DEVELOPMENT ALLOMETRY AND ITS IMPLICATION TO GRAIN YIELD IN BARLEY (HORDEUM VULGARE, L. EMEND. LAM.)

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ABSTRACT

DEVELOPMENTAL ALLOMETRY AND ITS IMPLICATION TO GRAIN YIELD IN BARLEY (HORDEUM VULGARE, L. EMEND. LAM.)

By

Zakri A. Hamid

Plant growth and development evolved around an integrated system which is dynamic throughout its entire ontogeny. Each organ is sequentially developed and although each may be affected by unique environmental stresses and different gene systems, the phenotypic expression of each of the plant organs is closely correlated. This relationship is essentially brought about by the nature of the apical meristem in higher plants, a role which has been explicitly defined by Sinnott (1921): "The size of any given organ depends upon the size of the growing point out of which it has been developed."

Evidence is presented to show that earlier developed organs have a profound influence on later formed structures. In the small grains, the proliferation of tillers is one of the first developmental processes at the organ level. There is a negative relationship between the number of tillers laid down by the plant and the size of the individual meristem on each tiller (size of the meristem is inferred from the size of the various organs that originate from it). The higher the number of tillers per unit area, the smaller would be the size of the culm diameter of each tiller, the average leaf area and the size of the head. In addition, highly significant correlations are observed between organs arising from a common meristem.

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The morphogenesis of organs within the plant is transcended by a need for balance among these structures, a condition largely brought about by a limiting external environment. This phenomenon is termed "developmental allometry."

The influence of developmental allometry confounds the already complex nature of plant growth and development. For instance, the data involving the leaf and culm characteristics of the five groups of crosses and backcrosses sampled at their F_7 or BS_6 generations did not follow a predictable pattern and appeared to be determined at random. One would have expected the value of the straight cross to be intermediate between the two complementary backcrosses but this was not the general case. Developmental allometry interferes with the effect of a genetic system per se thus resulting in the failure of prediction.

The culm diameter and the leaf area are not significantly associated with grain yield, although they may be strongly correlated with one or more of the three components of yield. The effect, if any, of either culm diameter or leaf area on grain yield is indirectly channeled via its interaction with the components of yield. Leaves and culms form an integral part of a cereal plant and their roles are obvious in the normal functioning of a crop stand. However, the results of this study imply that the photosynthetic surface and stem size are not the direct causative factors that determine the variation in grain yield found in the progeny populations.

With this gene pool and in this particular growing environment, the size and number of the appropriate components of W may be more critical than the size or number of the photosynthetic surfaces in causing differences in W among genotypes.

DEVELOPMENT ALLOMETRY AND ITS IMPLICATION TO GRAIN YIELD IN BARLEY (*HORDEUM VULGARE*, L. EMEND. LAM.)

By

Zakri A. Hamid

A DISSERTATION

Submitted to

Michigan State University
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To

Sandy and family

and

Mami and Bapi

"oats, peas, beans and barley grow

oats, peas, beans and barley grow

can you or I or anyone know

how oats, peas, beans and barley grow"

Anon

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INTRODUCTION

Much of the improvement of crop productivity through plant breeding has been realized by induction and deduction from empirical data. Emphasis on elucidation of the underlying physiological processes associated with the expression of crop yield is of rather recent origin. Over the years steady progress has been made. Such advances as have occurred have been achieved not so much from the application of fundamental concepts of plant growth and development as from the astute application of principles derived through painstaking methods of trial and error. For the most part, gains in crop improvement were made with very little assistance from basic botany. A vast amount of information has accumulated on the physicochemical processes of growth and differentiation in plants but the approaches for exploiting this store of knowledge towards the betterment of crop plants, notably the maximization of economic yield, has been frustratingly slow.

Today there is an increasing awareness that future gains in crop productivity, especially for crops that may already have reached their yield plateau, must rest on broader foundations. Plant scientists, especially breeders, physiologists and biochemists need to pool their talents in identifying those processes and characteristics that could be utilized in the engineering of a plant genotype with ideal yield potential (Brown et al., 1976; Wittwer, 1974; Wallace, Ozbun and Munger, 1972; Donald, 1968; Hageman, Leng and Dudley, 1967).

The relationship of variation in grain yield on one hand and any one physiological process in the plant on the other, for example photosynthetic efficiency, has not been fully established. Since grain yield is comprised mainly of carbon derivatives synthesized during photosynthesis, it would be intuitively logical to expect that higher rates of photosynthesis would result in better manifestation of crop yield. But to date there has been very meager experimental evidence that purports to show a direct association between photosynthetic efficiency and differences between cultivars in grain yield.

The well adapted cultivar is a stable organism. The multitude of the biochemical and physiological processes essential to the normal functioning of the plant system may already have been well integrated such that a state of homeostasis exists. It is a futile effort, in most cases, to try to isolate any one particular process or organelle from its _in situ_ condition and attempt to extrapolate the significance of its performance in relation to grain yield. What is observable _in vitro_ need not reflect the true "behavior" of the process in its natural intra-plant environment.

Plant growth and development evolved around an integrated system which is dynamic throughout its entire ontogeny. Each organ is sequentially developed and recent studies (Thomas _et al_., 1971 a, b, c; Grafius and Thomas, 1971), along with the data to be presented in this thesis, show that the earlier developed organs have a profound influence on later formed structures. The fate of each of these organs is intertwined even though each may be affected by different environmental stresses and by different gene systems. This common destiny is brought about by the allometric constraints set by the plant. The seat of this apparent control resides in the unique nature of higher plants where new cell pr

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production is restricted to the meristems.

The primordia of organs evolve from meristems and the central role of this embryonic structure has been explicitly pointed out as early as 1921 by Sinnott when he wrote, "The size of any given organ depends upon the size of the growing point out of which it has been developed." The preceding quotation is really an understatement of a general biological law on the nature of developmental relationships among plant organs in terms of size and number. The morphogenesis of organs within the plant is transcended by a need for balance among these structures, a condition largely brought about by a limiting external environment. This phenomenon is termed 'developmental allometry'. Sinnott's Law defines the constraints that each organ is restricted by in order that the developmental stability of the plant is not disrupted.

The influence of developmental allometry confounds the already complex nature of plant growth and development. Consequently when we address ourselves to the question of breeding for yield, it is imperative that we restrict our attention to the immediate crux of the problem until plant morphogenesis can be elucidated in very definite physicochemical terms.

Grain yield (W) in barley is a complex trait. Its morphological expression can best be understood through the analysis of its components, namely the number of fertile tillers (heads) per unit area (X), the number of kernels per head (Y) and the average kernel weight (Z). Genetic control of W is indirectly channeled via its components, with the earlier formed characters of the sequence assuming the major part of this control.

The physiological basis for the expression of economic yield involves the three interrelated processes of accumulation, translocation and stor

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storage. Photosynthates are manufactured in the chloroplasts of the plant surface and these are in turn allocated among the various structures. It is the partitioning of these assimilates into economic and non-economic organs that ultimately determines the magnitude of grain yield.

The following study seeks to show the significance of Sinnott's Law in the developmental allometry of cereal plants, the enduring role of earlier established organs in influencing the "form" of later traits and events and consequently the dynamics of the yield components in determining the shape of the yield parallelipiped.

LITERATURE REVIEW

One of the enduring areas of study in crop science is that aspect involving the determination of yield in crop plants. The justification for such an emphasis is straightforward. With a greater understanding of the mechanisms involved in the expression of yield, plant breeders would be in a better position to plan and execute their strategies for enhancing crop productivity.

One of the earliest attempts to dissect the complexity of yield was by Engledow and Wadham (1923) who partitioned grain yield of cereals into its numerous components. Subsequent research delved further into the underlying physiology implicated in the expression of yield. To date a substantial body of data has been collected on the mode of physiological action and regulation with respect to crop yield (Langer, 1967; Eastin *et al.*, 1969; Wallace *et al.*, 1972; Yoshida, 1972; Evans, 1975). Concomitantly, many advances were and are being made in the basic disciplines to identify the processes involved in photosynthesis, translocation of assimilates and partitioning of assimilates into the vegetative and reproductive structures of the plant. Notwithstanding all these achievements, there is still a void in our comprehension of this aspect of plant development. As lamented by no less a figure than Sir Otto Frankel, "The gap in our knowledge between the genetic controls and the actual processes of organ differentiation, which is perhaps greater in the higher plants than in other organisms, remains a great challenge to both geneticists and physiologists. At present a bridge is not in sight; but work from both approaches attempts to narrow the gap." (Frankel, 1976)

The analysis of crop yield entails the analysis of plant growth. The former is the end-point manifestation of a long sequence of developmental events from germination to maturity as evaluated in a plant community. The genetic potential may be inherent in the zygote but its final phenotypic expression is moderated by the environmental condition in which the plant grows. Bonnett (1964) describes morphogenesis as the development of the shape and arrangement of the parts of the plant, the time and sequence of development of the parts and the histology of the parts as they develop. He further states that it is an epigenetic process, one condition leads to another and does so in a channeled and controlled fashion.

The significance of the earlier formed structures on the development of organs laid down towards the end of the plant ontogeny has been recognized for some time. In a study involving Acer saccharum, Sinnott (1921) concluded that the size of a plant organ depends upon the size of the growing point from which it develops. Any factor which alters the size of the meristem will thus alter the size of the organs produced by this meristem. Crane and Finch (1930) observed that the size of buds has an effect in determining the size of shoots that grow from them. Stant (1954) found that where the meristem is long and narrow as in Elodea, the plant has well-developed internodes. Where it is relatively short and wide, as in Narcissus, the stem is much reduced and the internode is very short. In a comparative study of size differences in two strains of Cucurbita pepo, Maltzahn (1957) detected that the primordia of flowers and leaves are considerably larger in the large-fruited type. According to Aitken (1967), the size of the shoot apex is associated with the size of leaf, the species with small apices (e.g., ryegrass and red clover) having narrower leaf primordia and narrower leaves than those with large apices (e.g., peas and maize). He deduced that the association of the width of the shoot apex may be an important limiting factor to leaf size and hence total leaf area. Abbe _et al_. (1941) observed a developmental relationship between the shoot apex and leaf blade width in maize and concluded that it is possible to make a direct comparison between the size of the shoot apex and the width of the leaf blade from the earliest stages of development up to that of leaf 12. In _Sorghum bicolor_, Quinby (1970) suggested that hybrid vigor operates early in the embryonic growth period and results in larger meristems in hybrids. In his materials, the hybrids had larger sized leaves and heavier panicles than the parents.

