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NITROGEN UTILIZATION IN MICHIGAN WHEAT CULTIVARS, AS
RELATED TO GENOTYPE X ENVIRONMENT INTERACTION

Michigan State University

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AS RELATED TO GENOTYPE X ENVIRONMENT INTERACTION

By

Mark David Winslow

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ABSTRACT

NITROGEN UTILIZATION IN MICHIGAN WHEAT CULTIVARS, AS RELATED TO GENOTYPE X ENVIRONMENT INTERACTION

By

Mark David Winslow

The soft white winter wheat (Triticum aestivum L.) cultivar 'Tecumseh' is highly responsive to heavy applications of nitrogen (N) fertilizer, but is low-yielding if N is not applied. With the increasing cost of fertilizer, it is important to develop cultivars that use N efficiently. This research was conducted to examine the basis of Tecumseh's high N requirement and high N responsiveness.

Data were collected on the seasonal accumulation and straw-grain partitioning of reduced N in the above-ground portions of four cultivars ('Tecumseh', 'Ionia', 'Yorkstar', and 'Augusta'), as a function of three rates of N topdressing (0, 45, and 90 kg/ha), at three locations in 1980. The effect of N topdressing on yield, yield components, and harvest index, was also measured, in eight experiments over three years and three locations. To compare the effect of N with the effects of other environmental variables, yield and yield-component responses to improvement in site yield potential were measured, in fifteen sites over two years.

Tecumseh was as high or higher than the other cultivars in N accumulation per hectare, at all rates of applied N, by the end of the growing season. Tecumseh took up approximately twice as much soil N after anthesis as the other cultivars, and maintained a higher whole-plant concentration of N at all growth stages. It is concluded that

Tecumseh's high N requirement is not caused by a deficiency in capacity for uptake of soil N.

The high yield responsiveness of Tecumseh to N was associated with a high responsiveness of the yield component heads/m² (X). Tecumseh was also more yield-responsive than other cultivars to improvements in site yield potential, and this was also associated with a high X-responsiveness. Thus, genotype x environment interaction for Tecumseh results from an unusually high X-responsiveness; this is a general response to improved environments, rather than a specific response to N.

Tecumseh's high yield response to N was achieved with application of N at any time up until the crop reached the fully-tillered stage. In contrast, a high yield response to N for Ionia was achieved only when N was applied at the fully-tillered stage. This is interpreted as indicating an inherently lower level of inter-tiller competition in Tecumseh than in Ionia. Thus, Tecumseh's high X-responsiveness to improvements in the environment may be a result of a low level of inter-tiller competition, which allows this cultivar to achieve a high X despite the seasonal fluctuations in the supply of environmental resources that commonly occur in production situations.

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INTRODUCTION

Soon after its release in 1974, it was noticed that the Michigan soft white winter wheat (Triticum aestivum L.) cultivar 'Tecumseh' required heavier spring topdressings of nitrogen (N) fertilizer than other cultivars, in order to achieve satisfactory yields. Since N fertilizer is an expensive production input, it would be desirable to develop cultivars that have low N requirements. This research was conducted to discover the reasons for Tecumseh's high N requirement and high response to supplemental N. This information could be helpful in designing breeding strategies to improve the efficiency of N use in future cultivars.

Tecumseh's high N requirement might be caused by a deficiency in capacity for uptake of soil N. To test this hypothesis, data were collected on N accumulation in above-ground parts of four cultivars, as a function of different rates of N topdressing, in three environments. Other features of N accumulation and partitioning were also measured, to see if differences in utilization of N occurred among cultivars.

Since N application increases yield by increasing the values of the yield components, cultivar differences in yield component response to N might explain differences in yield response to N. To test this hypothesis, yield and yield component responses to N were measured over several years and locations.

It was recognized that there may be similarities between crop response to N and crop response to other growth-promoting factors, such as moisture and cool temperatures, which cause much of the differences in site yield potential among sites in the wheat-producing areas of Michigan. Thus, differential cultivar response to N may have the same basis as differential cultivar response to improvements in site yield potential, and may therefore be a model system in which to study "genotype x environment interaction." To examine these ideas, yield and yield-component performance across a set of sites of differing yield potential, were measured.

REVIEW OF LITERATURE

The intensive cultivation of cropland has reduced soil nitrogen (N) fertility to such a degree that the use of supplemental N fertilizer is necessary for high yields and profitable farming (45). However, the use of chemical N fertilizers has several drawbacks. It is expensive, accounting for approximately 10% of a farmer's production costs in Michigan (68). It is energy-intensive; one-third of the energy required to produce a corn crop in the United States goes toward the manufacture, distribution, and application of fertilizer N (86). Much of the fertilizer applied is lost through leaching or denitrification, which can cause serious environmental problems (88).

Despite these drawbacks, increased use of N fertilizer is essential if food production is to keep pace with population growth (105). Thus, agronomists are faced with the challenge of developing efficient systems of soil N fertility management and efficient crop cultivars. Vose (99, 100) and Epstein (20) argue that great potential exists for improving the efficiency of nutrient use in crops, by genetic means.

Evidence for genetic variability in N use efficiency has been reported in the literature. Chevalier and Schrader (13) measured the amount of nitrate and reduced N accumulated (per plant) by corn inbreds and hybrids in solution culture. They found differences among genotypes in the amount of nitrate taken up from solution and in the partitioning

of reduced N among plant parts. Mugwira et. al. (71), using 28-day old plants in solution culture, found that the wheat cultivar 'Arthur' (which has the same parentage as Tecumseh) took up more nitrate from the solution than did 'Atlas 66' when the concentration of nitrate in the solution was low. However, the difference between cultivars disappeared when concentration of nitrate was high in the solution. Thus, Atlas 66 was more responsive than Arthur, in terms of nitrate uptake per plant, to increases in nitrate supply. This group of workers also found differences among cultivars of triticale and rye, in nitrate uptake per plant. Lal et. al. (57) found that triticale cultivars accumulated more N per hectare than did wheat cultivars, but considerable within-species variation occurred for both crops. Harvey (44), in solution culture studies with corn and tomatoes, found cultivar differences in dry matter production per plant, as a function of solution nitrate concentration. He reported that cultivars that were low in dry matter production at low nitrate levels were more responsive (in terms of dry matter production) to increases in the nitrate level.

Gerloff (32) advocates the use of the variable "N efficiency ratio" ($\text{mg dry wt per plant} / \text{mg N absorbed per plant}$) as a measure of plant efficiency in the use of accumulated N for dry matter production. Using this criterion, cultivar differences were found in tomato (74) and ryegrass (101), on a per-plant basis, in solution culture experiments.

The finding that cultivars can differ in dry matter production per unit N absorbed implies that they differ in the efficiency of use of N in physiological processes. One explanation for this could be that cultivars differ in their capacity to convert the absorbed inorganic

nitrate into useful organic forms of N. The rate-limiting step in this process is the reduction of nitrate to nitrite by the enzyme nitrate reductase (16). Genetic differences in nitrate reductase activity (NRA) have been reported (16, 17, 30). It was hoped that genetic differences in NRA would correlate with differences in plant vigor, grain yield, and grain protein, and would therefore would provide a basis for selection in breeding programs. Unfortunately, however, the correlations have been weak (14, 16, 17, 82). It appears that inefficiencies in other N use processes, such as uptake and translocation, compensate for high NRA, so that gain in economic traits would not be achieved by selecting for high NRA alone (16, 17, 82).

The relationship of genetic variation in the efficiency of the various N use processes among cultivars, to grain protein production, has recieved considerable attention. Studies in wheat (70) and corn (47) indicate that certain high-protein cultivars accumulate more N from the soil (per hectare) or from solution culture (per plant), respectively, than do low-protein cultivars. However, a growth-chamber pot study conducted by Cataldo et. al. (11) revealed that a high-protein oat cultivar accumulated no more N than a low-protein cultivar; rather, high grain percent protein resulted from a lower accumulation of carbohydrate in the high-protein cultivar.

There does not appear to be any consistent association between grain percent protein and leaf N concentration. High-protein cultivars have been found to have leaf reduced N concentrations higher (79), lower (54), and equal (87) to those of lower-protein cultivars. One study advocated the use of seedling reduced N concentration as a screening criterion for identifying high-protein lines (48).

The study of Cataldo et. al. mentioned above found that the high

protein oat cultivar continued to accumulate N from the pot after anthesis, while the low protein cultivar did not. However, in a field study using six oat cultivars, including the two studied by Cataldo et. al., another group (79) obtained the opposite results for these two cultivars; the low-protein cultivar took up more N after anthesis than did the high-protein cultivar, per hectare. Thus, caution must be exercised in extending conclusions derived from growth-chamber pot experiments on single plants to make inferences about crop performance in the field. Among the six cultivars in the latter study, no correlation was found between post-anthesis N accumulation and grain percent protein. In a field experiment using cultivars of wheat studied in the present research, Heinrich (46) found that Tecumseh (which has a high grain percent protein) was greater in post-anthesis N uptake than lower-protein cultivars.

High-protein cultivars of wheat (53, 55, 87), oats (79), and rice (78) were found to translocate more N from the vegetative parts into the grain, than low-protein cultivars. However, another study in wheat found no such relationship (70). The study of Cataldo et. al. mentioned above found that the high-protein cultivar actually translocated less N from the vegetative parts to the grain, than did the low-protein cultivar.

Thus, it seems that there is no single physiological trait that can be used to predict or select for high grain percent protein. Rather, grain percent protein is the result of the interaction of many processes that may show compensatory shifts when one particular process is increased or decreased. Identification of genotypes superior for individual processes may be valuable in collecting parents for high-protein breeding programs, even if these parents are not particularly

high in grain percent protein themselves; "physiological complementation" (102) of these processes in segregating generations may lead to high-protein lines among the progeny. This idea of using parental component complementation to achieve progress in selection for complex traits was used successfully by Grafius et. al. (40).

Many breeders have noticed a negative correlation between yield and grain percent protein in segregating populations (8, 66, 77, 95). This correlation fits the expectation from a bioenergetic point of view (9, 81). Approximately twice as much glucose is required to synthesize one gram of protein as compared to one gram of carbohydrate (9). Hence, if the pool of assimilates is fixed, and if it limits grain production, any increase in protein production will be accompanied by a decrease in carbohydrate production (therefore yield will decrease). However, by increasing the capacity of a cultivar to assimilate solar energy in useful forms, gains in both yield and protein could be achieved (81). In actual breeding programs, simultaneous increases in yield and protein have been achieved (54). Thus, grain percent protein and yield can be increased simultaneously if both are selected for, but because of the negative correlation, progress will be slower than if just one or the other trait was emphasized in selection.

Although selection for higher grain percent protein slows progress for yield, cultural practices exist which can greatly increase protein, without sacrificing yield. (This observation casts doubt on the assumption underlying the bioenergetic argument described above, i.e. that assimilate supply limits yield and protein production in currently grown cultivars, since cultural N amendments also require plant energy for reduction and incorporation into protein). Late season N supplements, applied to the soil or foliage, boost grain percent protein (23,

33, 50, 69, 83, 85). The leaves play an important role in late-season N uptake and translocation to the grain, as demonstrated in leaf-removal experiments (70, 73). The flag leaf is particularly important in nitrate reduction (41, 70). A very important factor determining N uptake from the soil is soil available moisture; drouthy conditions reduce N uptake markedly (19, 89, 96). Drouth increases soil water tension, reducing mass flow of nutrients to the roots (98). Thus, adequate soil moisture is necessary for high protein production per hectare.

An interesting aspect of crop N use is the phenomenon of volatilization losses of N. Significant amounts of N are lost from the straw, primarily as ammonia (15, 49), in a maturing wheat crop. Presumably, the ammonia is a product of protein catabolism during remobilization of amino acids to the developing grain. Volatilization losses are greater at high temperatures (94).

The breeding of cultivars with greater yield responsiveness to heavy applications of fertilizer N, was a key factor in the spectacular yield increases achieved during the "Green Revolution" of the early 1960's. The new short-strawed cultivars withstood the increased growth stimulated by N without lodging (12). These cultivars had smaller, more erect leaves, so that the increased leaf area resulting from N application did not cause as much mutual shading as in traditional cultivars (5, 12, 18, 108). Mutual shading reduces net photosynthesis in the lower levels of the canopy, thus reducing net assimilation rate (12).

