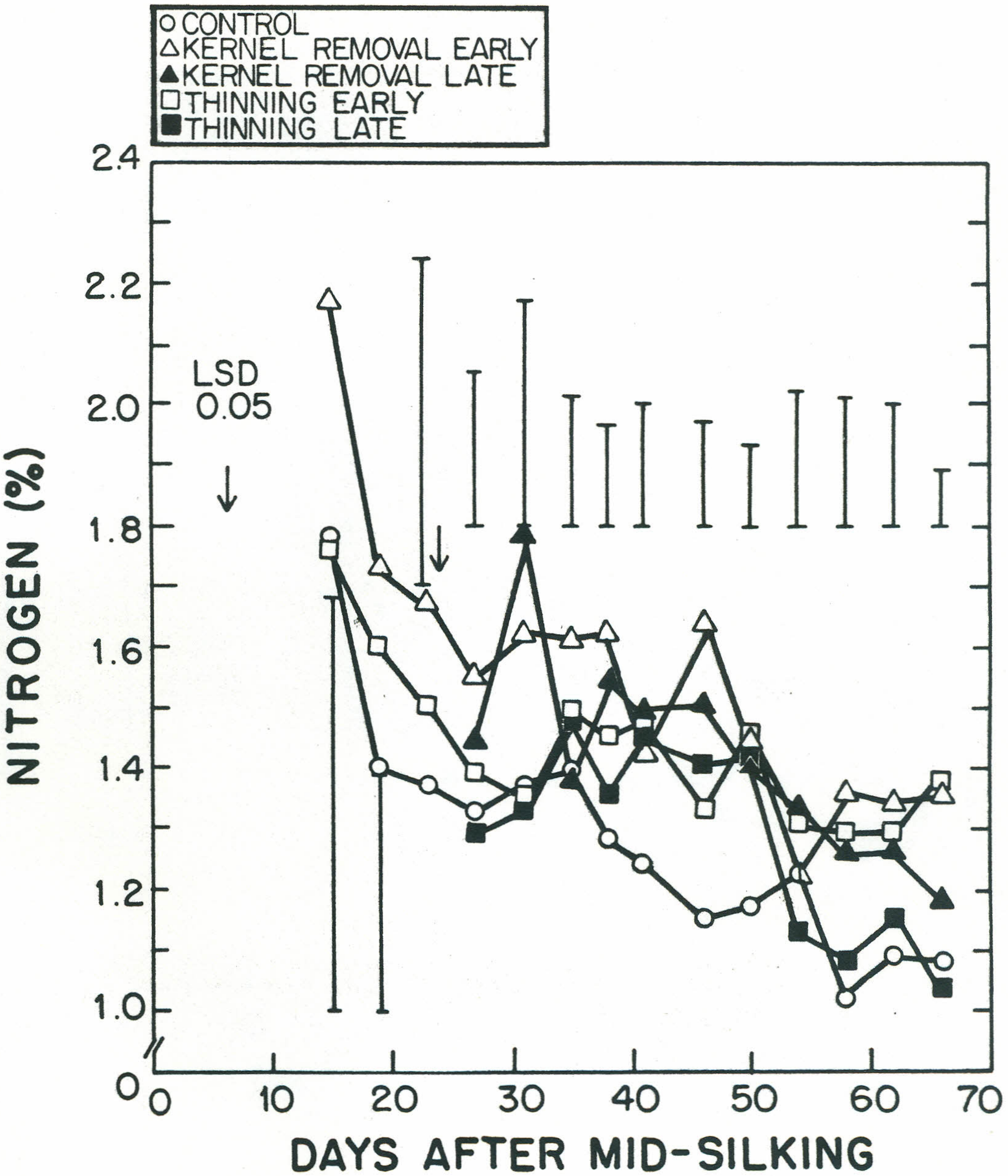
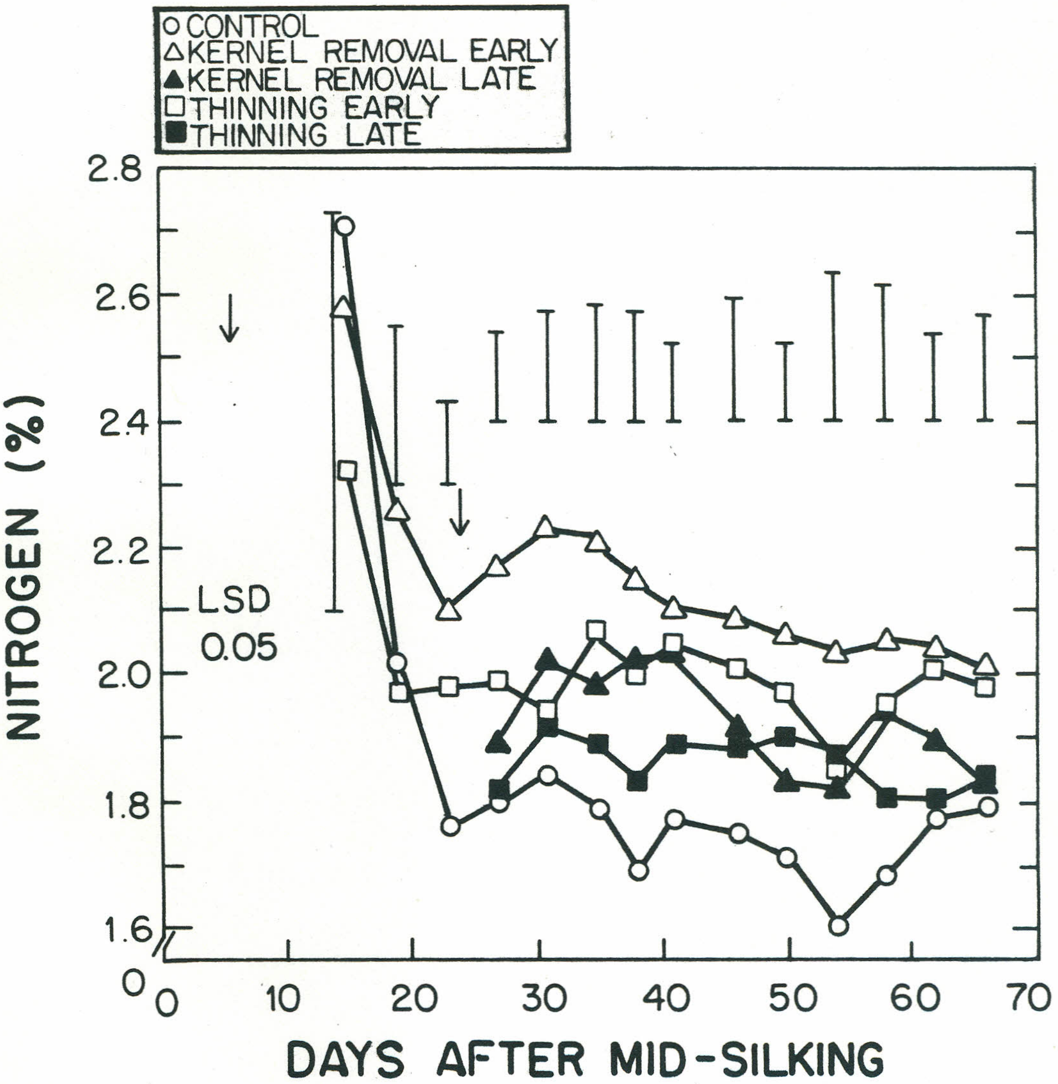

○ CONTROL
△ KERNEL REMOVAL EARLY
▲ KERNEL REMOVAL LATE
□ THINNING EARLY
■ THINNING LATE
LSD
0.05
NITROGEN (%)
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0
0
10
20
30
40
50
60
70
DAYS AFTER MID-SILKING

Figure 10. Effect of kernel removal and thinning on kernel nitrogen content. (Cultivar Pioneer 3780.) Arrows indicate times of treatment application.


○ CONTROL
△ KERNEL REMOVAL EARLY
▲ KERNEL REMOVAL LATE
□ THINNING EARLY
■ THINNING LATE
NITROGEN (%)
2.8
2.6
2.4
2.2
2.0
1.8
1.6
0
LSD
0.05
0
10
20
30
40
50
60
70
DAYS AFTER MID-SILKING