The problems of growth and development in living organisms have long fascinated biologists as attested to by the classical treatises of Thompson (1917) and Huxley (1932). The concepts developed by these authors along with those of Sinnott (1921, 1960) and Bonnett (1964) have some pertinence in a discussion of crop yield in cereals. The development of organs in plants is governed by certain allometric considerations. Each part and function is so closely correlated with the rest that the whole develops in an orderly fashion toward the growth of a mature individual (Sinnott, 1955; 1960). On the subject of plant architecture and yield in the grain legumes, Adams (1975) pointed out "the property of size or number" as part of an overall allometry in a plant. He cited as evidence the significant correlation between number of pods per plant

with main stem node number and that between the seed size and leaf size in Phaseolus vulgaris. Denis (quoted by Adams, 1975) using principal factor analysis to evaluate 22 structural traits in Phaseolus vulgaris showed that high yield potential is achieved by a balance between "factors of number" (e.g., number of nodes) and "factors of size" (e.g., stem diameter, leaf area). However, correlations between biological phenomena do not of themselves provide the ability to distinguish between cause and effect (Sinnott, 1960). In view of this the method of path coefficient (Wright, 1921; 1934) is often used to evaluate in a more realistic manner the ultimate determination of grain yield (Dewey and Lu, 1959; Fonseca and Patterson, 1968; Duarte and Adams, 1972; Pandey and Torrie, 1973; Thurling, 1974).

"When one considers the sequential nature of development, with all that it implies regarding gene action and genotype-environment interaction, the complexity of the problem becomes quite overwhelming" (Grafius, 1963). In a series of papers, Grafius and co-workers advanced the concept of a sequential developmental process of yield components (Grafius, 1963; 1969; Thomas et al., 1971 a, b, c; Grafius and Thomas, 1971). For their model in small grain crops, they defined yield, W, as being the multiplicative product of its components, i.e. $W = XYZ$. The number of heads per unit area is designated X, Y is the number of seeds per head and Z is the average kernel weight. The sequence of formation is from X to Y to Z.

The determination of grain yield at the level of the plant organ involves the dynamic interactions among the yield components. This intraplant competition is a property of the gene pool and the external factors in the environment. Adams (1967) postulated that two developing structures would register a negative correlation when they compete for a limiting nutrient supply. In a study of yield component compensation in several crop plants, he noted the prevalence of negative correlations between yield components.

Intertrait correlation is an important parameter for measuring the amount of stress that exists in the particular environment in which the crop is grown. In a sequential developmental process, the first event generally exerts an influence on the later forming ones (Grafius, 1969). Eastin and Sullivan (1974) pointed out in sorghum that environmental stresses at the time spikelet components are differentiated seriously reduce grain number and consequently yield itself. In terms of genetic effects, stresses occurring throughout the duration of growth tend to confound the observable genetic variance. Thomas _et_ _al_. (1971 c) examined the source of stress and its influence on sequential multiplicative traits and noted that this force tends to conceal the true nature of the source of control over the expression of the second and subsequent characters in a developmental sequence. Removing the influence of correlations, Thomas _et_ _al_. (1971 a) were able to extract the "true relative" genetic variance from the apparent genetic variance of the untransformed data and showed its significance to the mode of gene action in sequential traits. Lee and Kaltsikes (1972) applied the technique to a diallel set of sequential characters in _durum_ wheat and observed that the transformed data showed a higher level of nonadditive genetic effects with a concomitant decrease in heritability estimate for all yield components. In addition they corroborated the conclusion that the later characters in a sequence are under little or no real direct genetic control as derived by Thomas _et_ _al_. (1971 a, c) and Grafius and Thomas (1971).

More recently, Thurling (1974) found substantial component compensation in the oilseed rape species *Brassica napus* and *Brassica campestris*. Utilizing the appropriate transformation, he observed that yield component relationships were characterized by a strong environmental control of the type and degree of stress as well as by significant genetic control only of characters laid down early in the developmental sequence. Tai (1975) studied the genotype-environment interactions in potato (*Solanum tuberosum* L.). Within a given set of genotypes, he found that a cultivar which was able to produce a flexible number of tubers per stem (Y) according to the environmental conditions in that period gave more stable yield performance than those less capable of adjustment.

On the basis of physiological considerations, Donald (1968) proposed the breeding of crop ideotypes involving the modification of morphological structures. The idea is a sound one although his uniculm concept would not be practical with cereals like rice, wheat, barley or oats where the ability to tiller during adverse environmental conditions is analogous to an insurance policy. The plant type concept has been proven to be effective for breeding high yielding *indica* rice varieties at the International Rice Research Institute (Yoshida, 1972) and appears promising in the grain legumes (Adams, 1975).

The recent upsurge of interest in attempting to identify the physiological selection criteria for plant breeding (Frey, 1971; Wallace *et al.*, 1972; Wittwer, 1974; Evans, 1975) has seen greater emphasis being accorded to factors involved in the manufacture of photosynthates and their partitioning among the economic and non-economic structures of the crop. Current polemics center around whether the supply of assimilates (source) or the capacity for their storage (sink) limits crop yields. As Evans (1975) admitted, the question is "too polarized". Each case may have to be considered separately under its own set of conditions. However, when environmental conditions are not limiting and in crops where yield is derived from determinate inflorescences rather than vegetative organs, storage capacity may be limiting. Several lines of evidence have been given by Evans (1972) and Yoshida (1972). Grafius and Barnard (1976) have come to a similar conclusion with barley.

MATERIALS AND METHODS

Parents were selected on the basis of contrasting values for the yield components, namely the number of fertile tillers per 30 cm row (X), the number of kernels per head (Y) and the average weight per kernel (Z).

Five pairs of parents were involved in this experiment, their pedigrees being as follows:

Name/Number	Pedigree	Origin
1. B130	Traill 2X Kindred X C.I.7117-77 3X Trophy	ND
2. 'Dickson'	Traill^2 2X Kindred X C.I.7117-77	ND
3. Traill	Titan X Kindred	ND
4. X969-3	Very complex: includes Wis. Barbless, 'Olli', 'Newall', 'Pillsbury', Composite-cross selections	WI
5. 60-215-6	'Belownee' 2X 'Liberty' X Kindred^2	MI
6. 59-215-403	'Moore' X 'Montcalm'^{2} 2X Liberty X Kindred	MI
7. 60-216-12	Belownee 2X Liberty X Kindred^3	MI
8. 59-216-313	Moore X Montcalm 2X Liberty X Kindred	MI

The USDA Cereal Investigation numbers for the parental varieties (where available) are Dickson (C.I.10968), Traill (C.I.9538) and B130 (C.I.11864).

All eight parents have comparatively similar levels of grain yield (W) in the Michigan environment, but they vary in the values of their yield components, X, Y and Z. Crosses were made to exploit these differences.

For each pair, a single cross (AB) and the two respective complementary backcrosses (A^2B and AB^2) were made, giving a total of 15 progeny populations. Twenty random selections were made in each population in the F_4 or BS_3 generations. They were allowed to self until the F_7 or BS_6. Data collection and analyses were based on the latter. Twenty isolates per progeny were grown in four row plots .0254 m apart and 2.4 m long. In addition, 10 plots for each of the eight parental types and 20 plots for each of two check varieties (Larker C.I.10648 and Coho C.I.13852) were planted. The checks were used as sources of error variance for comparison among groups. Planting date was April 18, 1973. The plots were completely randomized.

Leaves were sampled in the following procedure: six culms were randomly selected from each plot. Measurements wre obtained from the three top leaves of each culm, i.e. flag leaf (L_f), second leaf from the top (L_2) and third leaf from the top (L_3). The leaf data collected were the length from the tip to the base of the lamina and the maximum leaf width. The average leaf area (S) was the mean of the area of these top three leaves. Due to the large number of leaves involved (approximately 7,000), the measurements were done in batches with the rest of the leaves being stored in a dry place.

Before any measurement was taken, each leaf was soaked in warm water to allow it to return to its original size and shape. Several leaves were then spread out on a piece of glass which had a grid measurement underneath. Another identical piece of glass was then applied on top of the leaves to press them flat.

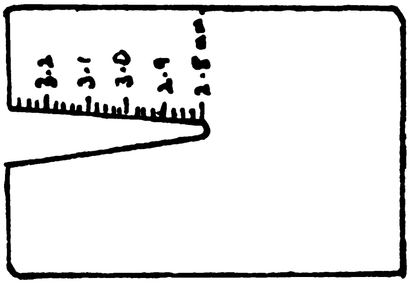
A random sample of leaves was also taken to determine the actual leaf area of the three types of leaf blade. The outline of each leaf was traced on a transparent paper of a uniform weight (in our case, a paper weight of 1 gm = 147.16 cm^2). Each tracing was cut and carefully weighed on a Mettler balance. The weight was then transformed into actual leaf area.

A regression of the actual leaf area on its corresponding length by width product was done using the equation

$$A = blm$$

where A is the actual leaf area, l = length of leaf, m = maximum width of leaf and b = regression coefficient. The b value of each type of leaf was later used to estimate leaf areas using the product (l x m). As will be shown later, our results were comparable to those obtained by other workers.

The average culm diameter (D) was computed from the measurements obtained at three specific points, namely the flag leaf node (N_f), the second node from the top (N_2) and the third node from the top (N_3). For a rapid assay, a simple but ingenious technique suggested by Evans (1972) was adopted. A gauge, as illustrated below, was carved out of a thin resilient paper, the size of a standard credit card and graduated markings in millimeters were lined along its inner edges. Rapid reading could be obtained by inserting the particular node of the culm into the gauge.



Estimates of kernels per head (Y) were derived from a random sample of 20 heads per plot preceding harvest. The central two rows were harvested for grain yield (W). The average kernel weight (Z) was calculated from a 3 gm sample per plot by using an electronic seed counter. The number of heads per 30 cm row (X) were obtained by dividing grain yield per 30 cm of row by the product of kernels per head and the average kernel weight.

Due to adverse field conditions, data on some of the progeny plots were not available. For the leaf and culm measurements, the range was from 12 to 20 except for cross 7 x 8^2 which had only six isolates. The harmonic mean was 16. For grain yield and its three components, the range was from 15 to 20 except for cross 7 x 8^2 with only five isolates. The harmonic mean was 15 and these means were used in calculating the respective least significant differences (LSD).

The correlation and regression analyses of the 15 crosses and backcrosses were done on the population means of either the F_7 or the BS_6 generations. Using the means of unselected populations helped to eliminate the effects of genetic linkage among traits assuming that epistasis was inoperative. Hence, we would expect that the statistical derivations based on these populations are indicative of developmental relationships among the characters.

A preliminary evaluation of the possible contributions of leaf area, culm diameter and the three yield components, X, Y and Z on W was done by using a multiple regression equation with W as the dependent variable and X, Y, Z, D and S as the independent variables. Based partly on the fact that no significant direct relationship was detected between W and either D or S, and partly on prior assumptions, the following path coefficient diagram was drawn to describe the expression of W and how it might be influenced by the mode of development of the morphological organs of the plant. A somewhat similar figure was advanced by Tai (1975).