Donald and Hamblin (18) point out that the shorter straw and smaller leaves of modern cultivars cause them to have a higher harvest index ($HI = \text{wt of grain} / \text{wt of whole plant}$). Thus, modern cultivars are

more N-responsive because they are less competitive (less mutual shading), and this is reflected in a higher HI. They propose selecting for HI to continue increasing N responsiveness.

Wellhausen (104) describes the greater N responsiveness of modern corn cultivars developed in Mexico. Traditional cultivars had been selected to give reliable, but low, yields on the continuously cropped land near the villages. No types of fertilizers were used in the traditional agricultural systems, so the soils were very low in fertility. The modern cultivars were selected from land races that had evolved in the few highly-fertile lakebottom areas. When grown in the nutrient-depleted areas, these modern cultivars yielded no more (and sometimes less) than the traditional cultivars. When fertilizer was supplied, however, the modern cultivars yielded twice as much as the traditional cultivars, and approximately seven times as much as when not fertilized. Hence, the use of fertilizer N and the breeding of cultivars more responsive to it have been inseparable components of the strategy for increasing yields in grain crops in modern times.

In the United States, corn production utilizes hybrid cultivars rather than the open-pollinated cultivars and synthetics of Mexico. There are differences among corn inbred lines in yield responsiveness to N (6). Hybrids may be more responsive than inbreds (10, 93).

It is accepted that modern small-grain cultivars are more yield-responsive to N than are traditional cultivars. Are there differences among modern cultivars themselves, with regard to N responsiveness? Several studies have come to different conclusions. Two studies found no differences in yield responsiveness to N among diverse collections of wheat cultivars (76, 84). Two other reports (67, 92) demonstrated significant differences among cultivars in response of the yield

components to N, but not of yield itself. Despite the lack of statistical significance, however, there was a tendency for the more yield-responsive cultivars to be those which were more responsive in the yield component heads per unit area (X), in one of the reports (92).

In eight studies, significant differences in yield response to N among small-grain cultivars were reported (25, 42, 58, 65, 72, 103, 106, 107). In four of these studies-- one with wheat (72), one with barley (103), one with oats (25), and one with rice (107)-- the yield components were measured. In all four, the cultivar with the highest yield response to N was the one that exhibited the highest X response to N. Thus, high X-responsiveness seems to be important in causing high yield-responsiveness to N, in modern small-grain cultivars.

Since X is the result of the growth and development of tillers, it is necessary to understand the processes controlling tiller development in order to understand X-response to N. Tillers are essentially branches, arising from axillary buds in the basal leaves of a grass culm. Conditions which favor plant growth as a whole, such as adequate moisture, fertility, and temperature, favor tillering (60). Active tillering is a process occurring in the vegetative stage of plant growth; once the apical meristem begins to differentiate into a reproductive structure (spike in wheat), tillering from the base of that culm is inhibited (3, 60). This inhibition is hormonal in nature (auxin), rather than being due to competition for nutrients among tillers (51, 52, 62, 63, 64). Tillers which have begun to elongate, but have not yet begun to differentiate their spike, will senesce and die if their parent culm is differentiating its spike (3, 63).

Aspinall (3), in a greenhouse pot experiment with barley, found that application of a nutrient solution reduced this inhibition; tiller

bud elongation was again stimulated, and senescence of smaller tillers prevented. In a subsequent experiment (4), he compared two cultivars, a high-tillering type and a low-tillering type, with regard to the degree of release of inhibition following apex removal and nutrient supplementation. Apex removal caused a greater increase in number of fertile heads in the low-tillering cultivar than in the high-tillering cultivar. Nutrient supplementation gave the same result. He concluded that, since release from inhibition was greater in the low-tillering cultivar, this cultivar must have a greater degree of apical dominance in the normal situation (without supplementation or apex removal). Note that this study was conducted during the heading stage of growth, which is later than the stage in which senescence of smaller tillers occurs, in field situations.

The point at which spike differentiation begins (and hence tillering ceases), is called the fully-tillered stage. Lang and Holmes (59) found that application of N fertilizer at this time gave the greatest yield response. They commented that earlier applications stimulated too much tillering, and that many of these tillers would not survive to bear seed. They did not specifically say whether the N application at the fully-tillered stage stimulated new tillering, reduced tiller senescence, or both. Gericke (31) found that delayed application (by two to four weeks) of N gave the maximum number of fertile tillers in oat plants in greenhouse pots. In field studies with oats, Frey (27) and Frey and Wiggans (28) found that a two-week delay in N application maximized yield, as a result of maximizing X. The fully-tillered stage occurs approximately two to four weeks after the beginning of spring growth in small grains (personal observations). Thus, it appears that delay of nutrient application until the fully-tillered stage maximizes

X-response to N, although genotypic differences for this response may exist.

The application of N fertilizer stimulates an increase in the yield components heads/m² (X) and seeds/head (Y), although cultivars differ as to which component is stimulated the most (25, 67, 72, 92, 103, 107). In contrast, the seed weight component (Z) is relatively unaffected by N supplementation.

To some extent, the response of Y to N supplementation is reduced as a result of the allometry of yield component development (37, 43). Allometry refers to the relationship of the size of different plant parts to one another. The concept arose from the observation of Sinnott (90) that "the size of any organ depends upon the size of the growing point out of which it has developed".

A grass plant begins shoot growth at a single apical meristem. As this meristem develops, leaf buds appear with small tiller bud meristems in their axils. Since these tiller buds are smaller than the apical meristem of their parent culm, the culms which are eventually derived from these tiller buds will be smaller than the parent culm, as per Sinnott's law. Thus, more distal culms will be progressively smaller.

The spike arises from the apical meristem of a culm. The apical meristem arises from the tiller bud meristem, from which that culm originated. Since more distal tiller buds are smaller, their culm apices are also smaller, and thus they give rise to smaller spikes. Thus, more distal tillers have smaller spikes, with fewer seeds. Therefore, as N fertilizer stimulates tillering, it increases the production of smaller culms, with smaller spikes, bearing fewer seeds. This is not to say that N causes a decrease in average Y; on the contrary,

N usually causes an increase in Y, as a result of better plant nutrition. However, this increase would probably be greater if not for the dampening effect of allometry.

Seed size is quite different from the other yield components, in terms of response to changes in resource supply. Many plant species, when coping with a limited resource supply, sacrifice seed number ($X \cdot Y$) but conserve seed size (Z) (91). Cereal crops appear to have evolved compensatory mechanisms to insure proper development of Z in the face of considerable stress. Pinthus and Sar-Shalom (80) found that late planting of a wheat crop reduced the seed fill period, but the rate of seed fill increased to compensate, with the result that normal Z was achieved. Gallagher et. al. (29), working with barley, found that stem carbohydrate reserves were mobilized to the grain to a greater degree in years of poor climate and in stressful environments, again as a compensatory mechanism to complete seed-filling. Fischer (24) found that shading of wheat plants during the grain-fill period had remarkably little effect on yield; presumably, stem reserves were mobilized to the grain to compensate for the reduction in current photosynthate.

Stebbins (91) offered an evolutionary justification for the constancy of Z. The seedling stage is the most vulnerable stage in the life cycle of the growing plant. An optimum seed size probably exists for a given species, in its ecosystem. Any smaller seeds will not have enough carbohydrate reserves to survive this stage. Larger seeds carry unnecessary carbohydrate that could have been used to increase the number of seeds produced by the parent plant. Thus, there may be a strong selection pressure towards the evolution of mechanisms that maintain Z at a fairly precise value.

N is just one of many environmental factors affecting yield. The

effect of environmental factors on yield can be clarified by examining their effect on the yield components (61). Optimum balances among the yield components may exist for maximizing yield, and these optima are probably different in different environments (35, 38). Thus, it appears plausible that cultivar differences in yield response to improvements in site yield potential, described by the phrase "genotype x environment interaction", may be caused by differences in yield component response (26).

If the yield components are important in determining yield and yield response to environmental variables, then breeders should be interested in changing the yield components to maximize yield. However, because of their developmental interdependency, the expression of the yield components in segregating populations exhibit negative (compensatory) correlations (1). Selection to increase one component results in a decrease in the others. There does appear to be some amount of uncorrelated variance, however; the difficult task is to find and utilize this variance.

Since Z is relatively isolated from the compensatory fluctuations that characterize X and Y, it has been the easiest to work with. Knott and Talukdar (56) were able to capitalize on the uncorrelated variance for this component in their gene pool. By backcrossing a high Z parent into an adapted cultivar and selecting for high Z, they eventually isolated lines which had the high X·Y (seeds per hectare) of the adapted recurrent parent, but had the high Z of the donor parent, and thus were higher yielding.

Grafius et. al. (40) were able to find uncorrelated variance for Y in their population, and by making the proper cross, obtained a progeny whose mean yield (unselected) was higher than that of the higher-yielding

parent. This is a characteristic of heterosis, but this was not true heterosis, since these progeny were homozygous (F_7 generation). The apparent heterosis was attributed to "component complementation", which is a result of the multiplicative interaction of component traits described by Grafius (34) and Adams and Duarte (2).

MATERIALS AND METHODS

The effect of spring nitrogen (N) topdressing on reduced N accumulation and on yield components of four soft white winter wheat cultivars adapted to Michigan, was measured in eight field experiments, over three years (1978-1980) and in three environments (Mendon, East Lansing, and Saranac). In addition, yield component responses across a set of environments of differing yield potential, were measured in fifteen sites, over two years.

N accumulation was measured in three of the experiments only. The experiments were at three different sites chosen to present a range of conditions of N availability and yield potential.

Mendon is in southwest lower Michigan (St. Joseph Co.) It is the warmest site, with an average of 2800 growing-degree days (40° base) between April 1 and July 31. This causes early maturity of the crop. The experiment was on a Nottawa sandy loam soil (Typic Argiudoll). This is a well-drained soil, and its low water-holding capacity combined with the high temperatures result in drouthy conditions at this site. Drouth stress combined with the early maturation make this site low in yield potential. The previous crop was corn, which had been supplied with fertilizer.

East Lansing is in south-central lower Michigan (Ingham Co.) The climate is cooler, with an average of 2400 growing-degree days between April 1 and July 31. Crop maturation is about ten days later than at

Mendon. The experiment was on a Capac loam soil (Aeric Ochraqualf), which is somewhat poorly drained. Moisture supply to the crop seemed adequate throughout the season. The combination of the cooler temperatures and adequate moisture supply make this a site of high yield potential. In an attempt to reduce soil N fertility prior to the experiment, a corn crop was grown the previous summer. It was not fertilized, and the stalks were incorporated into the soil to stimulate microbial immobilization of N.

Saranac is located in west-central lower Michigan (Ionia Co.) It is intermediate in temperature (2600 growing-degree days). The crop matures approximately seven days later than at Mendon. The experiment was on a Miami loam soil (Typic Hapludalf). This soil is well-drained, but moisture supply seemed adequate throughout the season. The adequate soil moisture but slightly high temperatures cause this site to be intermediate in yield potential. For all experiments at this site, the previous crop was soybeans incorporated into the soil before flowering, as a green manure. Thus, soil N fertility was probably high at this site before the experiments.

In this research, factorial experiments with a randomized complete-block design, were used. The number of replications varied from three to nine, depending on the experiment. All N accumulation experiments used six replications. Plots were 3.7 m long, with eight rows spaced 30 cm apart. Only the center four rows were harvested for grain yield, to avoid border effects.

N topdressing, in the form of urea or ammonium nitrate, was applied within the first two weeks of spring regrowth, using a mechanical spreader. This is the period of tiller initiation. Later soil applications were made by hand; foliar applications were made using a hand-

held sprayer.

