CULM DEVELOPMENT AND THE NATURE OF PLANT HEIGHT DIFFERENCES IN TRITICUM VULGARE (VILL.) HOST

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This is to certify that the

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Major professor

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ABSTRACT

CULM DEVELOPMENT AND THE NATURE OF DWARFISM IN *TRITICUM VULGARE* (VILL.) HAIT.

by Dirk H. Lenssen

The nature of plant height differences and [illegible] in three closely related, homozygous lines of wheat, [illegible] presented on total culm length, internode number, [illegible] cell number and length, and the effect of [illegible] these characters. Development of the [illegible] internodes is described for the three [illegible] weights and dimensions of [illegible] determined.

Differences in culm length were [illegible] length, both within and between [illegible] of internode number was [illegible]

Differences in length of [illegible] and 1328 were due to cell number, whereas [illegible] size was responsible. Both were [illegible] between Genesee and 1518.

ABSTRACT

CULM DEVELOPMENT AND THE NATURE OF HEIGHT DIFFERENCES IN TRITICUM VULGARE (VILL.) HOST

by Dirk M. Leeuwrik

The nature of plant height differences was investigated in three closely related, homozygous lines of wheat. Data are presented on total culm length, internode number and length, cell number and length, and the effect of environment on these characters. Development of the main culm and individual internodes is described for the three varieties. Embryo weights and dimensions of growing points and young seedlings were determined.

Differences in culm length were generally due to internode length, both within and between varieties. The contribution of internode number was negligible.

Differences in length of comparable internodes of Genesee and 1328 were due to cell number, whereas in 1518 and 1328 cell size was responsible. Both were involved in the difference between Genesee and 1518.

Dirk M. Leeuwrik

Height differences based on cell number appear to originate during embryogenesis while those based on cell length arise after germination. Thus, two independent developmental processes are involved.

Although the varieties differed slightly in their growth rates, the actual duration of extension growth appeared to be the more important contributing factor to length differences at maturity.

Compensatory mechanisms were evident at both cellular and component levels. The variability encountered at these levels was greater than that of the complex trait.

A strong positive relationship existed between variance and height, especially in the tall variety, and there was some evidence of differential homeostasis of homozygous parents.

The greater variation and the compensation encountered at the component and cellular levels lead to the conclusion that the genetic study of height is not aided by the independent study of its components. On the other hand, the strong association of variability and height and the indication of differential homeostasis probably due to the compensatory mechanisms at component levels, tend to obscure genetic segregation of the complex trait.

CULM DEVELOPMENT AND THE NATURE OF PLANT HEIGHT DIFFERENCES IN TRITICUM VULGARE (VILL.) HOST

By

Dirk M. Leeuwrik

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INTRODUCTION

Studies of plant height date back to the beginning of genetics as a science; Mendel used plant height as one of the heritable traits in studies with peas. Cereals in general, and wheat in particular, have received a fair share of the genetic studies of plant height, but the picture has not been resolved completely.

Plant height is a quantitatively inherited character which, although strongly influenced by environment, generally displays a high heritability and is easily and simply measured. For this reason it has been a popular subject for genetic studies designed to reconcile the behavior of quantitative traits with Mendelian principles. Plant height has been a useful trait for studies of environment-genotype interactions, the relative contributions of component characters to a "complex" trait and the genetic behavior of such characters. There is a trend at present to identify components of a quantitative trait biologically in order to simplify genetic explanations. For size differences those explanations must ultimately lie in the heredity of cell size, number, shape and organization.

The data presented here come from a series of investigations made to (a) more fully understand the nature of heritable height differences in Triticum vulgare (Vill.) Host, (b) to determine where, when and how these differences first express themselves in the development of the wheat plant and (c) to identify logical components which could be studied separately in order to elucidate the inheritance of height.

REVIEW OF LITERATURE

Monocotyledonous stems have been studied for over a century. Many of the older papers deal with detailed anatomy and morphology with the main emphasis on systematic and taxonomic implications. Duval, in 1869, described the anatomy of the stems, leaves and rhizomes of Gramineae (13). Guilland (31) published the comparative and developmental anatomy of some monocotyledonous stems, not including those of grasses.