The path coefficient analysis as outlined by Wright (1921, 1934) is a powerful tool for analyzing the relationship between two or more variables. The path coefficient expresses the direct influence of one variable on another and the analytical method allows the partitioning of the cross-product linear correlation into its direct and indirect effects. However, for the method to be valid, the experimenter must assign the cause-and-effect system *a priori*, as illustrated in Figure 1.

The phenotypic correlations are partitioned into their direct and indirect effects as follows:

1. $r_{XY} = a$
2. $r_{YZ} = b + ae$
3. $r_{ZW} = c + bf + de + abd + aef$
4. $r_{XW} = d + ce + af + abc$
5. $r_{XZ} = e + ab$
6. $r_{YW} = f + bc + ad + ace$
7. $r_{XD} = g$
8. $r_{XS} = h$
9. $r_{DY} = p'$
10. $r_{SY} = q'$
11. $r_{DS} = t'$

The unknown path coefficients are solved by simultaneous equations.

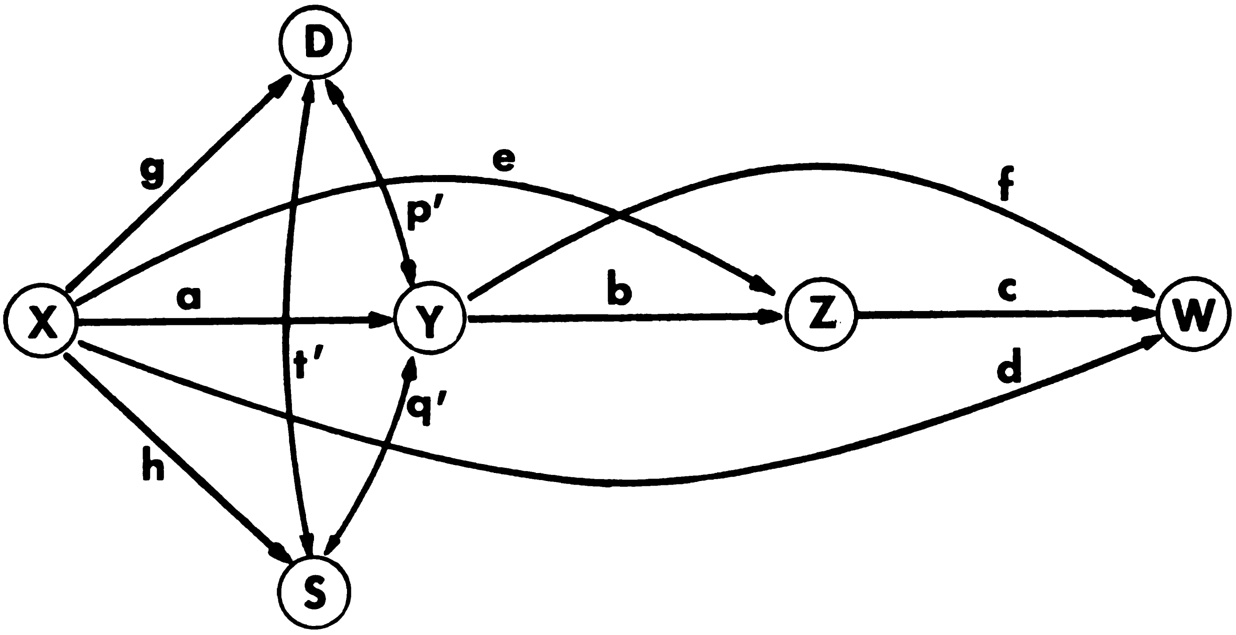


Figure 1. Designation of cause-and-effect of plant organs influencing grain yield per unit area (W). Where X = number of tillers per unit area; Y = number of kernels per head; Z = average kernel weight; D = culm diameter; and S = average leaf area. Single arrowed lines denote path coefficients and double arrowed lines denote correlation coefficients.

RESULTS

The regression coefficients (b) of the actual leaf area on the product of length (l) x maximum width (m) are shown in Table 1. They vary somewhat among the three different leaves. The results are comparable to the values derived by other workers. Watson *et al.* (1958) reported mean b values of 0.76 ± .0044 for a field experiment and 0.73 ± .0038 for a greenhouse experiment involving the same varieties. However, their experiments did not discriminate among the different leaves on a plant. Carleton and Foote (1965) found a b value of between .66 and .75 in three barley varieties at two different stages of growth. They believed that the use of a single regression coefficient for one whole experiment was sufficient for an accurate estimation of leaf area. Fowler and Rasmusson (1969) found a regression coefficient ranging from .65 to .69 for L_f and from .64 to .71 for L_1 leaves in five barley populations. They suggested the use of a coefficient of .67 for the L_f and .70 for the L_1 and lower leaves. In these studies a different b value for each of the three types of leaves was used. The estimated leaf area correlated well with the actual leaf area (Table 2).

Table 3 shows the leaf and culm characteristics of the eight parental varieties. There were substantial differences in leaf and culm sizes among the parental pairs that made up the five groups of crosses. For example, there was a wide difference in leaf and culm sizes between Parent 1 and Parent 4 or between Parent 3 and Parent 5. These differences

Table 1. Regression coefficients (b) of actual leaf area on the product of length (l) x maximum width (m).

Leaf type	Sample size	b
Flag leaf (L_f)	93 leaves	.638 ± .0106
Second leaf from top (L_2)	93 leaves	.624 ± .0078
Third leaf from top (L_3)	93 leaves	.642 ± .0098

Table 2. Correlation coefficients of actual leaf area with estimated leaf area.

Leaf type	Coefficient
L_f	$.892^{**}$
L_2	$.863^{**}$
L_3	$.749^{**}$

$^{**}P \leq .01$

Table 3. Parental values for flag leaf (L_f), second leaf from the top (L_2), third leaf from the top (L_3), total leaf area (of the three uppermost leaves) per culm (TLA/culm), average leaf area (S), culm diameter at flag leaf node (dN_f), culm diameter at second node from the top (dN_2), culm diameter at third node from the top (dN_3) and average culm diameter (D), where l = length of leaf, m = maximum width of leaf and A = leaf area.

Parent	L_f				L_2				L_3						
	dN_f (mm)	l (cm)	m (cm)	A (cm^2)	dN_2 (mm)	l (cm)	m (cm)	A (cm^2)	dN_3 (mm)	l (cm)	m (cm)	A (cm^2)	TLA/culm (cm2)	S (cm^2)	D (mm)
1. B130	2.51	13.33	1.03	8.74	3.31	22.25	1.28	17.79	3.59	25.03	1.23	19.70	46.22	15.42	3.14
2. Dickson	2.48	13.40	1.12	9.59	3.25	22.22	1.33	18.45	3.59	24.48	1.26	19.83	47.87	15.96	3.11
3. Traill	2.36	12.40	1.16	9.17	3.19	21.25	1.35	17.85	3.50	25.09	1.30	21.13	48.14	16.06	3.02
4. X969-3	2.80	16.79	1.31	14.03	3.72	24.00	1.44	21.65	3.91	24.94	1.24	19.79	55.47	18.50	3.48
5. 60-215-6	2.19	12.89	1.12	9.15	2.79	18.85	1.26	14.81	2.99	21.31	0.95	13.08	37.05	12.35	2.66
6. 59-215-403	2.32	11.70	0.98	7.28	3.08	21.15	1.20	15.82	3.40	24.02	1.10	16.99	40.09	13.37	2.93
7. 60-216-12	2.46	12.12	1.09	8.44	3.16	19.30	1.25	15.09	3.36	22.52	1.04	15.12	38.65	12.88	3.00
8. 59-216-313	2.79	16.25	1.11	11.67	3.51	25.22	1.36	21.35	3.85	27.46	1.31	23.08	56.10	18.71	3.38
LSD .05	0.19	1.36	0.08	0.98	0.18	2.15	0.11	2.29	0.17	2.65	0.06	2.70	4.60	1.53	0.12

Table 4. Mean square values in the parental populations for the flag leaf (L_f), second leaf from the top (L_2), third leaf from the top (L_3), total leaf area (of the three uppermost leaves) per culm (TLA/culm) and the average leaf area (S). The error variance is derived from two check varieties planted at random throughout the nursery where l = length of leaf, m - maximum width of leaf and A = leaf area.

Source	d.f.	L_f			L_2			L_3			TLA/culm	S
		l	m	A	l	m	A	l	m	A		
Between parents	7	36.974**	.094**	45.601**	46.974**	.059**	69.448**	33.939**	.163**	106.643**	529.838**	58.871**
Within parents	72	1.748	.008	2.391**	1.614	.011	2.995	2.104	.018**	9.187	26.023	2.891
Error	38	2.251	.008	1.178	5.673	.015	6.414	8.612	.005	8.894	25.915	2.880

** $P \leq .01$

Table 5. Mean square values in the parental populations for culm diameters at the flag leaf node (dN_f), at the second node from the top (dN_2), the third node from the top (dN_3) and the average culm diameter (D). The error variance is derived from two check varieties planted at random throughout the nursery.

Source	d.f.	dN_f	dN_2	dN_3	D
Between parents	7	.4503**	.7518**	.8242**	.6447**
Within parents	72	.0351	.0352	.0442	.0326*
Error	38	.0422	.0411	.0358	.0177

** $P \leq .01$

* $P \leq .05$

were further confirmed by the variances in Table 4 (for leaf characteristics) and Table 5 (for culm diameter). The error variance was obtained from the varieties Coho and Larker, the two checks planted at random throughout the nursery. This basis of comparison was made because the parents were planted in blocks. Both between and within variances were tested using the error variance. There are highly significant differences ($P \leq .01$) among parents for the various leaf dimensions and the culm diameters.

The parental values for the three yield components, X, Y and Z and grain yield are given in Table 6. There is a wide range in the yield components among the parents, but their yield levels are of the same magnitude. The contrasting values of the components were the criteria for the selection of the five groups of crosses. Table 7 shows the analysis of variance for X, Y, Z and W in the parental populations. As mentioned previously, the source of variance for error was derived from the two check varieties, Coho and Larker. Highly significant differences ($P \leq .01$) were evident for the components of yield but no difference was detected for W.

The leaf and culm data of the five groups of crosses and backcrosses in their F_7 or BS_6 generations are shown in Table 8. One would have expected the value of the straight cross to be intermediate between the two complementary backcrosses, but this was not the case. The values within each of the five groups did not follow a predictable pattern and appeared to be determined at random. For instance, with respect to dN_f, out of five groups of crosses and backcrosses, only the group involving parents 1 and 4 have the single cross intermediate between the two backcrosses. For the flag leaf area, the straight crosses consisting of

Table 6. Parental values for number of fertile tillers per 30 cm (X), number of kernels per head (Y), average weight per kernel (Z) and grain yield per plot (W).