In the N accumulation experiments, all plant material (including surface roots) in a 30 cm section of row (randomly chosen from within the second row of the plot) was harvested for N and yield component analysis, at each of three growth stages (fully tillered, anthesis, maturity). The samples were rinsed free of soil and dried at 70°C for 48 hours. At the fully-tillered and anthesis stages, the entire sample was weighed for use in total dry matter calculations, and then used in the N determination. At the maturity stage, ten culms were randomly selected from the sample, and used for the N determination. Grain samples were drawn from the plot yield bag for N determination.

Samples for N determinations were ground in a Wiley mill to pass through a screen with 0.5 mm hole diameter. The powder was stirred thoroughly, and a 30 mg portion taken for the N measurement. Reduced N was measured using an automated micro-kjeldahl apparatus (the Technicon Auto Analyzer; Technicon Corp., Tarrytown, NY) (21). This procedure uses a colorimetric assay for ammonia-- the Berthelot reaction (97). Addition of nitrate to plant samples did not change the measurements (46), indicating that only reduced forms of N are measured in this procedure.

Yield components and harvest index were measured in the following manner. After removing the ten culms for the N determination, the number of heads in the remaining portion of the sample was counted (ranging around 40 heads). The portion was weighed and threshed, and the number of heads divided into the weight of threshed grain, to obtain the average head weight. Harvest index was calculated by dividing the weight of the threshed grain by the weight of the portion before threshing. Total dry matter for the plot was calculated by dividing the harvest index into

the plot grain yield. Seed weight was determined by counting the number of seeds in a five g sample taken randomly from the plot yield bag. The number of seeds per head was calculated by dividing the average head weight by the average seed weight.

Yield and yield-component data were also collected from the MSU Regional-Advanced Winter Wheat Nurseries (01 series) in 1979 and 1980. These trials test 30 entries (adapted cultivars and advanced lines) using a 5 x 6 rectangular lattice design with three replications. Plots were 3.7 m long, with four rows spaced 30 cm apart. The same entries were used at all sites within a year, and 26 of the 30 entries were the same in both years. Data were collected at eight sites in 1979 and at seven sites in 1980.

All four rows were harvested for grain yield. Before harvest, a random sample of ten heads was collected from each plot. The average head weight calculated from this sample was divided into the plot grain yield, to get the number of heads per plot. Seed weight and number of seeds per head were determined as in the N accumulation experiments described above.

Four cultivars were studied in the N accumulation experiments. These cultivars are adapted to Michigan and are of considerable economic importance in the state.

Ionia was the first cultivar released from the MSU breeding program (1972). Its pedigree is Redcoat/3*Genesee. It was grown on 15% of the wheat acreage in 1978. It is tall and low-tillering, with large seeds.

Tecumseh was the next MSU release (1974), and was the most widely grown cultivar in Michigan in 1978 (30% of the acreage). Its genetic background is quite different from that of the other cultivars. It has

the same complex parentage as 'Arthur' (a popular Purdue release). Tecumseh matures approximately seven days earlier than the other cultivars, which may account for its lower yield. It is short-strawed, high-tillering, and high in grain percent protein.

Yorkstar is a 1967 release from Cornell. Its pedigree is Norin 10/Brevor//Yorkwin/3/3*Genesee. It yields well in Michigan, and was grown on 13% of the wheat acreage in 1978. It is intermediate in yield components and height.

Augusta is a new release from the MSU program (1980). Its pedigree is Genesee/Redcoat//Yorkstar. It is similar in height and yield components to Yorkstar.

RESULTS AND DISCUSSION

Data describing the crop N status at the three sites used for the N accumulation experiments, are presented in Table 1. At Mendon, the crop was lowest in N accumulation per hectare, plant N concentration, and yield. Moisture stress probably limited N uptake and grain yield at this site. East Lansing was intermediate for the N variables and for yield, but showed the greatest yield response to N. This is a reflection of the low soil N fertility at the beginning of this experiment (see Materials and Methods), combined with adequate moisture, which promotes uptake of N. The greatest N accumulation, plant N

Table 1.-- Crop N status and yield performance at three locations in 1980.

Location	Mean [†]			Mean [‡] yield response to N
	N accumulated in crop	Whole-plant N conc'n. at anthesis	Grain yield	
	kg/ha	%	q/ha	%
Mendon	84 a*	1.23 a	33.6 a	42
East Lansing	146 b	1.52 b	43.3 b	69
Saranac	187 c	1.82 c	46.9 c	12

*Means within a column followed by different letters are significantly different at the 5% level, by Duncan's Multiple Range Test.

[†]Experiment grand means (averages of 72 observations, over four cultivars and three rates of N topdressing.)

[‡]Mean response of four cultivars.

concentration, and yield occurred at Saranac. This resulted from the high N fertility status of the soil at the beginning of the experiment. Because of the high soil N fertility, yield response to supplemental N was low at this site.

Thus, the three sites exhibited a range of conditions of N supply and yield potential. Despite the dissimilarity of the environments, however, the cultivar patterns of N accumulation and dry matter production were remarkably consistent over experiments. For this reason, the data were averaged over sites, and are presented in Figures 1 and 2. Data for the individual experiments can be found in Appendix A.

Figure 1 shows that, despite being the lowest in dry matter accumulation per hectare, Tecumseh was as high or higher than the other cultivars in N accumulation per hectare, at maturity. It is seen from Figure 2 that Tecumseh lags slightly behind the other cultivars in N accumulation at anthesis, but the differences among cultivars for N accumulation are much less than the differences in dry matter accumulation. In other words, Tecumseh maintained a significantly higher whole-plant N concentration than the other cultivars, at all growth stages. The values for whole-plant N concentration at anthesis were 1.60%, 1.53%, 1.52%, and 1.44%, for Tecumseh, Augusta, Yorkstar, and Ionia, respectively ($LSD_{.05} = 0.05\%$). Tecumseh also took up approximately twice as much N after anthesis, as did the other cultivars (see below). Based on these observations, it is concluded that Tecumseh's high N requirement is not a result of a deficiency in capacity for uptake of soil N. Tecumseh appears to be at least as (if not more) capable of N uptake as the other cultivars, which nevertheless yield considerably more than Tecumseh, in conditions of low soil N fertility.

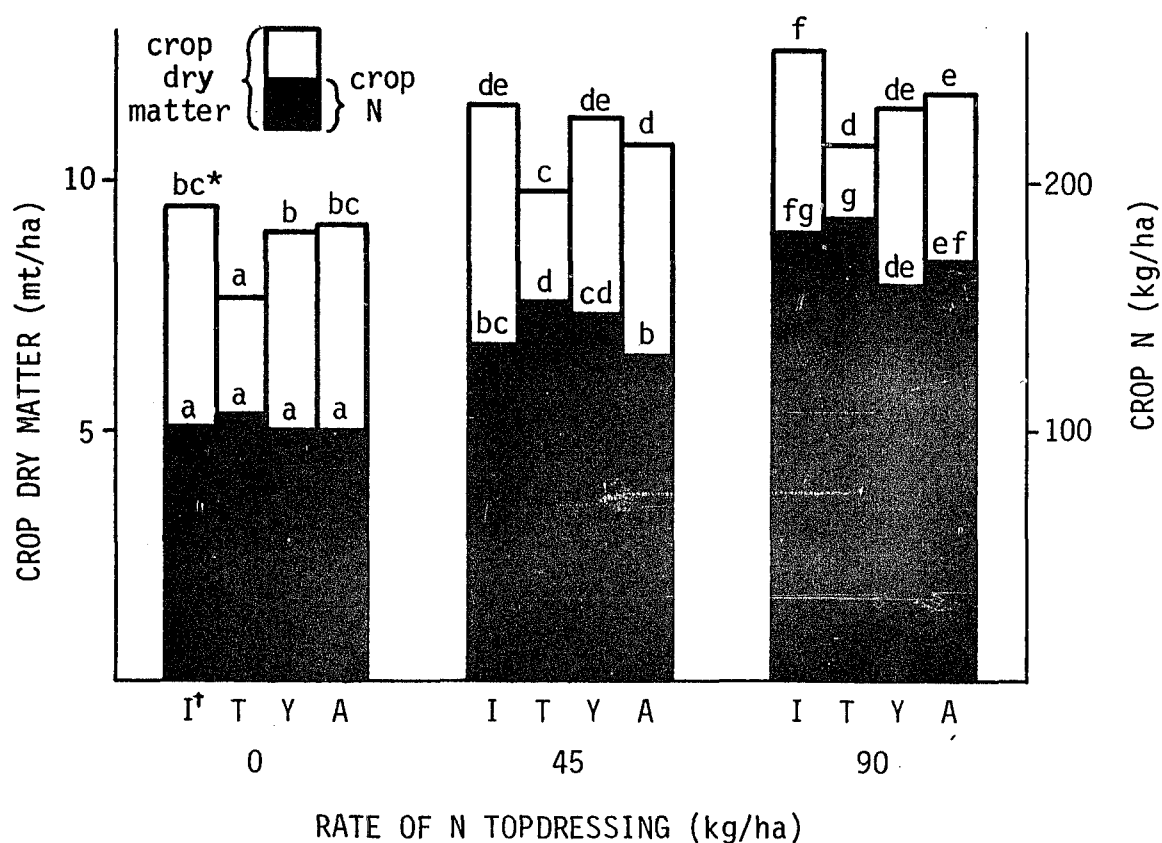


Figure 1.-- Effect of N topdressing on dry matter production and N accumulation in four wheat cultivars, at maturity.

*For a given variable (crop dry matter or crop N), bars topped by the same letter are not significantly different at the 5% level, by Duncan's Multiple Range Test. Data are means of 18 observations, over three locations.

[†]I=Ionia, T=Tecumseh, Y=Yorkstar, A=Augusta.

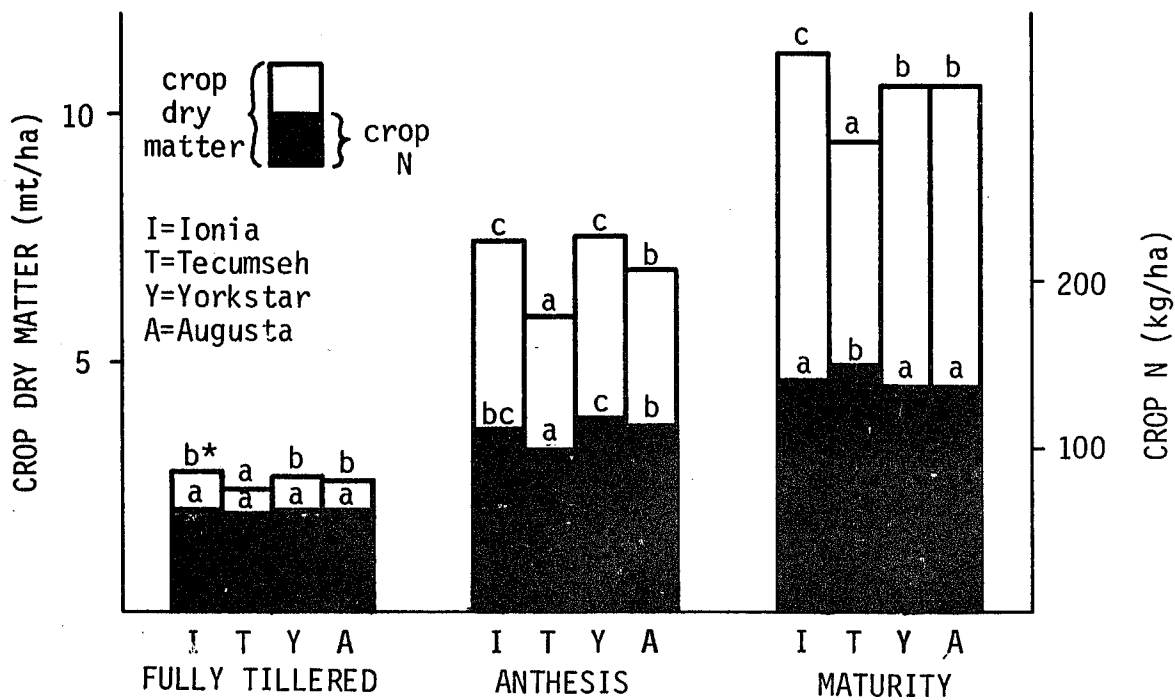


Figure 2.-- Dry matter production and N accumulation over three growth stages, for four wheat cultivars.