Van Tieghem (63) distinguished between slow- and fast growing stems, and terminal and intercalary growth. He identified the latter with fast growing stems and explained that internodes elongate while nodes do not. Drawing on some of Sachs' data (49) he pointed out that the pattern of elongation of internodes was the same as for the entire stems. Athanassoff (13) pointed out that the grass stem is a flowering stalk and he therefore preferred the term culm.

At the turn of the century studies were conducted to relate various culm characteristics to resistance to lodging. Papers on this aspect have been reviewed by Percival (46) and Athanassoff (13). Attention was mainly directed to vascular organization and nodal anatomy, which seemed to be a natural outgrowth of earlier work by Andersson (10) and others.

Percival (46) and Athanassoff (13) published the first comprehensive studies pertaining to stem development in wheat. Percival described the cereal culm as erect, elastic, cylindrical,

furrowed, smooth or scabrid, the upper parts being green and hence assimilatory. The majority of culms had six nodes but the occurrence of five or seven was not infrequent. The length of individual internodes increased from base to apex with little exception.

In stem development, Percival explained, the hypocotyl remained short and the second internode of the epicotyl lifted the crown with terminal bud to just below the soil surface. When the crown reached its position the rhizome ceased growth, internodes remained short and buds developed in the axils of leaves.

When the plant entered the reproductive stage i.e. when inflorescences originated at the apex of the branches, lateral bud formation ceased. Elongation of the young stem was effected by the apical meristem but also by the intercalary meristems at the base of each internode, which continued to lengthen each internode after the upper part of it had ceased to grow.

Percival briefly described the anatomy of the culm and presented some estimates of cell size. Although he indicated the great variation in cell size which occurred, no attempt was made to relate these to gross dimensions.

Athanassoff (13) has given an excellent and thorough account of the growth and development of individual internodes and culms of Triticum turgidum in terms of morphology,

anatomy and histology. Many of his general observations confirm those made by Percival. In addition he gave detailed descriptions of the anatomical and histological changes along the developing internode and stem.

The researches of Prat (47) (48) indicated that the relationship between the internodes of some cereal and grass culms can be expressed mathematically by the formula $Y = An^k$, Y being the length of internode, n its rank and A and k constants. Prat called this the biometrical gradation of the internodes and showed that this relationship holds fairly well for T. vulgare. There appeared to be a definite association with maturity as, in general, the biometric gradation increased when the life cycle of the plant became shorter.

Probably the most significant contribution of Prat's studies has been his demonstration of the effect of the developing spike on culm development and his subsequent development of a theory of the regulatory effect of histochemical gradients in morphogenetic processes.

Johnson (37) investigated the effect of light intensity, photoperiod and location on the length and internodal pattern of five winter wheat varieties of different heights. All varieties normally produced five above-ground, extended internodes, irrespective of location or relative height. Moisture stress reduced internode lengths.

In a later paper Johnson (38) reported on culm morphology and development in three varieties of winter wheat of different heights. He concluded that differences in culm length were determined by internode length rather than number. Differences in internode length between varieties became progressively greater in higher and longer internodes. Three internodes elongated simultaneously according to a definite pattern of sequential development, with the peduncle being slightly out of phase with the others.

Whereas Johnson found that the major elongation of the inflorescence of winter wheat was concurrent with that of the third internode, Bonnett (17), in oats, found that the major increase in size of the panicle occurred during the elongation of the peduncle.

Similar minor differences in development occur in early stages of growth. For instance, the work of Avery (14) and McCall (42) show that the first expansive internodal growth occurs in the first internode of oats, the second internode in maize and in the third internode in wheat.

Kaufman (39) has stated that in rice, as in wheat, the expansion of internodes occurs during the transition and reproductive phase and occurs acropetally. Thus stem elongation is slow during the vegetative stage but extremely rapid during the reproductive phase. Rapid extension of relatively short duration is the dominant feature of shoot development during the latter stage.