Parent	X (#)	Y (#)	Z (mg)	W (gms)
1. B 130	21.8	41.0	35.7	516
2. Dickson	17.2	47.3	36.5	473
3. Traill	19.0	45.8	36.3	500
4. X969-3	18.7	51.6	36.0	536
5. 60-215-6	29.4	28.3	36.2	479
6. 59-215-403	24.2	37.1	34.3	486
7. 60-216-12	27.8	27.4	38.7	471
8. 59-216-313	17.5	46.0	39.6	445
LSD .05	2.9	3.3	1.6	42

Table 7. Mean square values of the parental populations for number of fertile tillers per 30 cm (X), number of kernels per head (Y), average weight per kernel (Z) and grain yield per plot (W). The error variance is derived from two check varieties planted at random throughout the nursery.

Source	d.f.	X	Y	Z^{++}	W
Between parents	9	216.3^{**}	696.4^{**}	4146^{**}	4111.1
Within parents	90	7.3	19.7	342	1875.6
Error	36	10.4	13.6	303	2229.4

** $P \leq .01$

++ 1×10^{-8}

Table 8. Leaf and culm characteristics in the five groups of crosses and backcrosses for the flag leaf (L_f), second leaf from the top (L_2) third leaf from the top (L_3), total leaf area (of the three uppermost leaves) per culm (TLA/culm), average leaf area (S), culm diameter at flag leaf node (dN_f), culm diameter at second node from the top (dN_2), culm diameter at third node from the top (dN_3) and average culm diameter (D) where l = length of leaf, m = maximum width of leaf and A = leaf area.

	L_f				L_2				L_3						
Cross	dN_f (mm)	l (cm)	m (cm)	A (cm^2)	dN_2 (mm)	l (cm)	m (cm)	A (cm^2)	dN_3 (mm)	l (cm)	m (cm)	A (cm^2)	TLA/culm (cm^2)	S (cm^2)	D (mm)
1 X 2	2.70	13.00	1.07	8.86	3.46	22.94	1.30	18.60	3.71	25.93	1.19	19.79	47.26	15.75	3.29
1^2 X 2	2.56	13.05	1.08	9.03	3.29	21.68	1.30	17.54	3.53	25.36	1.23	19.94	46.51	15.50	3.12
1 X 2^2	2.66	13.39	1.10	9.42	3.50	22.13	1.34	18.45	3.80	24.75	1.27	20.11	47.98	16.00	3.30
1 X 4	2.64	13.55	1.12	9.72	3.58	21.81	1.33	18.15	3.85	24.50	1.21	19.05	46.92	15.64	3.35
1^2 X 4	2.53	13.37	1.07	9.15	3.24	21.33	1.23	16.41	3.55	24.65	1.14	18.07	43.63	14.54	3.06
1 X 4^2	2.68	14.56	1.17	10.84	3.48	22.90	1.38	19.70	3.76	24.88	1.27	20.26	50.79	16.93	3.31
3 X 5	2.32	12.66	1.12	9.07	2.98	20.02	1.25	15.68	3.33	22.53	1.09	15.78	40.53	13.51	2.88
3^2 X 5	2.40	13.12	1.21	10.18	3.26	21.05	1.34	17.58	3.59	24.65	1.24	19.57	47.32	15.77	3.08
3 X 5^2	2.36	13.20	1.16	9.81	2.97	20.64	1.24	16.05	3.23	22.47	1.06	15.29	41.16	13.72	2.85
6 X 8	2.72	13.39	1.06	9.06	3.47	22.81	1.32	18.66	3.76	24.45	1.31	20.54	48.26	16.09	3.32
6^2 X 8	2.46	13.35	0.99	8.44	3.30	22.56	1.20	17.03	3.47	23.99	1.17	18.00	43.47	14.49	3.08
6 X 8^2	2.64	14.25	1.07	9.74	3.41	22.65	1.33	18.84	3.74	24.95	1.26	20.22	48.80	16.27	3.26
7 X 8	2.64	14.92	1.09	10.38	3.41	23.72	1.30	19.29	3.65	26.27	1.27	21.37	51.04	17.01	3.23
7^2 X 8	2.54	12.72	1.14	9.22	3.29	20.36	1.28	16.21	3.54	23.26	1.12	16.75	42.19	14.06	3.12
7 X 8^2	2.50	14.20	1.08	9.87	3.30	22.59	1.27	17.94	3.55	25.06	1.24	19.93	47.74	15.91	3.12
LSD .05	0.15	1.07	0.16	0.78	0.15	1.70	0.09	1.81	0.14	2.10	.05	2.13	3.64	1.20	0.10

1 x 2, 3 x 5 and 7 x 8 all show values outside the range of their respective backcrosses. The randomness of the results are further evidenced in the L_2 where only 1 x 2 shows an intermediate value between the backcrosses with regard to dN_2 and where the intermediate leaf areas are found only in straight crosses involving parents 1 with 4 and 6 with 8. This apparent lack of stability underscores the important role of developmental allometry. What the latter does is to confound the effect of a genetic system per se resulting in the failure of prediction.

Tables 9 and 10 are the analyses of variance for the various leaf and culm characteristics in the 15 cross populations. Highly significant differences exist among the crosses for all the traits measured.

The values of the yield components X, Y and Z, and grain yield in the five groups of crosses and backcrosses are shown in Table 11. Here again, as in the data for the leaf and culm characteristics, the straight cross does not fall between the two backcrosses as would be expected. The analysis of variance for these traits are given in Table 12.

The developmental correlations among the leaf areas of L_f, L_2 and L_3 and among these leaves with the average kernel weight in the five groups of crosses and backcrosses are given in Table 13. The closer the leaves were located to each other the more correlated they were. The flag leaf (L_f) is more correlated to L_2 than with L_3. The correlation of L_2 with L_3 was highly significant. Presumably they were subjected to the same internal and external factors during their development. There was no significant association of the size of the kernel with the size of any of the top three leaves. A subtle implication revealed by this relationship is the possibility that the rate of grain growth and hence

Table 9. Mean square values in the five groups of crosses and backcrosses for the flag leaf (L_f), second leaf from the top (L_2), third leaf from the top (L_3), total leaf area (of the three uppermost) leaves per culm (TLA/culm) and the average leaf area (S). The error variance is derived from two check varieties planted at random throughout the nursery where l = length of leaf, m = maximum width of leaf and A = leaf area.

		L_f			L_2			L_3				
Source	d.f.	l	m	A	l	m	A	l	m	A	TLA/culm	S
Between crosses	14	7.164**	.056**	7.398**	20.709**	.043**	28.954**	21.150*	.103**	60.793**	198.862**	22.096**
Within crosses	258	2.442	.011	2.610*	3.532	.008	4.706	3.329	.007	4.299	21.990	2.443
Error	38	2.251	.008	1.178	5.673	.015	6.414	8.612	.005	8.894	25.915	2.880

** $P \leq .01$

* $P \leq .05$

Table 10. Mean square values in the five groups of crosses and backcrosses for culm diameters at the flag leaf node (dN_f), at the second node from the top (dN_2), the third node from the top (dN_3) and the average culm diameter (D). The error variance is derived from two check varieties planted at random throughout the nursery.

Source	d.f.	dN_f	dN_2	dN_3	D
Between crosses	14	.3513**	.5941**	.6014**	.4771**
Within crosses	258	.0452	.0500	.0433	.0303*
Error	38	.0422	.0411	.0358	.0177

* $P \leq .05$

** $P \leq .01$

Table 11. Yield and yield component values in the five groups of crosses and backcrosses where X = number of fertile tillers per 30 cm; Y = number of kernels per head; Z = average kernel weight and W = grain yield per plot.

Cross	X (#)	Y (#)	Z (mg)	W (gms)
1 X 2	19.2	48.4	35.3	520
1^2 X 2	21.2	45.5	33.8	516
1 X 2^2	20.8	44.6	36.3	534
1 X 4	19.5	46.9	36.6	527
1^2 X 4	22.7	40.4	36.4	518
1 X 4^2	20.2	49.6	36.8	581
3 X 5	23.4	38.8	34.2	489
3^2 X 5	21.5	42.8	36.5	531
3 X 5^2	25.8	35.7	35.5	502
6 X 8	21.0	40.4	37.0	496
6^2 X 8	23.8	38.0	35.2	502
6 X 8^2	18.5	42.6	37.9	470
7 X 8	19.9	41.3	35.8	455
7^2 X 8	22.3	35.4	39.1	481
7 X 8	19.8	41.8	37.6	488
LSD .05	2.3	2.6	1.3	33

Table 12. Mean square values in the five groups of crosses and backcrosses for number of fertile tillers per 30 cm (X), number of kernels per head (Y), average kernel weight (Z) and grain yield per plot (W). The error variance is derived from two check varieties planted at random throughout the nursery.

Source	d.f.	X	Y	Z^{++}	W
Between crosses	14	70.5**	342.0**	3340**	11953.1**
Within crosses	238	11.0*	28.1**	959**	2632.0
Error	36	10.4	13.6	303	2229.4

* $P \leq .01$

** $P \leq .05$

++ 1×10^{-8}

Table 13. Developmental correlations among flag leaf (L_f), second leaf from the top (L_2), third leaf from the top (L_3) and average kernel weight (Z). Data based on the five groups of crosses and backcrosses. (13 d.f.)

$L_f \cdot L_2 = .487$

$L_f \cdot L_3 = .330$

$L_2 \cdot L_3 = .908^{**}$

$L_f \cdot Z = .309$

$L_2 \cdot Z = .194$

$L_3 \cdot Z = .145$

** $P \leq .01$

Table 14. The population means of the five traits and grain yield (W) in the five groups of crosses and backcrosses. Each population is based on 20 random selections made in the F_4 or BS_3 and allowed to self until the F_7 or BS_6. The traits are the average leaf area (S), the culm diameter (D), the number of fertile tillers per 30 cm (X), the number of kernels per head (Y) and the average kernel weight (Z).