*Within growth stages, bars topped by the same letter are not significantly different at the 5% level, by Duncan's Multiple Range Test. Data are means of 18 observations, over three locations and three rates of N topdressing.

The highest-yielding cultivars were Augusta and Yorkstar; however, it is seen in Figures 1 and 2 that these cultivars were no higher in N accumulation per hectare than the lower-yielding cultivars Ionia and Tecumseh. Thus, it seems that the breeding of higher-yielding cultivars does not require genetic advance in capacity for N uptake. However, these higher-yielding cultivars were lower in grain percent protein (see below).

Several features of seasonal accumulation and straw-grain partitioning of N for these four cultivars, are presented in Table 2. Tecumseh accumulated approximately twice as much N after anthesis as did the other cultivars. This late-season surge of N uptake caused Tecumseh to have the highest total seasonal accumulation of N at maturity (Figure 2, maturity stage). In an experiment with late-season foliar and/or soil N supplements, Tecumseh also showed a high capacity for late N

Table 2.-- Pre- and post-anthesis accumulation of N, and grain-straw partitioning of N, for four wheat cultivars.

	N accumulated by crop:		Vegetative $\Delta N^{\dagger}$	Grain N	N harvest index ‡
	pre- anthesis	post- anthesis			
	kg/ha				
Ionia	111	42	-60	102	0.70 b*
Tecumseh	98	70	-30	100	0.63 a
Yorkstar	117	32	-62	95	0.67 ab
Augusta	108	40	-60	100	0.70 b

*Means followed by the same letter are not significantly different at the 5% level, by Duncan's Multiple Range Test. All data are means based on 54 observations, over two locations and three rates of N topdressing.

[†]Net change in N content of non-grain portion of crop after anthesis.

[‡]N in grain (kg/ha) divided by total crop N (kg/ha).

uptake (Appendix B). Despite being the highest in total seasonal N accumulation, Tecumseh accumulated no more N in the grain portion of the crop, than the other cultivars (Table 2). This was a result of a lower net translocation of N from the vegetative plant parts into the grain, for this cultivar. Tecumseh's low efficiency of translocation is reflected in a low N harvest index. Thus, Tecumseh's high capacity for N uptake is negated (in terms of grain protein production per hectare) by a compensating inefficiency in its capacity to translocate N into the grain portion of the crop.

The relationship between grain protein production and yield for the four cultivars, is illustrated in Table 3. The cultivars accumulated remarkably similar amounts of N in the grain portion of the crop, per hectare. However, they differed in grain yield. Thus, differences in grain percent protein among cultivars was primarily a result of differences in carbohydrate accumulation per hectare, rather than in

Table 3.-- Relationship between grain N and yield for four wheat cultivars.

Cultivar	Grain N	Grain yield	Grain protein [†]
	kg/ha	q/ha	%
Augusta	88 b*	44.7 d	9.8 a
Yorkstar	84 a	42.9 c	9.9 a
Ionia	88 b	40.8 b	10.8 b
Tecumseh	88 b	36.7 a	12.1 c

*Means within a column followed by different letters are significantly different at the 5% level, by Duncan's Multiple Range Test. Data are means of 54 observations, over three locations and three rates of N topdressing.

[†]Adjusted to 14% moisture.

N accumulation. This conclusion was reached in a study of oat cultivars differing in groat percent protein, as well (11). Using the data of Table 3, the correlation between grain percent protein and grain yield is strongly negative ($r = -0.984^*$, $p < 0.05$). This negative correlation fits the trend seen in the literature (see Literature Review).

Data showing the effect of early-season N topdressing on yield, yield components, and harvest index, are averaged over six experiments and presented in Table 4, for two cultivars. Data for the specific location-years can be found in Appendix C. In all six experiments, Tecumseh showed the greatest yield response to N. In five of the experiments, this was associated with the largest increase in the yield component heads/m² (X) for Tecumseh, as compared to the other cultivars. Ionia, on the other hand, had the largest response of all cultivars for the yield component seeds/head (Y), in three of the six experiments. Seed weight (Z) was relatively unaffected by N topdressing. Thus, the two cultivars have different strategies of N response: Tecumseh is more X responsive (and most yield-responsive), while Ionia is more Y-responsive. Augusta and Yorkstar seem to have more "balanced" responses than these two.

The association between high head-number (X) responsiveness and high yield responsiveness to N for Tecumseh, fits a trend in the literature (see Literature Review). Why should X-responsiveness be more important than Y-responsiveness, as a mechanism for high yield responsiveness to N? Three possible reasons are offered below.

First, the ontogeny of yield component development is in the order X, Y, Z. Since N is usually applied early in the season, N supply is optimal for stimulating an increase in X. The Y component response must

Table 4.-- Effect of N topdressing on yield variables of two wheat cultivars.

Variable	Cultivar	Topdressing rate, kg/ha		LSD* 0.05	response to topdressing %
		0	90		
Yield, q/ha	Ionia	33.1	42.4	1.6	28
	Tecumseh	27.3	38.8		42
Heads/m ²	Ionia	304	349	24	15
	Tecumseh	388	494		27
Seeds/head	Ionia	26.2	29.7	1.4	13
	Tecumseh	21.2	23.0		8
Seed wt, mg	Ionia	44.4	44.2	0.51	0
	Tecumseh	35.7	35.8		0
Harvest Index	Ionia	0.368	0.379	0.008	3
	Tecumseh	0.372	0.390		5

*Least significant difference for comparison of individual means. Data are means of 60 observations, over three years and three locations.

utilize what little N may be remaining, or what can be mobilized from the tiller vegetative tissues. Hence, N supply is more restricted to the developing spike, than it is to the tiller.

A second reason is that Y is restricted by developmental controls. X results from a vegetative process (tillering), while Y results from a reproductive process (spike differentiation). Vegetative processes are primarily controlled by nutrient supply, while reproductive processes (in determinate inflorescences) are controlled by developmental limits, such as photoperiod and temperature. These limits dampen the capacity of Y to respond to increases in the supply of nutrients.

A third reason is the dampening influence of allometry, as described in the Literature Review. N stimulates the development of more distal culms, but because they arise from smaller meristems, they will have smaller spikes, and hence a smaller Y. This reduces the magnitude of the Y response to N.

Table 4 shows that N topdressing did not have a great effect on the harvest index (HI). N caused only a slight (but statistically significant) increase in HI; this increase was similar for both cultivars. Thus, N does not affect the partitioning of dry matter between grain and straw differently for these cultivars. These findings are somewhat at odds with those of Donald and Hamblin (18). They reported that N consistently decreased HI, though slightly. They also found that this decline was less in more N-responsive cultivars. These modern cultivars were less competitive, hence vegetative growth stimulated by N did not create deleterious levels of mutual shading (see Literature Review). Perhaps the different plant types and more ample moisture supply in Michigan create an ecosystem of lower competition, as compared to the situation in Australia. If this is true, the

increased vegetative growth in response to N would not necessarily cause a decline in HI. Increased number of seeds per head (as a result of both increased number of spikelets per head and seeds per spikelet) seem to cause the increase in HI in the Michigan situation (personal observations).

Does Tecumseh respond to increases in site yield potential across a range of production environments, in a fashion similar to its response to N, i.e. by a large X-response? To answer this question, yield and yield-component data were plotted as a function of location mean yield, over the set of test sites used in the MSU wheat breeding program. These data are shown in Figure 3. The values of the dependent variables (yield and its components) are plotted as a percentage of the mean value at a particular location-year. This allows presentation of the data for yield and its components on a single graph. In this figure, deviation of a point above or below the 100% level indicates a value greater or less than that of the "average cultivar", respectively. A regression line slope significantly different from zero indicates "genotype x environment interaction", i.e. that the particular cultivar is responding differently than the average cultivar to increases in site yield potential.

Figure 3 shows the data for Tecumseh; several other cultivars are shown in Appendix D. Tecumseh expressed significant genotype x environment interaction for yield; and this is seen to have been caused by an unusually high X response. The other two yield components behave similarly to those of the average cultivar. No significant genotype x environment interaction was found for the other cultivars (Appendix D). Thus, it is concluded that Tecumseh's high yield response to improvements in site yield potential, like its response to N, is caused by

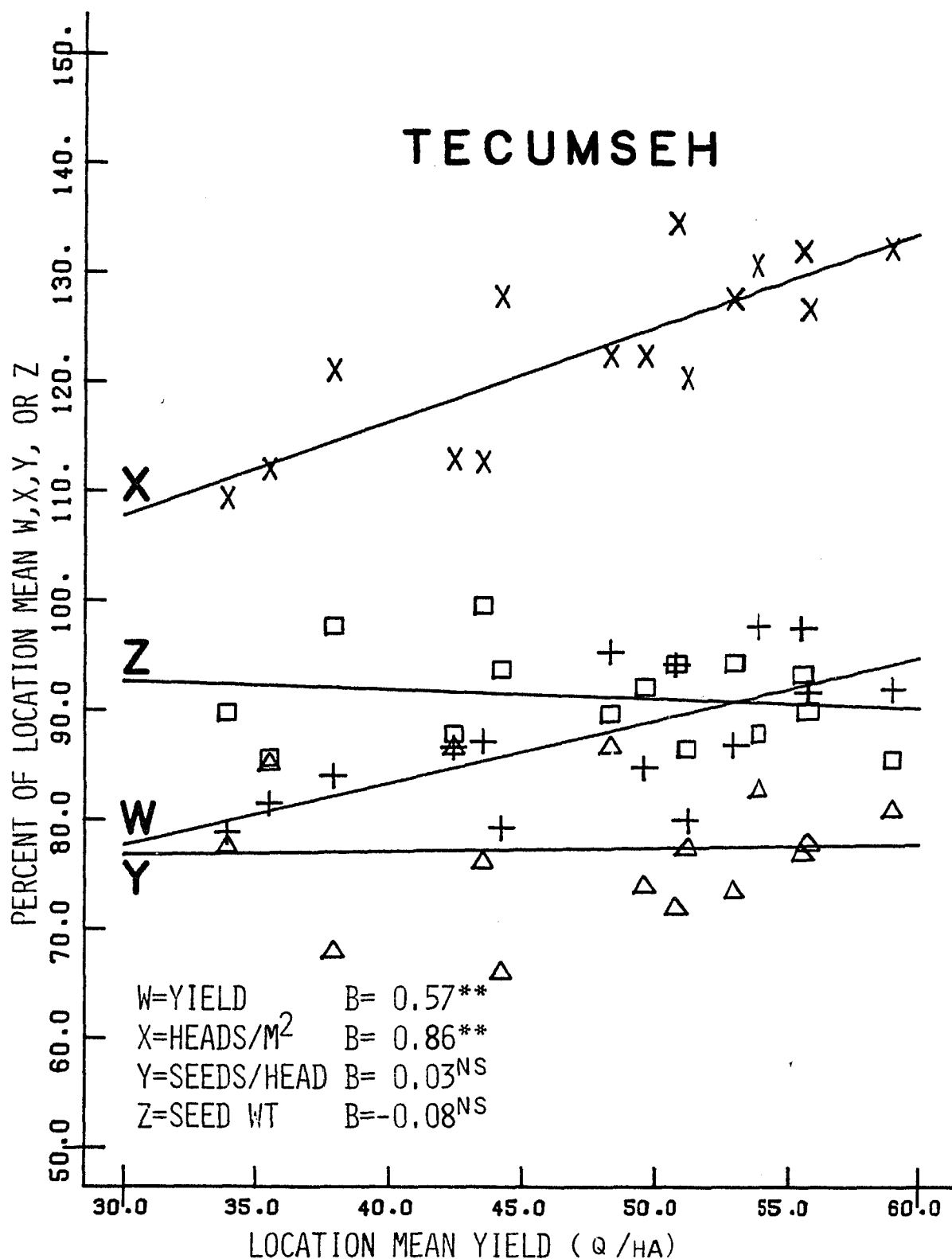


Figure 3.-- Effect of increasing site yield potential on the yield and yield components of Tecumseh wheat, relative to the gene pool mean.

**Slope significantly different from zero at the 1% probability level.

NS= slope not significantly different from zero.

an unusual capacity for X response. Thus, X-responsiveness for Tecumseh seems to be a general growth response to improvements in environmental resource supply, rather than a specific response to N. (The main factors believed to differentiate sites in Michigan with regard to yield potential are moisture supply and temperature).

Since X-responsiveness is important in explaining Tecumseh's high yield responsiveness, experiments were conducted to examine some of the features of yield component response in these cultivars. The effect of varying plant population level on yield and yield components is shown in Figure 4. With increasing seeding rate, X increased dramatically, but a compensating decline in Y (and to a lesser extent Z) kept yield almost constant. Thus, the increase in interplant competition brought about by a sixteen-fold increase in seeding rate causes compensatory adjustments in X and Y, such that Z is almost unaffected. HI was also almost unaffected. This indicates that the proportion of grain to culm dry matter remained constant, despite large declines in the dry weight of both these two components. This is an excellent example of the importance of allometry in crop development. Since both the vegetative and spike portions of the culm arise from the same original apical meristem, reduction in growth of both due to crowding will be highly correlated. The near constancy of HI in the N experiments reported earlier was also a reflection of this growth correlation.

The effect of increasing site yield potential on the yield components of the "average cultivar" (means of 30 entries), for two years, is presented in Figure 5. X and Y fluctuate in a compensatory manner across sites, while Z is almost unaffected. The yield and yield component balances of particular locations change from year to year. For example, Tuscola was the third-lowest yielding site in 1979,

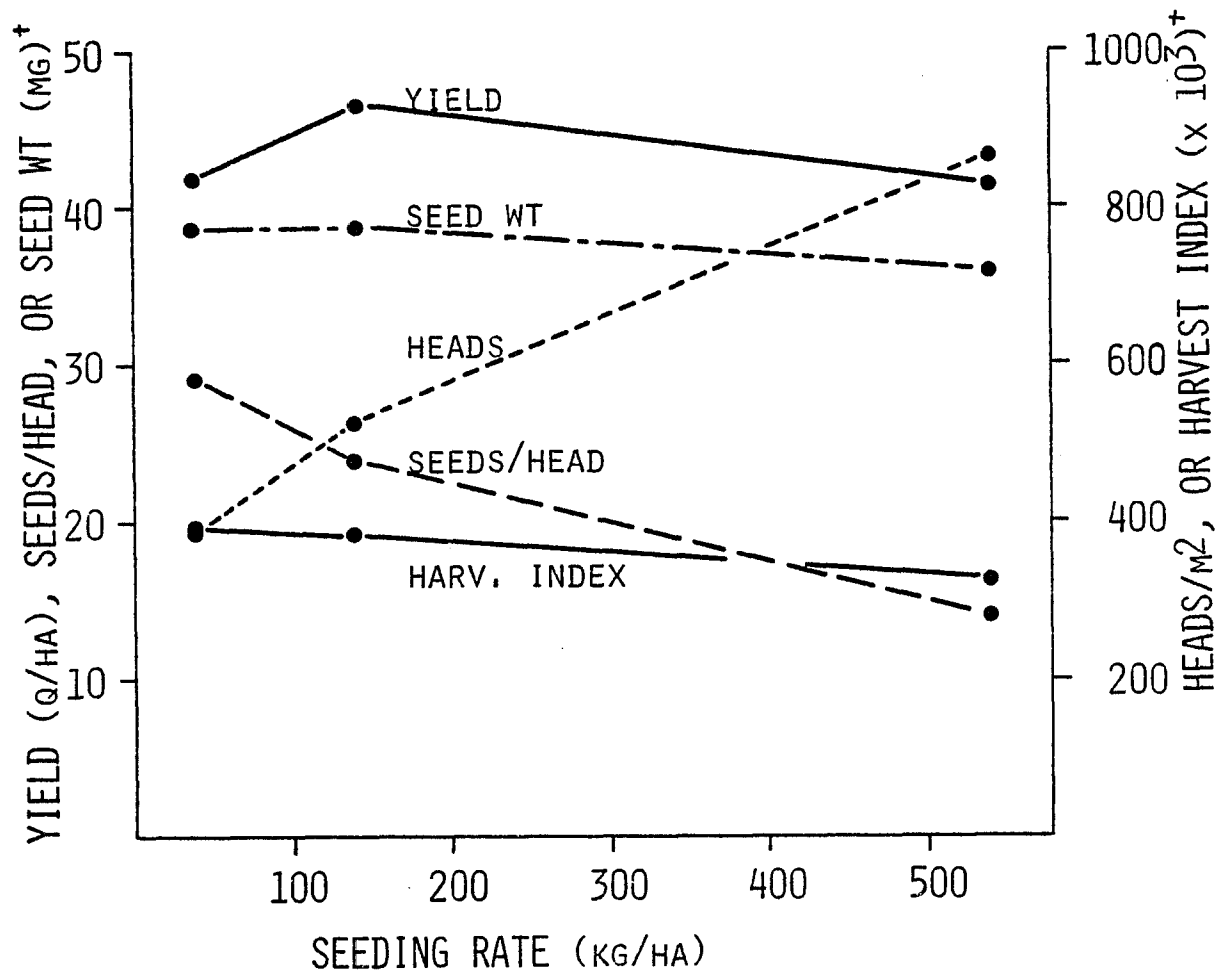


Figure 4.-- Effect of seeding rate on yield variables in wheat. Saranac, 1980.

[†]Means of 24 observations, over three N rates and three cultivars.

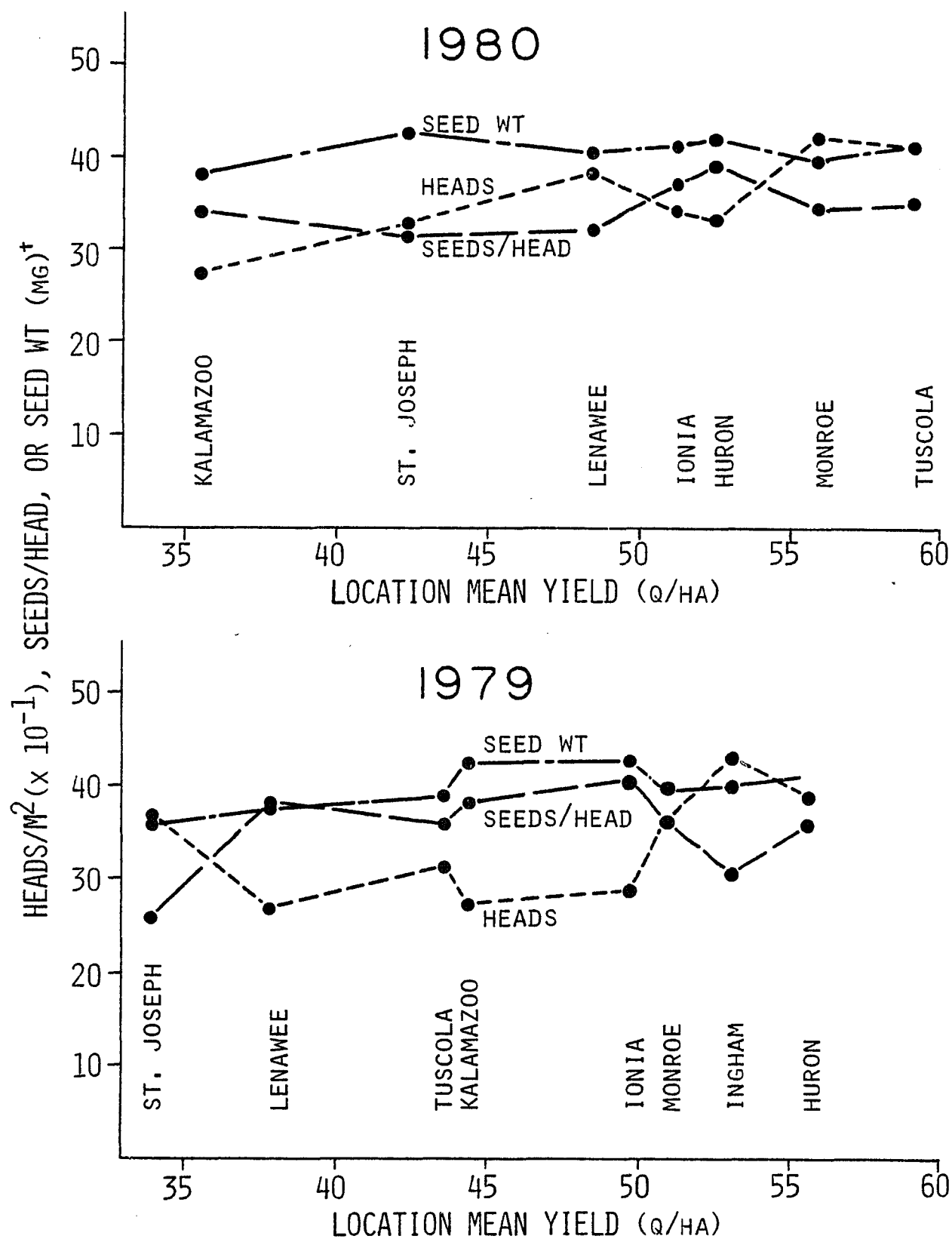


Figure 5.-- Variation of yield components across sites of differing yield potential.

†Means of 90 observations (30 genotypes x 3 replications).

and was characterized by a low X and moderate Y. In 1980, it was the highest-yielding site, with a high X and moderate Y. Lenawee was a low-X, high-Y site in 1979, but it was high-X, low-Y in 1980.

The compensatory fluctuations in X and Y across sites and across years, probably reflect variation in the seasonality of allocation of growth-promoting environmental resources such as moisture and cool temperatures. Since the yield components develop sequentially, seasonal variation in resource allocation will promote the different components differently, depending on how closely the period of ample resource availability coincides with the period of growth of the particular components (1). If resources are available early in the season, X will be promoted; if they are available later, Y will be promoted; if resources are evenly distributed over the season, X and Y will be relatively balanced.

Z is seen to be relatively isolated from component compensation for variation in site yield potential (Figure 5). It was also found to be relatively unaffected by N topdressing (Table 4) and altering the plant population level (Figure 4). Small grains have developed buffering systems to maintain Z at an optimum level (see Literature Review). Thus, variation in this component is not likely to be important in explaining genotype x environment interaction.