Cross	S (cm^2)	D (mm)	X (#)	Y (#)	Z (mg)	W (gms)
1 X 2	15.75	3.29	19.2	48.4	35.3	520
1^2 X 2	15.50	3.12	21.2	45.5	33.8	516
1 X 2^2	16.00	3.30	20.8	44.6	36.3	534
1 X 4	15.64	3.35	19.5	46.9	36.6	527
1^2 X 4	14.54	3.06	22.7	40.4	36.4	518
1 X 4^2	16.93	3.31	20.2	49.6	36.8	581
3 X 5	13.51	2.88	23.4	38.8	34.2	489
3^2 X 5	15.77	3.08	21.5	42.8	36.5	531
3 X 5^2	13.72	2.85	25.8	35.7	35.5	502
6 X 8	16.09	3.32	21.0	40.4	37.0	496
6^2 X 8	14.49	3.08	23.8	38.0	35.2	502
6 X 8^2	16.27	3.26	18.5	42.6	37.9	470
7 X 8	17.01	3.23	19.9	41.3	35.8	455
7^2 X 8	14.06	3.12	22.3	35.4	39.1	481
7 X 8^2	15.91	3.12	19.8	41.8	37.6	488
LSD .05	1.2	0.10	2.3	2.6	1.3	33

Table 15. Developmental correlation coefficients of culm diameter (D), leaf area (S), head size (YZ), the number of fertile tillers per 30 cm (X), the number of kernels per head (Y), the average kernel weight (Z) and grain yield per plot (W) (13 d.f.)

	X	D	S	Y	Z	YZ
D	-.832**					
S	-.823**	.806**				
Y	-.721**	.689**	.696**			
Z	-.325	.357	.213	-.147		
YZ	-.824**	.804**	.768**	.936**	.208	
W	-.035	.250	.186	.632*	-.131	.582*

** $P \leq .01$

* $P \leq .05$

Table 16. Correlation coefficients (13 d.f.) of the estimates of leaf canopy area[1] (A_1, A_2, A_3) with average leaf area (S), length of leaf (1), maximum width of leaf (m) and the total leaf area (of the three uppermost leaves) per culm (TLA/culm).

	A_1	A_2	(A_1+A_2)	A_3[1]	1	m	S
A_2	1.000						
(A_1 + A_2)	1.000	1.000					
A_3[1]	.873	.873	.873				
1	.693**	.693**	.693**	.821**			
m	.292	.292	.292	.291	.495		
S	.626*	.626*	.626*	.707**	.905**	.815**	
TLA/culm	.626*	.626*	.626*	.707**	.905**	1.000	

[1] Grafius, J. E. and J. Barnard. 1976.

** $P \leq .01$ * $P \leq .05$

its weight is not limited by the size of the photosynthetic structure. Some recent studies on the "carbohydrate balance sheets" in wheat have revealed that more assimilates are available for grain filling than are used (Evans and Rawson, 1970; Rawson and Evans, 1971; Wardlaw, 1971). Since no significant differential response was detected among the three types of leaves relative to the size of the grain, and since L_f, L_2 and L_3 are strongly correlated, the average size of the leaves (S) was used in further analyses of the developmental relationships among plant organs.

Table 14 shows the values of five traits in the five groups of crosses and backcrosses involved in the correlation and regression analyses with grain yield.

The correlation coefficients assumed to be developmental in nature are given in Table 15. A striking relationship observed is that of the number of fertile tillers per unit area (X) with all the other plant organs involved in this study. It is found that X is negatively correlated at a highly significant level with culm diameter (D), leaf area (S) and size of the head (H). The pattern is clear: when the number of tillers increases, the sizes of the organs on each tiller tend to decrease. In other words, a genotype with a high number of tillers tends to have small culm diameters, small leaves and small heads. These relationships are plotted in Figures 2, 3 and 4. In Figure 2, D is plotted against X for the 15 cross populations and the significant regression line reaffirms the inverse relationship. Similarly, Figures 3 and 4 point out the inverse associations of X with S and H, respectively.

Highly significant inter-organ relationships are also observed in Table 15 such as that of D with S, D with H and S with H. Interestingly enough, the vegetative traits of D and S are not significantly correlated

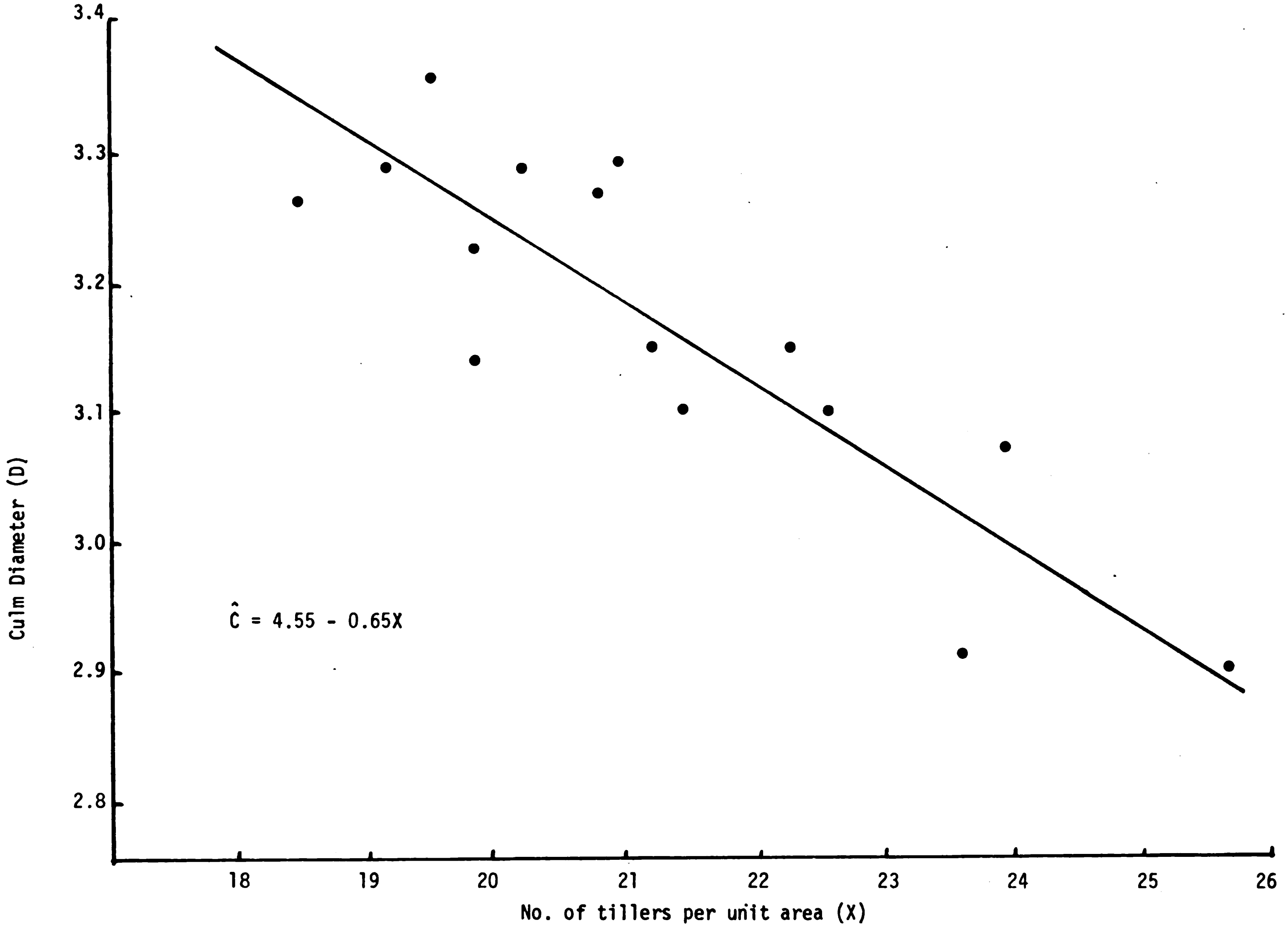


Figure 2. Regression of culm diameter (D) on the number of fertile tillers per 30 cm (X).

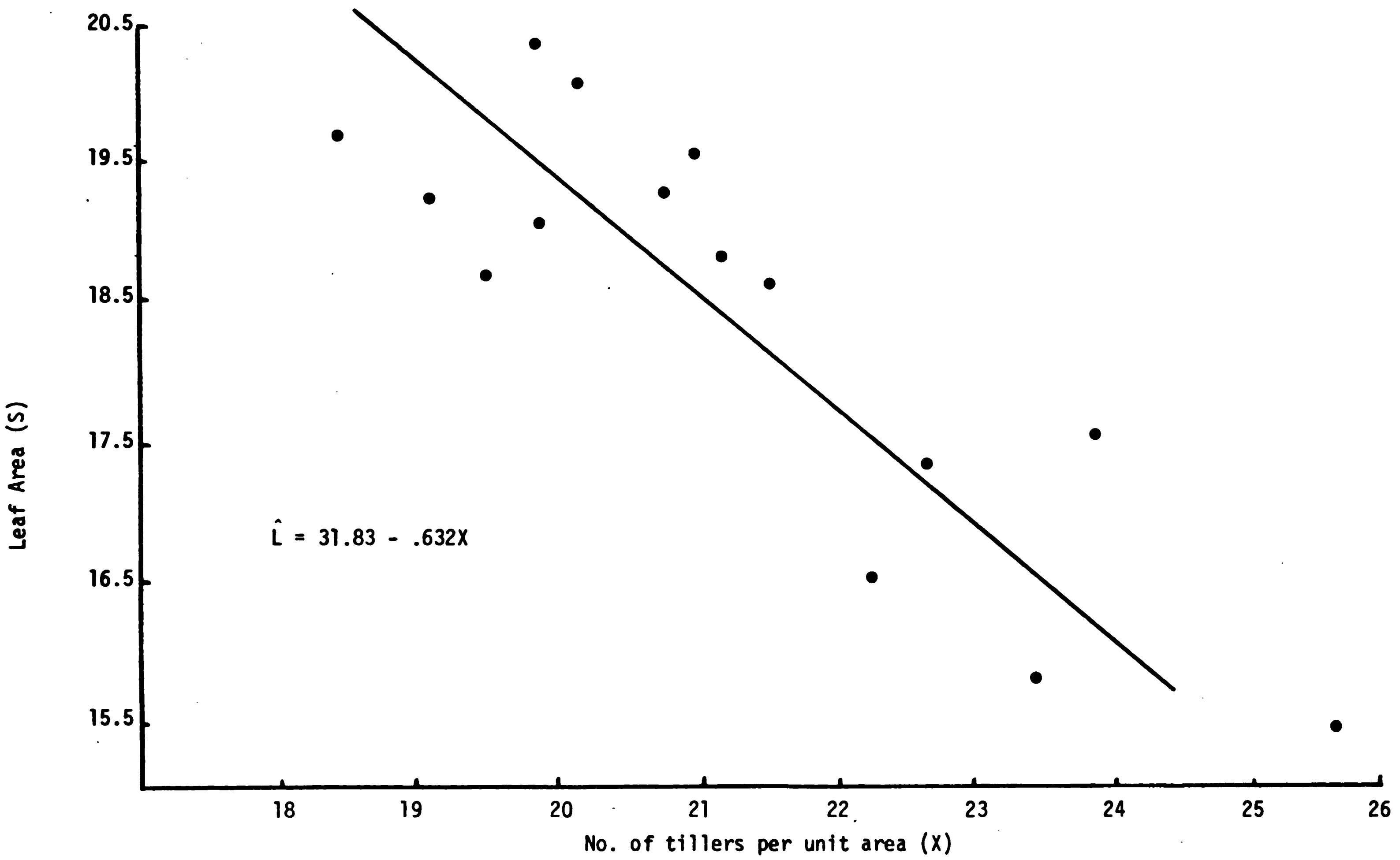


Figure 3. Regression of average leaf area (S) on the number of fertile tillers per 30 cm (X).