Do genotypes with inherently different balances of the yield components differ in their ability to compensate for seasonal fluctuations in resource supply? Grafius (35, 36), Grafius and Okoli (38) and Grafius and Thomas (39) argue that yield component optima exist for different environments, which supports this possibility. An experiment was conducted in which N was supplied at different dates, for Ionia and Tecumseh (Figure 6). Yield response to N was maximum for

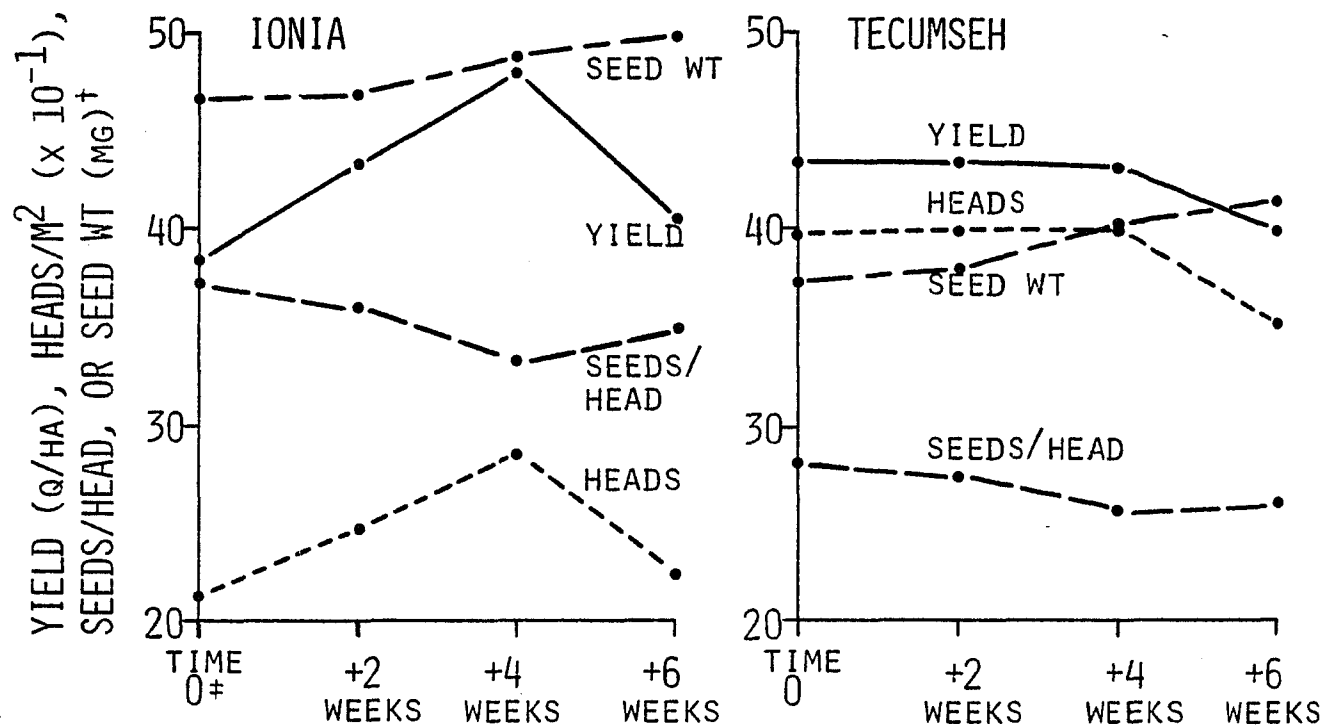


Figure 6.-- Effect of different dates of application of N topdressing on yield and yield components of two wheat cultivars.

†Means of six observations; Saranac, 1979.

‡130 kg/ha N as ammonium nitrate applied at time 0 (beginning of spring regrowth), +2 weeks, +4 weeks (fully tillered stage), or +6 weeks (heading).

Ionia when the N was applied at the fully-tillered stage (four weeks after the beginning of spring regrowth). Application of N at the other dates markedly reduced the response. In contrast, application of N any time in the first four weeks caused an identical yield response, in Tecumseh. These response variations were caused by response variations in X. Y changed less, in compensation for the change in X. Thus, differential X response to date of N application caused differential yield response, in the high-tillering cultivar Tecumseh, as compared to the low-tillering cultivar Ionia.

These differences can be interpreted in terms of the different levels of apical inhibition in low- and high-tillering cultivars, suggested by Aspinall (4) (see Literature Review). The fully-tillered stage is the point of maximum inter-tiller competition, since at this time, older tillers assume apical dominance, inhibiting growth of younger tillers. Any tiller that survives this competitive "bottleneck" has a high probability of surviving to produce seed. Since nutrient supplementation reduces apical inhibition (4), it reduces the amount of inter-tiller competition, and this effect will be maximal if the nutrients are supplied at the time of maximum competition (fully-tillered stage).

If low-tillering cultivars have a greater degree of apical dominance, as Aspinall argued (4), then inter-tiller competition at the fully-tillered stage is probably greater for these types. Aspinall also found that nutrient supplementation released this apical dominance to a greater extent in the low-tillering cultivar, presumably because of the greater degree of dominance that existed before the nutrient treatment. If these conclusions can be extended to the present study, the following explanation of the different responses of Ionia and

Tecumseh to different dates of N application seem plausible.

Early application of N stimulates tillering in Ionia, but because of the higher level of inter-tiller competition, few of these tillers survive through the competitive bottleneck of the fully-tillered stage. Application of N at the fully-tillered stage relieves this competition, allowing many tillers to survive and bear seed, which appears as a large X response. Early application of N stimulates tillering in Tecumseh as well, but since inter-tiller competition is less, the competitive bottleneck of the fully-tillered stage is less restrictive, and a high proportion of these tillers survive to maturity. Thus, the large X response of Tecumseh will occur over a range of dates of N application.

If these hypotheses are true, then the low yield responsiveness of Ionia to N may be an artifact of the early date of application of N commonly used in commercial production. It is more convenient to apply N early in the season, because spring rains may make fieldwork impossible for considerable periods of time. However, these data and conclusions suggest that producers of Ionia wheat may be sacrificing yield with this practice.

The high responsiveness of Tecumseh to N and to improvements in other environmental factors may be a result of the flexibility of its tillering response to seasonal variations in resource supply. Tecumseh can increase X despite differences in the date of maximum resource allocation in different environments. Thus, on the average, it appears to be more responsive to improvements in the environment.

Yield component balance and response may thus be an important factor in explaining genotype x environment interaction. N may serve as a "model" environmental variable which can reveal such interactions.

Yield components are easily measured, and their response to N may simulate their response to environments, especially if date of application is used as an independent variable (along with rate of application). Different dates of application simulate the seasonal variation of resource allocation that occurs in production environments, and hence model an important factor influencing genotype x environment interaction.

SUMMARY AND CONCLUSIONS

1. Tecumseh's high N requirement does not result from a deficiency in capacity for N uptake.
2. Tecumseh accumulates approximately twice as much N after anthesis as several other cultivars, which are more typical of the MSU gene pool.
3. Tecumseh is less efficient in translocating N from vegetative plant parts into the grain, than several other cultivars.
4. Differences in grain percent protein among four cultivars (Ionia, Tecumseh, Yorkstar, and Augusta) are due to differences in carbohydrate accumulation in the grain, rather than N accumulation.
5. Tecumseh's high yield responsiveness to N is caused by a high response of the yield component heads/m² (X).
6. Tecumseh's high yield response to improvements in site yield potential is also caused by a high X response.
7. The seed weight component (Z) is relatively unaffected by fluctuations in the supply of environmental resources. X and Y (seeds/head) adjust in a compensatory fashion to limitations in resource supply.
8. The low-tillering cultivar Ionia is very sensitive to the seasonality of resource allocation. Nutrient supplements applied at the

fully-tillered stage cause a maximum yield response in this cultivar. This observation is interpreted as indicating a high level of inter-tiller competition in this cultivar.

9. The high-tillering cultivar Tecumseh is less sensitive to the seasonality of resource allocation. Nutrient supplements applied at any time up until the fully-tillered stage cause a similar yield response in this cultivar. This observation is interpreted as indicating a low level of inter-tiller competition in this cultivar.
10. The low level of inter-tiller competition in Tecumseh, which allows it to utilize nutrients or other environmental resources across a range of dates, may thus explain the high X-responsiveness of this cultivar, both in terms of response to N and to variations in site yield potential. This low level of inter-tiller competition may thus be the cause of genotype x environment interaction for Tecumseh.

APPENDICES

APPENDIX A

EFFECT OF N TOPDRESSING ON DRY MATTER AND N ACCUMULATION AT THREE GROWTH STAGES, FOR FOUR WHEAT CULTIVARS: DATA FROM SPECIFIC LOCATIONS, IN 1980

APPENDIX A

Table A1.-- Effect of N topdressing on dry matter production and N accumulation at three growth stages in four wheat cultivars, at Mendon.

Variable	Growth stage	Topdressing rate, kg/ha	Cultivar				LSD* 0.05
			Ionia	Tecumseh	Yorkstar	Augusta	
Dry matter, mt/ha	Fully tillered	0	3.84	2.98	3.18	3.53	
		45	3.68	3.03	3.53	3.77	0.57
		90	4.21	3.27	3.95	3.52	
	Anthesis	0	6.81	4.90	6.82	5.96	
		45	6.58	6.17	7.84	7.43	1.19
		90	8.00	6.37	7.43	7.50	
	Maturity	0	7.79	6.67	7.86	7.96	
		45	9.18	7.98	9.38	9.44	0.94
		90	10.3	8.56	10.6	10.1	
N accumulated, kg/ha	Fully tillered	0	52.9	43.4	46.0	49.0	
		45	53.8	50.2	59.7	57.6	10
		90	75.0	61.0	65.6	62.5	
	Anthesis	0	69.5	55.3	75.8	62.3	
		45	72.3	79.5	97.6	90.9	18
		90	111	91.0	98.1	110	
	Maturity	0	65.2	57.6	58.9	66.1	
		45	70.7	96.1	89.9	78.9	16
		90	104	107	91.7	101	

*Least significant difference for comparison of individual means. Data are means of six observations.

APPENDIX A

Table A2.-- Effect of N topdressing on dry matter production and N accumulation at three growth stages in four wheat cultivars, at East Lansing.

Variable	Growth stage	Topdressing rate, kg/ha	Cultivar				LSD* 0.05
			Ionia	Tecumseh	Yorkstar	Augusta	
Dry matter, mt/ha	Fully tillered	0	1.78	1.60	1.87	1.61	0.39
		45	1.76	1.79	1.94	1.97	
		90	1.96	1.74	1.76	1.76	
	Anthesis	0	5.60	4.16	5.74	5.96	1.4
		45	8.63	5.45	8.67	6.51	
		90	9.22	6.89	8.23	7.82	
	Maturity	0	7.58	6.64	7.88	7.66	1.2
		45	11.2	10.1	12.0	11.0	
		90	13.1	11.8	12.0	12.7	
N accumulated, kg/ha	Fully tillered	0	30.4	28.9	33.4	29.0	10
		45	46.7	53.4	60.3	52.4	
		90	61.7	61.0	55.3	62.8	
	Anthesis	0	62.3	52.4	64.2	66.6	29
		45	120	86.0	141	89.6	
		90	160	147	144	163	
	Maturity	0	94.3	98.0	92.0	91.4	26
		45	133	147	170	139	
		90	193	212	172	210	

*Least significant difference for comparison of individual means. Data are means of six observations.

APPENDIX A

Table A3.-- Effect of N topdressing on dry matter production and N accumulation at three growth stages in four wheat cultivars, at Saranac.

Variable	Growth stage	Topdressing rate, kg/ha	Cultivar				LSD* 0.05
			Ionia	Tecumseh	Yorkstar	Augusta	
Dry matter, mt/ha	Fully tillered	0	3.07	2.55	3.21	2.86	
		45	2.69	2.76	2.64	2.62	0.61
		90	2.89	2.76	2.66	2.78	
	Anthesis	0	6.17	4.79	7.16	5.94	
		45	8.16	7.19	8.40	6.85	1.4
		90	8.14	7.53	7.82	8.22	
	Maturity	0	12.9	10.1	11.2	11.8	
		45	14.2	11.4	12.3	11.9	1.4
		90	14.5	12.1	12.0	12.6	
N accumulated, kg/ha	Fully tillered	0	55.0	52.0	62.5	57.7	
		45	85.0	84.7	82.8	83.1	16
		90	96.4	97.2	95.1	96.1	
	Anthesis	0	74.8	68.5	94.3	75.9	
		45	148	126	144	129	10
		90	182	178	194	187	
	Maturity	0	144	164	147	140	
		45	199	214	182	174	27
		90	240	240	210	197	

*Least significant difference for comparison of individual means. Data are means of six observations.

APPENDIX B

EFFECT OF LATE-SEASON N SUPPLEMENTS ON GRAIN N AND YIELD VARIABLES OF
THREE WHEAT CULTIVARS

APPENDIX B

Cultivar differences in capacity to accumulate N late in the season were investigated in an experiment testing the effect of late-season foliar and/or soil N applications on N accumulation in the grain (Table B1). Both soil and foliar N treatments increased N accumulation in the grain, although the effect was greater for the soil treatment. The foliar treatment caused a slight amount of leaf burn, resulting in reduced seed weight and lowered yields. The increase in grain percent protein following foliar N application was thus partially a result of lower carbohydrate accumulation in the grain portion of the crop. N accumulation in the grain following the combined soil and foliar treatments was less than that following soil treatment alone, suggesting that foliar damage reduced the crop's ability to take up N from the soil. This supports the findings of Mikesell and Paulsen (70) and Neales et. al. (73) that the leaves are important in uptake of soil N.

Tecumseh showed the greatest increase in N accumulation (difference between treated and untreated plots) for both the soil and foliar treatments, although cultivar differences were not significant. Augusta showed very little increase in N accumulation from either treatment.

APPENDIX B

Table B1.-- Effect of late-season foliar and soil N applications on grain N and yield variables of three wheat cultivars. Saranac, 1980.

Parameter	Cultivar	N treatment [†]				LSD 0.05
		none	soil	foliar	soil + foliar	
N accumulated in the grain, kg/ha	Ionia	92	120	95	114	
	Tecumseh	85	116	98	112	11
	Augusta	93	110	93	112	
Grain percent protein [*]	Ionia	10.8	14.4	12.2	14.4	
	Tecumseh	12.2	14.9	13.8	15.2	0.57
	Augusta	9.6	11.5	11.6	12.3	
Seed weight, mg	Averaged over cultivars	41.1	41.5	39.2	39.8	1.1
Grain yield, kg/ha	Averaged over cultivars	44.0	44.4	39.7	42.3	2.5

[†]Soil treatment: 90 kg/ha N as ammonium nitrate sidedressed at anthesis.
Foliar treatment: approximately 170 kg/ha N applied as a foliar spray
(12% urea solution) four days after anthesis.

^{*}Adjusted to 14% moisture.

APPENDIX C

EFFECT OF N TOPDRESSING ON YIELD VARIABLES OF SEVERAL WHEAT CULTIVARS:
DATA FROM SPECIFIC LOCATION-YEARS

APPENDIX C

Table C1.-- Effect of N topdressing on yield variables of two wheat cultivars. Saranac, 1978, experiment 1.

Variable	Cultivar	Topdressing rate, kg/ha		LSD* 0.05	response to topdressing %
		0	90		
Yield, q/ha	Ionia	31.7	35.0	3.1	10
	Tecumseh	23.6	26.9		14
Heads/m ²	Ionia	238	229	35	-4
	Tecumseh	243	291		20
Seeds/head	Ionia	31.5	36.2	3.5	15
	Tecumseh	26.7	26.5		-1
Seed wt, mg	Ionia	41.1	40.9	1.1	-1
	Tecumseh	35.1	34.3		-2
Harvest Index	Ionia	0.395	0.401	0.011	2
	Tecumseh	0.369	0.377		2

*Least significant difference for comparison of individual means. Data are means of 24 observations.

APPENDIX C

Table C2.-- Effect of N topdressing on yield variables of four wheat cultivars. Saranac, 1978, experiment 2.

Variable	Cultivar	Topdressing rate, kg/ha		LSD* 0.05	response to topdressing
		0	90		
					%
Yield, q/ha	Ionia	22.2	30.3		36
	Tecumseh	21.6	33.6	4.4	56
	Yorkstar	24.1	32.1		33
	Frankenmuth	28.2	37.2		32
Heads/m ²	Ionia	170	201		18
	Tecumseh	242	333	60	38
	Yorkstar	211	263		25
	Frankenmuth	241	286		19
Seeds/head	Ionia	30.9	36.6		19
	Tecumseh	25.9	28.3	4.6	9
	Yorkstar	32.7	35.8		10
	Frankenmuth	33.0	35.0		6
Seed wt, mg	Ionia	41.8	41.1		-2
	Tecumseh	34.0	35.2	1.2	4
	Yorkstar	34.9	32.2		-8
	Frankenmuth	36.0	34.4		-4

*Least significant difference for comparison of individual means. Data are means of nine observations.

APPENDIX C

Table C3.-- Effect of N topdressing on yield variables of three wheat cultivars. Saranac, 1979.

Variable	Cultivar	Topdressing rate, kg/ha		LSD* 0.05	response to topdressing %
		0	90		
Yield, q/ha	Ionia	45.0	48.6		8
	Tecumseh	32.3	45.0	5.0	39
	Yorkstar	42.4	48.0		13
Heads/m ²	Ionia	255	265		4
	Tecumseh	312	419	39	34
	Yorkstar	238	288		21
Seeds/head	Ionia	35.7	37.4		5
	Tecumseh	24.0	25.8	2.1	7
	Yorkstar	39.9	38.6		-3
Seed wt, mg	Ionia	47.7	47.2		-1
	Tecumseh	42.0	40.0	1.4	-5
	Yorkstar	43.0	41.8		-3

*Least significant difference for comparison of individual means. Data are means of nine observations.

APPENDIX C

Table C4.-- Effect of N topdressing on yield variables of four wheat cultivars. Mendon, 1980.

Variable	Cultivar	Topdressing rate, kg/ha		LSD* 0.05	response to topdressing
		0	90		
					%
Yield, q/ha	Ionia	26.0	36.4	2.5	40
	Tecumseh	23.8	34.5		45
	Yorkstar	29.4	41.5		41
	Augusta	29.5	42.6		44
Heads/m ²	Ionia	288	343	64	19
	Tecumseh	498	529		6
	Yorkstar	331	387		17
	Augusta	421	424		1
Seeds/head	Ionia	21.4	23.0	3.0	7
	Tecumseh	14.1	18.1		28
	Yorkstar	22.6	25.5		8
	Augusta	18.3	24.6		34
Seed wt, mg	Ionia	43.1	46.2	0.87	8
	Tecumseh	34.9	36.8		5
	Yorkstar	40.1	42.1		5
	Augusta	39.3	41.1		5
Harvest Index	Ionia	0.335	0.353	0.024	5
	Tecumseh	0.359	0.403		12
	Yorkstar	0.378	0.394		4
	Augusta	0.373	0.422		13

*Least significant difference for comparison of individual means. Data are means of six observations.

APPENDIX C

Table C5.-- Effect of N topdressing on yield variables of four wheat cultivars. East Lansing, 1980.

Variable	Cultivar	Topdressing rate, kg/ha		LSD* 0.05	response to topdressing
		0	90		
					%
Yield, q/ha	Ionia	30.2	53.5	4.3	77
	Tecumseh	26.5	47.5		79
	Yorkstar	33.7	51.3		52
	Augusta	33.2	56.4		70
Heads/m ²	Ionia	355	533	95	50
	Tecumseh	420	680		62
	Yorkstar	382	546		43
	Augusta	389	556		43
Seeds/head	Ionia	19.3	22.9	3.8	19
	Tecumseh	19.6	20.1		3
	Yorkstar	382	546		43
	Augusta	21.8	26.4		21
Seed wt, mg	Ionia	45.1	44.6	1.4	-1
	Tecumseh	32.9	35.2		7
	Yorkstar	39.0	38.6		-1
	Augusta	39.6	38.8		-2
Harvest Index	Ionia	0.398	0.408	0.016	3
	Tecumseh	0.399	0.405		2
	Yorkstar	0.428	0.430		0
	Augusta	0.433	0.443		2

*Least significant difference for comparison of individual means. Data are means of six observations.

APPENDIX C

Table C6.-- Effect of N topdressing on yield variables of four wheat cultivars. Saranac, 1980.

Variable	Cultivar	Topdressing rate, kg/ha		LSD* 0.05	response to topdressing
		0	90		
					%
Yield, q/ha	Ionia	43.7	50.8	4.3	16
	Tecumseh	35.9	45.4		26
	Yorkstar	44.9	46.2		3
	Augusta	49.3	51.8		5
Heads/m ²	Ionia	519	520	96	0
	Tecumseh	610	710		16
	Yorkstar	471	509		8
	Augusta	452	513		13
Seeds/head	Ionia	18.2	22.3	3.4	23
	Tecumseh	16.9	19.2		14
	Yorkstar	25.1	25.3		1
	Augusta	27.5	28.0		2
Seed wt, mg	Ionia	47.5	45.1	1.8	-5
	Tecumseh	35.3	33.4		-5
	Yorkstar	39.8	36.0		-10
	Augusta	40.4	36.7		-9
Harvest Index	Ionia	0.342	0.352	0.026	3
	Tecumseh	0.360	0.373		4
	Yorkstar	0.403	0.387		-4
	Augusta	0.419	0.414		-1

*Least significant difference for comparison of individual means. Data are means of six observations.

APPENDIX D

EFFECT OF INCREASING SITE YIELD POTENTIAL ON THE YIELD AND YIELD
COMPONENTS OF SEVERAL WHEAT CULTIVARS

APPENDIX D

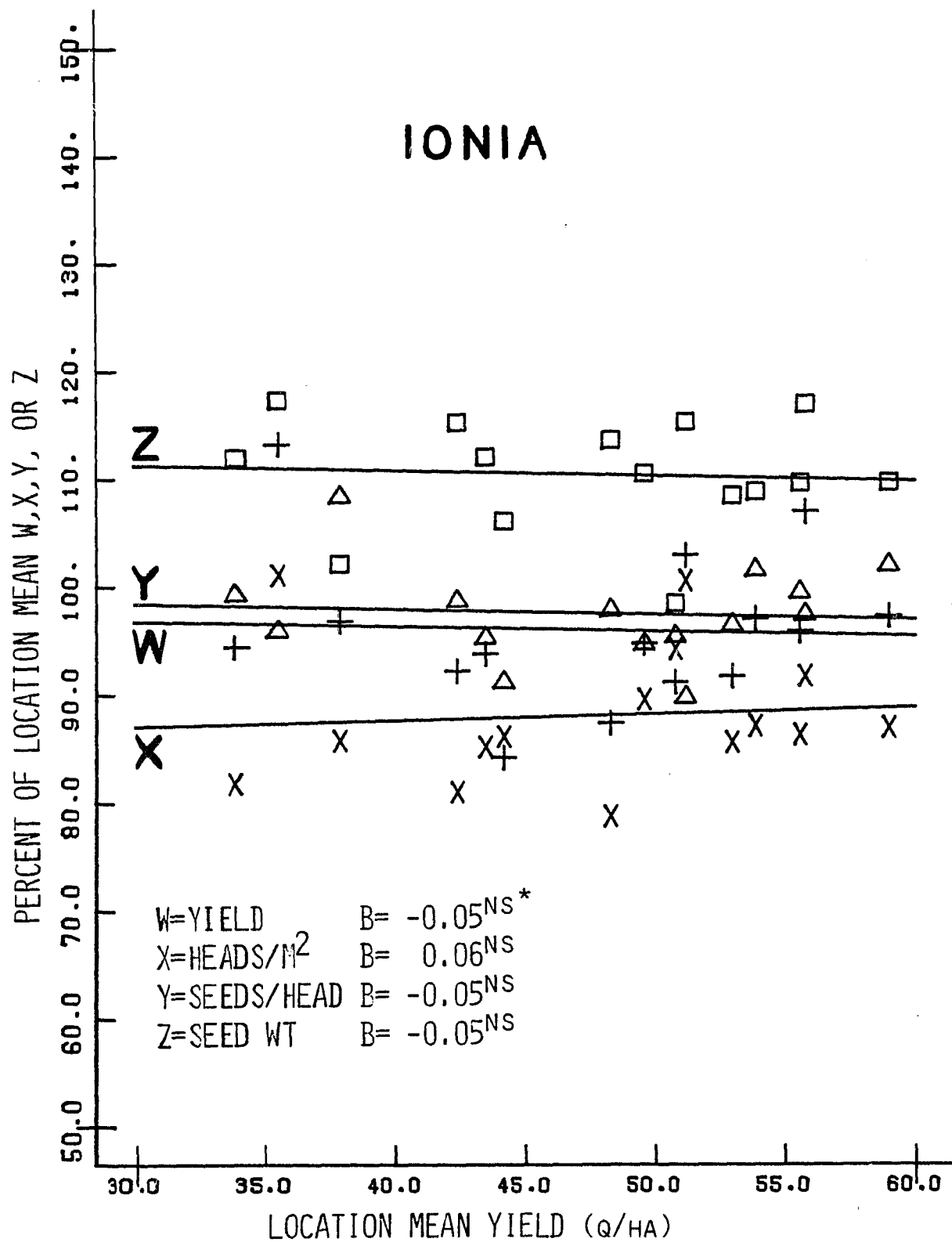


Figure D1.-- Effect of increasing site yield potential on the yield and yield components of Ionia wheat, relative to the gene pool mean.