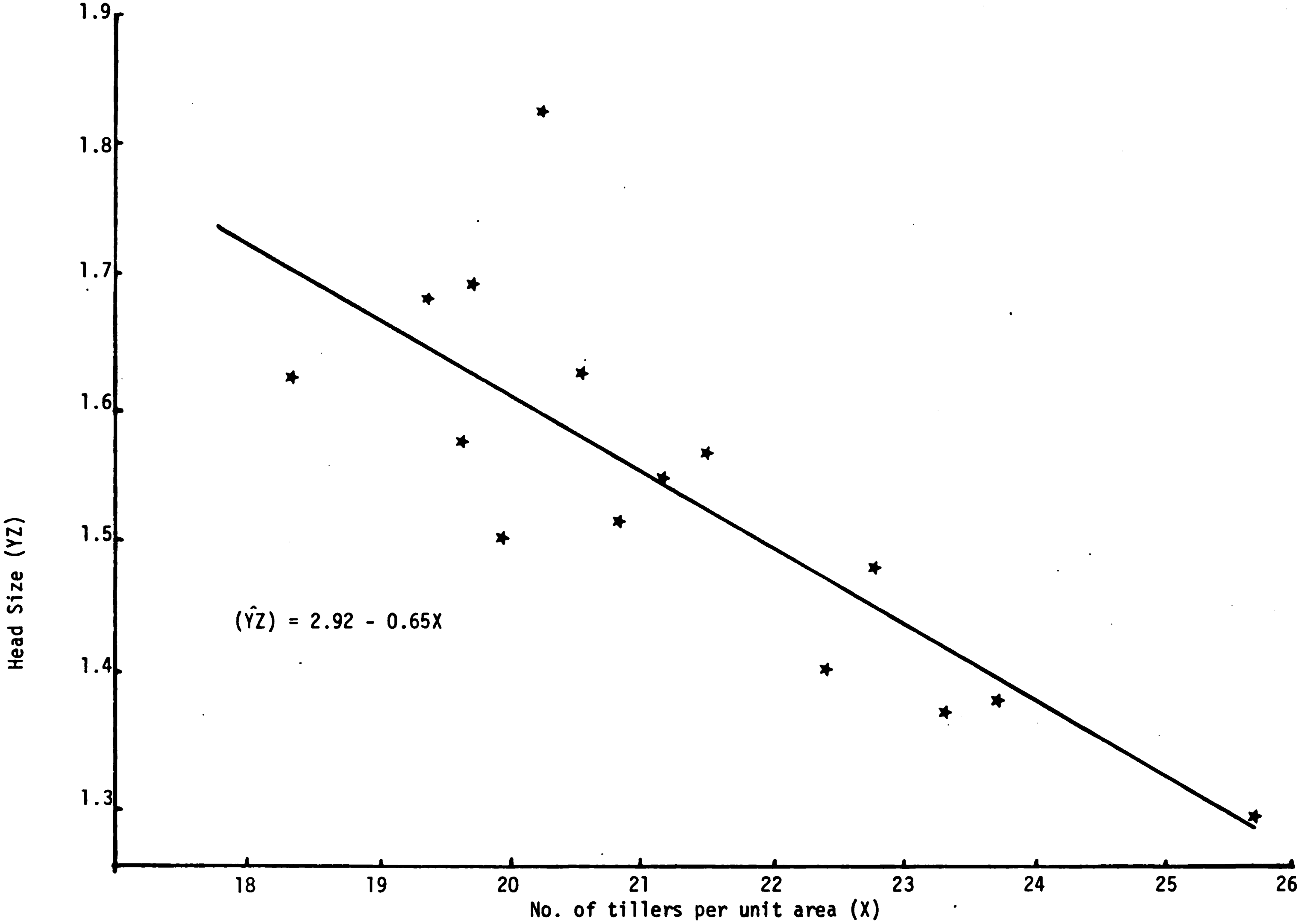


Figure 4. Regression of head size (YZ) on the number of fertile tillers per 30 cm (X).

with W, even though they may be strongly associated with one or more of the three components of yield. The genetic control of grain yield is indirectly manifest through the genic system of its three components (Grafius, 1965). The effect, if any, of either culm diameter or leaf area on W is indirectly channeled via its interaction with the components of yield. The analysis of variance on the multiple regression of yield per unit area on number of fertile tillers per 30 cm, number of kernels per head, average kernel weight, average leaf area and culm diameter is shown on Table 17. The mean square value for regression is highly significant ($P \leq .01$) and the coefficient of determination ($R^2 = .9635$) indicates that much of the variance in the dependent variable (W) can be accounted for by the variation in the five independent variables (X, Y, Z, S and D). Table 18 provides a measure of the degree of contribution of each independent variable on W. The *Beta* weight (standard partial regression coefficient) values indicate that Y and X determine most of the variation in W followed to a smaller extent by Z. It is observed that S and D respectively, has null influence on the variance of W. Even when each of these two variables is taken out of the multiple regression equation, the coefficient of determination does not appear to be reduced. The R^2 deletes for S and D are .9635 and .9624, respectively. In contrast, when Y is deleted from the equation the R^2 is markedly diminished ($R^2 = .2180$).

Table 16 provides the correlation coefficients of the leaf parameters measured in this study with the estimates of leaf canopy integrated over time as derived by Grafius and Barnard (1976). Data on canopy closure were sampled at strategic intervals during the crop growth, namely at the fifth leaf stage (approximate cessation of tillering), heading stage

Table 17. Analysis of variance on the multiple regression of grain yield per unit area (W) on numbrer of fertile tillers per 30 cm (X), number of kernels per head (Y), average kernel weight (Z), average leaf area (S) and culm diameter (D). $R^2 = .9635$

Source	df	Mean Squares
Regression	5	2535.049**
Error	9	53.343

** $P \leq .01$

Table 18. Multiple regression statistics for yield per unit area (W) as the dependent variable, and number of fertile tillers per 30 cm (X), number of kernels per head (Y), average kernel weight (Z), average leaf area (S) and culm diameter (D) as the independent variables.

Variables	Beta weights	Significant level	Partial corr. coefficients	R^2 deletes
X	1.4317	< 0.0005	.9578	.5582
Y	1.6866	< 0.0005	.9764	.2180
Z	.5535	< 0.0005	.8994	.8090
S	.0140	.913	.0376	.9635
D	.0709	.614	.1715	.9624

(cessation of floral development) and date of maximum closure. The area of the leaf canopy for three periods of growth were estimated, i.e., A_1, A_2 and A_3. Good agreement is observed between their estimates and the present parameters except for maximum width of leaf (m), which is apparently a very stable trait in the populations.

Grain yield is essentially determined by its three components. With this gene pool and in this particular environment the "edge" that is most important to W is Y as evidenced by the parameters summarized on Table 18. Number of tillers per unit area is the next important character, while Z has the least direct effect on W.

Figure 5 illustrates a perspective on the developmental allometric relationships of organs and their consequences on yield in cereal crops. The values were obtained from the derivation of Figure 1. Within any specific environment and gene pool, the development of plant organs in terms of their gross size and number is closely interrelated. This relationship exists even though plant organs are laid down sequentially and each may be affected by a different mode of environmental stress. The inverse relationships between X on one hand, and D, Y and S respectively, on the other, and the positive associations among D, Y and S themselves, testify to this developmental allometry. The possible paths from the numerous morphological traits to the ultimate character of grain yield in Figure 5 shows X as having negative influences on culm diameter, leaf area, number of kernels per head and size of kernel. No path is drawn from either D or S to W since the preliminary analysis (Table 18) indicates that no such direct relationship exists between them.

Leaves and culms form an integral part of a cereal plant and their roles are obvious in the normal functioning of a crop stand. However, the results of this study imply that the photosynthetic surface and stem size are not the direct causative factors that determine the variation in grain yield found in the progeny population.

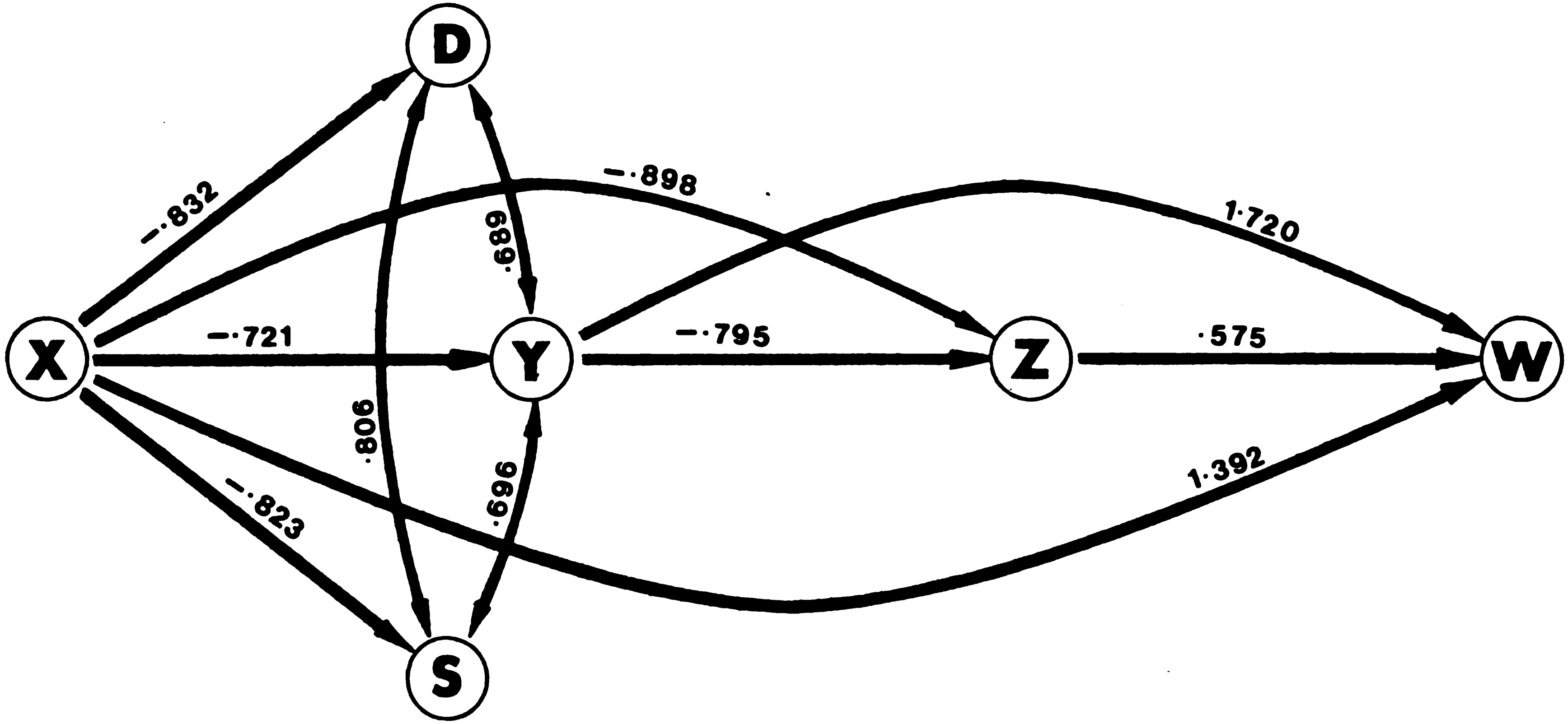


Figure 5. Developmental allometry and the influences of plant organs on the expression of grain yield per unit area (W). X = number of tillers per unit area; Y = number of kernels per head; Z = average kernel weight; D = culm diameter; and S = average leaf area. Single arrowed lines denote path coefficients and double arrowed lines denote correlation coefficients.