*NS= slope not significantly different from zero.

APPENDIX D

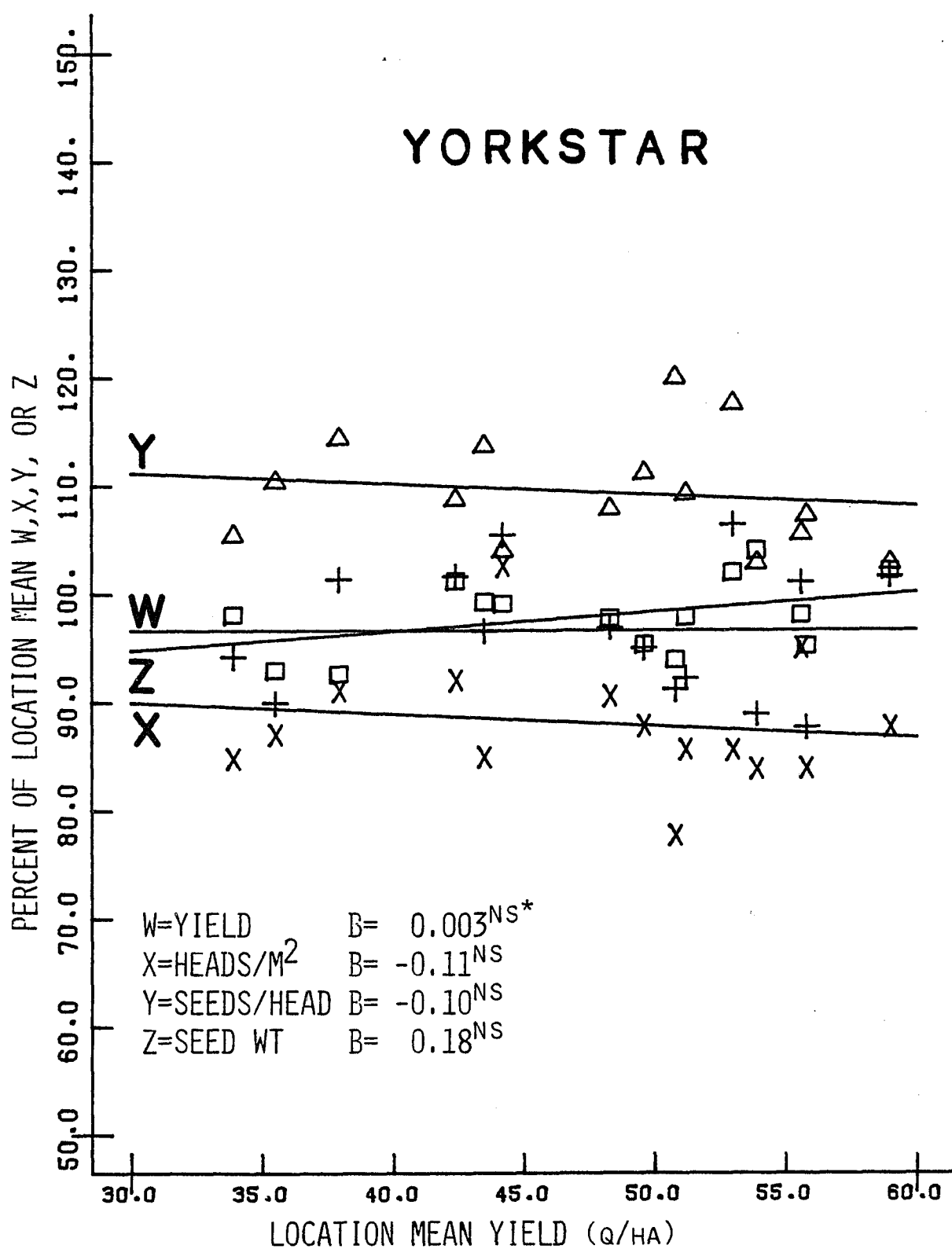


Figure D2.-- Effect of increasing site yield potential on the yield and yield components of Yorkstar wheat, relative to the gene pool mean.

*NS= slope not significantly different from zero.

APPENDIX D

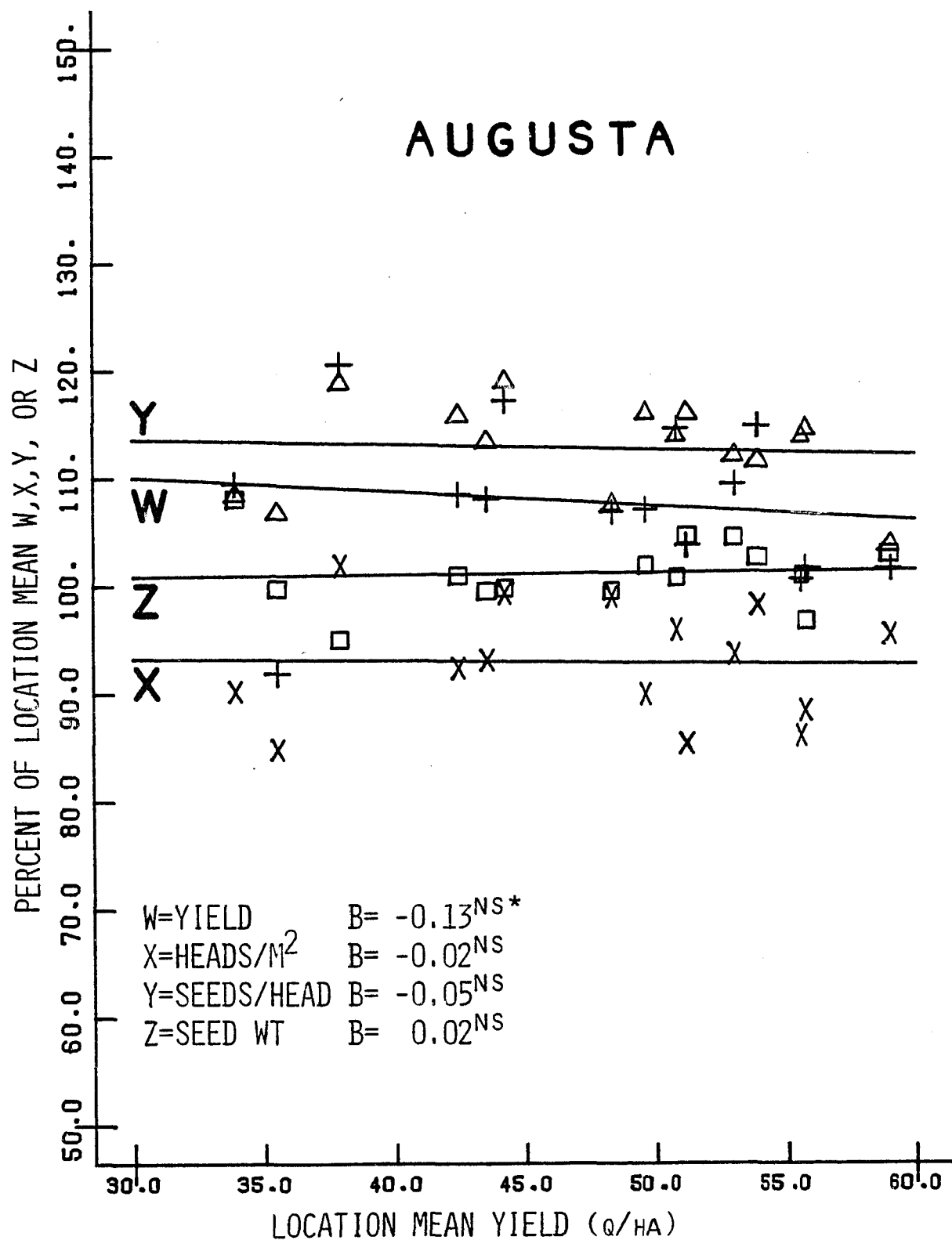


Figure D3.-- Effect of increasing site yield potential on the yield and yield components of Augusta wheat, relative to the gene pool mean.

*NS= slope not significantly different from zero.

APPENDIX D

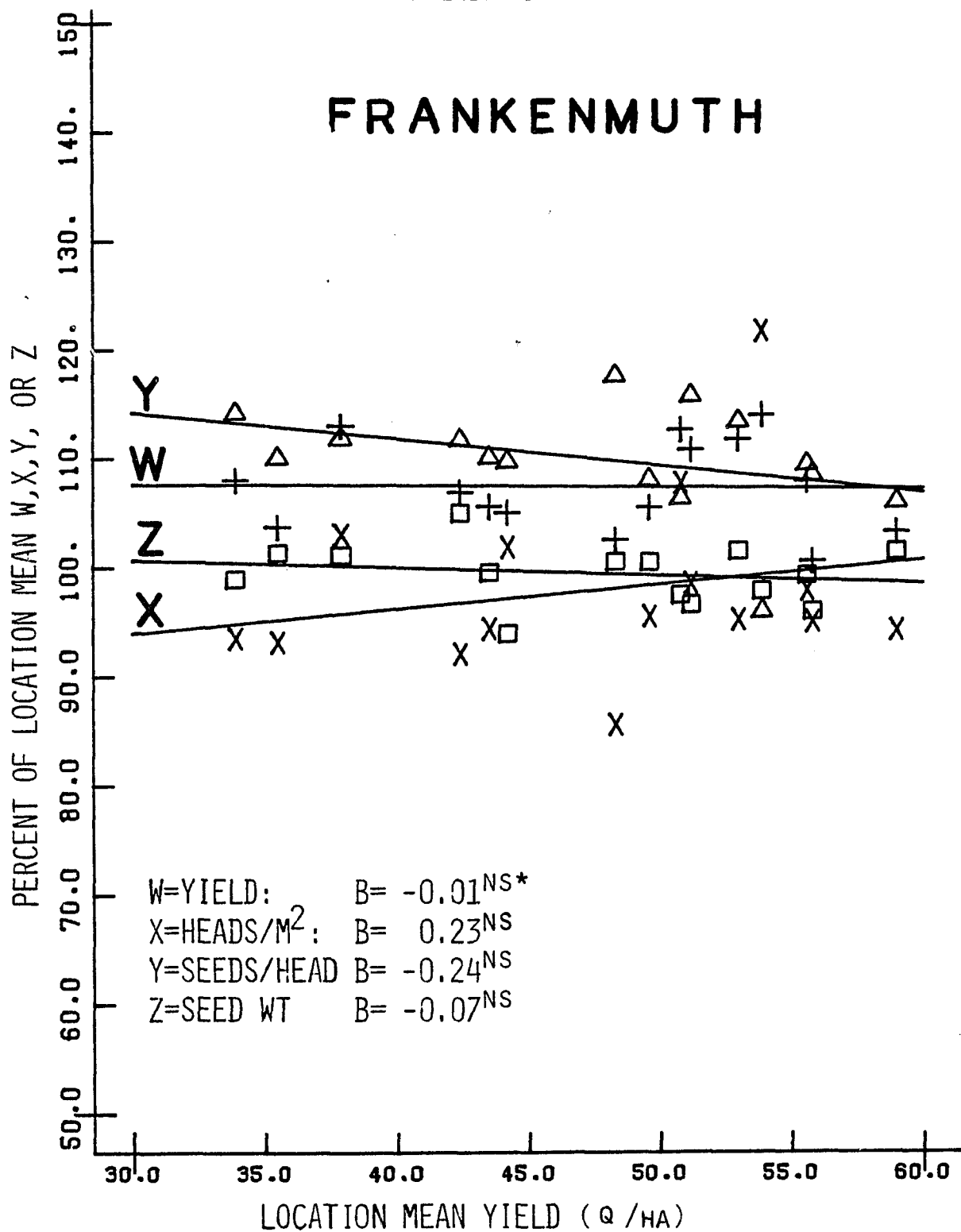


Figure D4.-- Effect of increasing site yield potential on the yield and yield components of Frankenmuth wheat, relative to the gene pool mean.

*NS= slope not significantly different from zero.

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