DISCUSSION

Allometric Relationships Among Plant Organs

The correlation analysis was calculated using the means of unselected populations of the F_7 or BS_6 generations. Hence the effect of genetic linkages is minimized so that any correlation observed among traits would most likely be developmental in nature.

In the small grains, the proliferation of tillers is one of the first developmental processes at the organ level. There appears to be a significant relationship in which the number of tillers laid down by the plant has far reaching effects on the growth and development of organs which occur later in the plant's ontogeny. This apparent causation has its underlying origin in the role and nature of the meristem. Most mature plant cells are enclosed in thick cellulose walls and in normal circumstances are incapable of further division. Mitotic cell division occurs only at certain regions in the plant, namely at the apices of the shoot and root or at lateral points where meristems are located. In the cereal plant the above-ground organs evolve from the shoot meristem and each of these organs is sequentially laid down, beginning with establishment of the main stem, followed by proliferation of the tiller primordia and subsequent development of other plant structures such as the leaf, the culm diameter of each tiller and the floral primordia.

The results here have shed strong inferences on the nature of these relationships. There is a direct association between the number of tillers laid down by the plant and the size of the individual meristem on each tiller. (In the present case, the size of the meristem can be inferred from the size of the various plant organs.) The higher the X, the smaller would be the size of the meristem for each tiller.

Given that plant organs arise from the same meristem, one would expect to find strong inter-organ associations as a matter of course. This is well illustrated in the findings. The correlation coefficients of culm diameter with average leaf area and head size are $.806^{**}$ and $.804^{**}$, respectively. In addition, average leaf area is significantly correlated with head size ($.768^{**}$). These relationships obviously reflect the basic underlying system of organization existing in the plant (the discussion here is mainly restricted to the interactions of systems at the organ level). The development of the plant as a whole organism as programmed in its heredity interacting with its environment, necessitates the formation of its various morphological structures into some specific integrated form. There is always a dynamic balance between the number of units (tillers) laid down and the size of the components on each unit (i.e., head size, leaf size and culm diameter). This balance is essential in order to maintain the stability of the plant which often is grown in an environment of limiting resources.

The developmental correlations observed among organs have broad implications in plant morphological architecture. The characteristics of any well adjusted plant type would have to be set within the constraints of Sinnott's Law. In constructing a crop ideotype, the plant breeder would have to take these allometric relationships into consideration. For example, it is unlikely that a heavily tillered plant with small culms will have large leaves and big heads. What would be more practical is a plant with many tillers, small culm diameter, small leaves and many small heads. The high yielding rice varieties developed at the International Rice Research Institute in recent years have medium to high numbers of tillers and short, upright leaves (Chandler, 1969). While the basic concept for the construction of this plant type is essentially agronomic adaptability to the rice growing environment, it is evident that Sinnott's Law is operative in such a case. It might be well to point out that short, narrow leaves would be more erect than long, broad leaves (Yoshida, 1972).

Relationships of Morphological Structure to Grain Yield

In Table 16, the r value of average leaf area with grain yield is found to be non-significant. Working with similar materials, Grafius and Barnard (1976) attempted to relate leaf canopy integrated over time to W but found no significant relationship. The leaf dimensions used in this study correlate well with the leaf parameters estimated by Grafius and Barnard (Table 17). More exact agreement between canopy area and individual leaf area is not expected because of the confounding effects of the number of tillers per 30 cm of row and its negative correlation with leaf size and tendency towards non-erectness (planophile) habit of leaf orientation.

There is a general consensus that from 80 to 90% of the carbohydrates in the grain are obtained from CO_2 fixation after anthesis and many workers have stressed the importance of the upper leaf area, stem and ear to grain filling (see physiological references cited by Wardlaw, 1968). Undoubtedly such physiological studies are relevant to identify the photosynthetic sites involved and their relative contribution to post-anthesis accumulation of assimilates in the grain.

However, the determination of grain yield (W), specifically the observed differences among a set of genotypes that is normall involved in a breeding program, entails a more complex process and would not be resolved by an explanation of a vis-a-vis relationship of photosynthetic efficiency and W. In the first place, the expression of economic yield in cereals is the end point of those three major physiological processes, namely, accumulation (of assimilates), translocation and storage. Any one process could be limiting, but in this set of data, the non-significant relationship between W and average leaf area, and also the corroborative results obtained by Grafius and Barnard, strongly suggest that photosynthetic efficiency is not the determining factor in the variation of W in the 15 cross populations. Recent works by Berdahl et al. (1972) shows no consistent yield advantage of small over large leaves or vice versa. Evans and Dunstone (1970) and Khan and Tsunoda (1970) have observed that in cereals, the higher yielding cultivars have lower photosynthetic rates.

It is not a case of a limiting supply of assimilates but rather what strategy the plant adopts for a certain environment in partitioning the assimilates into the economic and non-economic structures of the "sink". In such a situation translocation ability and/or storage capacity may be the limiting steps. The size and number of the appropriate components of W may be more critical than the size or number of the photosynthetic surfaces in causing differences in W among genotypes.

It must be emphasized that W is a complex trait and in barley, size of grain is only one of its components. The determination of W commences with the proliferation of tillers, through to the onset of the number of kernels per head and ends with grain filling. Each component is sequentially developed and, except for some degree of overlapping, the development of each is isolated in time. As a consequence different environmental stresses modify the expression of each component trait. Other things being equal, it is the mode of interactions among these three components that would ultimately determine the shape of the optimum yield parallelipiped.

The multiple regression statistics (Table 18) of W with X, Y, Z, D and S confirm the major roles imparted by these yield components on W. Number of kernels per head appears to have the strongest influence on W, followed by X and lastly by Z. The stress matrix among X, Y and Z are $r_{XY} = .721^{**}$, $r_{XZ} = -.325$ and $r_{YZ} = .147$. These values are not static, but reflect the prevailing stresses existing in the particular environment in which the crop is grown and its specific gene pool (Adams, 1967; Grafius, 1969). These stresses are the result of inter-trait competition as elucidated in the concept of a sequential developmental process of the components of yield (Grafius, 1969; Thomas et al., 1971 a, b, c; Grafius and Thomas, 1971). The basic premise rests on the assumption that environmental resources for plant growth and development are not equally available throughout the growing season, and furthermore, those resources that are exploited at one stage of development would not be available for use in later stages of the plant's ontogeny. Grafius and Thomas (1971) demonstrated that stress induced by competition for resources by sequentially developed traits has an oscillatory form of curve and the success or failure of a cultivar relies on its ability to balance the allocation of the existing environmental resources on those component(s) that is/are strongly associated with W.

With the present data, as in most other small grains in the Michigan environment (Grafius and Okoli, 1974), the importance of Y and/or the combination of XY in determining the biological optimum shape is underscored. In Figure 5 it is shown that the effects on W are mostly determined by X and Y, the two components that are set early in the developmental sequence. Using transformation techniques to remove correlations between sequential traits, Thomas *et al*. (1971 a, b) were able to show that true genetic control over variation in W is mainly exerted by those characteristics laid down early in the sequence and that this control tends to diminish with traits formed later in ontogeny. Recent works by Thurling (1974) on rapeseed species *B. napus* and B. *campestris*, and by Tai (1975) on potatoes, lend strong support to this concept. Grafius *et al*. (in press) were able to predict progeny mean yield on the basis of parental (XY) alone.

The importance of the trait set early during morphogenesis, namely X, can be visualized in Figure 5. The plant reaction to opt for any one level of X triggers a chain reaction affecting all later formed organs as exemplified by Sinnott's Law. By virtue of its direct association with meristem size, X assumes a pivotal role in determining sizes of plant organs and eventually the determination of economic yield itself. This decision on X could be modified by external factors such as nutrients (Aspinall, 1961, 1963), water (Wardlaw, 1971), temperature, light intensity and daylength (Cannell, 1969; Friend, 1965) or internally by hormone levels. It has been shown by Leopold (1949) that apical dominance is involved in the control of tillering and auxin has been postulated to be the hormone mediating this function. However, amidst

all these extenuating factors, one must give cognizance to the fact that although the initial control originates in the gene, the magnitude of stress matrix among organs has a bearing on their phenotypic expressions. It is an intraplant response invoked by external forces in the environment. Plant organs abide by certain allometric conformations to maintain the integrity of the plant system and the vegetative structures may not necessarily be directly involved in causing variation of grain yield.

SUMMARY AND CONCLUSION

Eight parents were selected on the basis of contrasting values of the three yield components. They have comparatively similar levels of grain yield but they vary in their yield components. Five groups of crosses and backcrosses were made in order to exploit these differences.

The data obtained consisted of grain yield per unit area (S), number of fertile tillers per 30 cm (X), number of kernels per head (Y), average kernel weight (Z), average leaf area (S) and culm diameter (D).

The results obtained indicate that the earlier developed organ (in this case, X) exerts influence on later formed structures. The higher the number of tillers per unit area, the smaller would be the size of the culm diameter of each tiller, the average leaf area and the size of the head. Furthermore, a strong positive correlation exists between any two organs arising from a common meristem.

To account for all these relationships, the phenomenon of 'developmental allometry' is hypothesized. This condition is brought about because the development of organs within the plant is subjected to an overall need for balance among these numerous structures.

Grain yield is not significantly associated with either the culm diameter or the leaf area, although the two latter traits may be strongly correlated with one or more of the three components of yield. It is concluded that with this gene pool and in this particular growing

environment, the components of the grain yield would be more limiting than the size of the photosynthetic surface or other plant structures (e.g., diameter of culm) in causing variation of grain yield among cultivars.

LITERATURE CITED

1. Abbe, E. C., L. F. Randolph, and J. Einset. 1941. The developmental relationship between shoot apex and growth pattern of leaf blade in diploid maize. Amer. J. Bot. 28:778-782.

2. Adams, M. W. 1967. Basis of yield component compensation in crop plants with special reference to the field bean, Phaseolus vulgaris. Crop Sci. 7:505-510.

3. Adams, M. W. 1975. Plant architecture and yield in the grain legumes. In Report of the TAC working group on the biology of yield of grain legumes. TAC Secretariat, FAO, Rome.

4. Aitken, Y. 1967. Leaf primordia formation in some agricultural species. J. Aust. Inst. Agr. Sci. 33:212-214.

5. Aspinall, D. 1961. The control of tillering in the barley plant. I. The pattern of tillering and its relation to nutrient supply. Aust. J. Biol. Sci. 14:493-505.

6. Aspinall, D. 1963. The control of tillering in the barley plant. II. The control of tiller-bud growth during ear development. Aust. J. Biol. Sci. 16:285-304.

7. Berdahl, J. D., D. C. Rasmusson, and D. N. Moss. 1972. Effect of leaf area on photosynthetic rate, light penetration and grain yield in barley. Crop Sci. 12:177-180.

8. Bonnett, O. T. 1964. Morphogenesis in the organism and the expression of complex traits. Crop Sci. 4:500-503.

9. Cannell, R. Q. 1969. The tillering pattern in barley varieties. I. Production, survival and contribution to yield by component tillers. J. Agr. Sci. Camb. 72:405-422.

10. Carleton, A. E. and W. Foote. 1965. A comparison of methods for estimating total leaf area of barley plants. Crop Sci. 5:602-603.

11. Brown, A. W. A., T. C. Byerly, M. Gibbs, A. San Pietro (eds.) 1976. Crop productivity - Research Imperatives. Proceedings of an international conference sponsored by Mich. State Univ. Agr. Exp. Sta. and C. F. Kettering Foundation. 399 pp.

12. Chandler, R. F. 1969. Plant morphology and stand geometry in relation to nitrogen. p. 265-285. In J. D. Eastin, F. A. Haskins, C. Y. Sullivan and C. H. M. van Bavel (eds.) Physiological aspects of crop yield. ASA and CSSA, Madison, Wisconsin.

13. Crane, H. L. and A. L. Finch. 1930. Growth character, leaf size and bud development in the pecan. Proc. Amer. Soc. Hort. Sci. 27:404-443.

14. Dewey, D. R. and K. H. Lu. 1959. A correlation and path coefficient analysis of components of crested wheat grass seed production. Agron. J. 51:515-518.

15. Donald, C. M. 1968. The breeding of crop ideotypes. Euphytica 17:385-403.

16. Duarte, R. and M. W. Adams. 1972. A path coefficient analysis of some yield component interrelations in field beans (Phaseolus vulgaris L.). Crop Sci. 12:579-582.

17. Eastin, J. D., F. A. Haskins, C. Y. Sullivan, and C. H. M. van Bavel (eds.) 1969. Physiological aspects of crop yield. ASA and CSSA, Madison, Wisconsin. 393 pp.

18. Eastin, J. D. and C. Y. Sullivan. 1974. Yield considerations in selected cereals. In R. L. Bieleski, A. R. Ferguson and M. M. Chesnel (eds.) Mechanisms of regulation of plant growth. Royal Soc. of New Zealand, Wellington. Bull. 12:871-877.

19. Engledow, F. L. and S. M. Wadham. 1923. Investigations on yield in the cereals. I. J. Agr. Sci. Camb. 13:390-439.

20. Evans, G. C. 1972. The quantitative analysis of plant growth. Univ. of Calif. Press, Berkeley and Los Angeles. 734 pp.

21. Evans, L. T. 1972. Storage capacity as a limitation on grain yield. Int. Rice. Res. Inst. Rice Breeding 499-511.

22. Evans, L. T. 1975. Crop physiology: some case histories. Cambridge Univ. Press. 374 pp.

23. Evans, L. T. and R. L. Dunstone. 1970. Some physiological aspects of evolution in wheat. Aust. J. Biol. Sci. 23:725-741.

24. Evans, L. T. and H. M. Rawson. 1970. Photosynthesis and respitation by the flag leaf and components of the ear during grain development in wheat. Aust. J. Biol. Sci. 23:245-254.

25. Fonseca, S. and F. L. Patterson. 1968. Yield component heritabilities and inter-relationships in winter wheat (Tritucum aestivum L.). Crop Sci. 8:614-617.

26. Fowler, C. W. and D. C. Rasmusson. 1969. Leaf area relationships and inheritance in barley. Crop Sci. 9:729-731.

27. Friend, D. J. C. 1965. Tillering and leaf production in wheat as affected by temperature and light intensity. Can. J. Bot. 43:1063-1076.

28. Frankel, O. H. 1976. Floral initiation in wheat. Proc. Roy. Soc. Lond. B. 192:273-298.

29. Frey, K. J. 1971. Moving off the yield plateau. ASA Special Pub. 20:15-58.

30. Grafius, J. E. 1963. Breeding for yield. In Barley Genetics I. Proc. 1st Intern. Barley Genet. Symp., Wageningen, Pudoc, Wageningen. 267-277.

31. Grafius, J. E. 1965. A geometry of plant breeding. Mich. State Univ. Agr. Exp. Sta. Res. Bull. #7, p. 59.

32. Grafius, J. E. 1969. Stress: a necessary ingredient of genotype by environment interaction. In Barley Genetics II. Proc. 2nd Intern. Barley Genet. Symp., Pullman, Washington St. Univ. Press, Pullman. pp. 346-355.

33. Grafius, J. E. and J. Barnard. 1976. The leaf canopy as related to yield in barley, Hordeum vulgare L. Agron. J. 68(2):398-402.

34. Grafius, J. E. and L. B. Okoli. 1974. Dimensional balance among yield components and maximum yield in an 8 x 8 diallel of barley. Crop Sci. 14:353-355.

35. Grafius, J. E. and R. L. Thoams. 1971. The case for indirect genetic control of sequential traits and the strategy of deployment of environmental resources by the plant. Heredity 27: 433-442.

36. Grafius, J. E., R. L. Thomas, and J. Barnard. 1976. The effect of parental component complementation on yield and components of yield in barley, Hordeum vulgare L. Crop Sci. (in press)

37. Hageman, R. H., E. R. Leng, and J. W. Dudley. 1967. A biochemical approach to corn breeding. Adv. Agron. 10:45-86.

38. Huxley, J. S. 1932. Problems of relative growth. Dover Edition (1972) New York. 312 pp.

39. Khan, M. A. and S. Tsunoda. 1970. Evolutionary trends in leaf photosynthesis and related leaf characters among cultivated wheat species and its wild relatives. Jap. J. Breeding 20: 133-140.

40. Langer, R. H. M. 1967. Physiological approaches to yield determination in wheat and barley. Field Crop Abstracts 20 (2):101-106.

41. Lee, J. and P. J. Kaltsikes. 1972. Diallel analysis of correlated sequential characters in Durum wheat. Crop Sci. 12:770-772.

42. Leopold, A. C. 1949. The control of tillering in grasses by auxin. Am. J. Bot. 36:437-440.

43. Maltzahn, K. E. von. 1957. A study of size differences in two strains of Cucurbita pepo I. Gross size differences. Can. J. Bot. 809-830.

44. Pandey, J. P. and J. H. Torrie. 1973. Path coefficient analysis of seed yield components in soybeans (Glycine max (L.) Merr.) Crop Sci. 13:505-597.

45. Quinby, J. R. 1970. Leaf and panicle size of sorghum parents and hybrids. Crop Sci. 10:251-254.

46. Rawson, H. M. and L. T. Evans. 1971. The contribution of stem reserves to grain development in a range of wheat cultivars of different height. Aust. J. Agr. Res. 22:851-863.

47. Sinnott, E. W. 1921. The relation between body size and organ size in plants. Amer. Naturalist 55:385-403.

48. Sinnott, E. W. 1955. The biology of the spirit. The Viking Press, New York. 180 pp.

49. Sinnott, E. W. 1960. Plant morphogenesis. McGraw-Hill, New York. 550 pp.

50. Stant, M. Y. 1954. The shoot apex of some monocotyledons III. Growth organization. Ann. Bot. n.s. 18:441-447.

51. Tai, G. C. C. 1975. Analysis of genotype environemnt interactions based on the method of path coefficient analysis. Can. J. Genet. Cytol. 17:141-149.

52. Thomas, R. L., J. E. Grafius, and S. K. Hahn. 1971a. Genetic analysis of correlated sequential characters. Heredity 26: 177-188.

53. Thomas, R. L., J. E. Grafius, and S. K. Hahn. 1971b. Transformation of sequential quantitative characters. Heredity 26:189-193.

54. Thomas, R. L., J. E. Grafius, and S. K. Hahn. 1971c. Stress: an analysis of its source and influence. Heredity 26:423-432.

55. Thompson, D'Arcy N. 1917. On growth and form. Abridged Edition (1961). J. T. Bonner (ed.) Cambridge Univ. Press. 345 pp.

56. Thurling, N. 1974. Morphophysiological determinants of yield in rapeseed (Brassica campestris and Brassica napus). II. Yield components. Aust. J. Agr. Res. 25:711-721.

57. Wallace, D. H., J. L. Ozbun, and H. M. Munger. 1972. Physiological genetics of crop yield. Adv. Agron. 24:97-146.

58. Wardlaw, I. F. 1968. The control and pattern of movement of carbohydrates in plants. Bot. Rev. 34:79-105.

59. Wardlaw, I. F. 1971. The early stages of grain development in wheat in response to water stress in a single variety. Aust. J. Biol. Sci. 24:1047-1055.

60. Watson, D. J., G. N. Thorne, and S. W. French. 1958. Physiological causes of differences in grain yield between varieties of barley. Ann. Bot. n.s. 22:321-352.

61. Wittwer, S. H. 1974. Maximum production capacity of food crops. Bioscience 24(4):216-224.

62. Wright, S. 1921. Correlation and causation. J. Agr. Res. 20: 557-585.

63. Wright, S. 1934. The method of path coefficients. Ann. Math. Stat. 5:161-215.

64. Yoshida, S. 1972. Physiological aspects of grain yield. Ann. Rev. Plant Physiol. 23:437-464.