Dimensions of plants and plant organs are the result of a complexity of cell size, shape, number and organization interrelationships. Sinnott (54) (55) has written that shape is primarily determined by the relative frequencies of cell division in various planes and ultimate control of form therefore resides in individual cells.

The question of whether an organism is the final result of the behavior of an organized population of individual cells or whether the cell as a unit is subordinate to the organism has occupied research workers in biology for a long time. Sachs (50) in 1893 discussed plant and organ size in relation to cellular organization. He speculated as to the significance of the apparent restriction of cell size to a specific amount of nuclear material and cytoplasm and originated the concept of "energids." Amelung (8) followed this with quantitative data on mean cell size of different organs in various plants. He tried to relate cell size to organ size and was surprised to find the constancy of cell size in organs of different size and purpose.

Sierp (53) summarized his research in the following manner: (1) Cell size in any particular tissue of a plant species is not constant. (2) Environmental influence on cell size is great. (3) Despite this, cell size has, for any tissue, a characteristic average value, which is heritable. (4) A difference in plant- or organ size can be due to any of the

following: (a) reduction in cell size, (b) simultaneous reduction in cell size and cell number, (c) reduction in cell number and increase in cell size.

Brotherton and Bartlett (18), comparing etiolated- with normal internodes of Phaseolus multiflorus, found that the greater length of the etiolated internodes was due to both cell elongation (66%) and cell division (34%). Since cell extension was decreased by light the latter represented a very disturbing influence in inheritance studies of size, because ultimately, any quantitative biological variation must be due to variation in cell size, cell number or both.

Abbe (3) attempted to find the histological reason for dwarfism in Zea mays. The main difference in length from the normal types appeared to be due to differences in length of the lower internodes. Houghtaling (34) presented data on cell size and number in four varieties of tomato and some F_2 populations of crosses between them. She found that quantitative differences in cortical and pith tissues were mainly due to cell number and concluded that cell number was a heritable character.

That the picture is not always a simple one is shown by Bindloss (15), who found that in a certain dwarf tomato the cell size was actually greater than in normal varieties. She found that tall varieties had a proportionally greater

meristem and were able to produce more cells. The cells in the dwarf types, however, ceased dividing earlier and elongated for a longer period. The relationship of cell size and cell number to stem length shifted throughout the ontogeny of the plant and was genetically controlled.

Sharman (52) has given a good account of leaf initiation and internode formation during early ontogeny in maize. Periclinal cell divisions proceed laterally from the point of initiation of the leaf primordium around both sides of the apical meristem until the margins nearly meet. Differential rates and planes of cell division within the collar which is thus formed produce a domelike structure which encloses the shoot apex. In the lower half of the original collar, cells begin to divide anticlinally forming a rib meristem with which the first growth of the internode is initiated.

Abbe et al (1) put developmental aspects of the maize shoot on a more quantitative basis. They demonstrated that the shoot apex must attain a certain size before differentiation of parts begins. For each general size increase of the shoot apex with successive plastochrons there is a minimum and a maximum size. Cell size approximates constancy throughout growth of the apex and thus cell number increases in each successive stage in a parallel fashion to external dimensions.

Nilson et al (45) reporting on the relation of parenchyma and epidermal cell length to internode length in winter wheat

demonstrated that in both cell types length differed significantly between internodes. Whereas internode length increased from base to apex of the plant, cell length changed in a reverse manner. There was a direct relationship between cell number and internode length. Epidermal and parenchyma cell numbers increased in total number with increasing length of culm.

Cell length and number are delimited by differential rates and duration of cell division and elongation, which were studied by Kaufman et al (40) in Avena sativa. Concentrating mainly on the development of epidermal tissue of the internode next to the peduncle (P-1) they described intercalary meristem activity, cell morphology, localization of "cytokinetic activity" and differentiation pattern during internode elongation. They confirmed the findings of Athanassoff (13) and Prat (48) that growth and cellular differentiation are basipetal.

Kaufman et al (40) also showed that cell division is not subject to any rhythms but occurs continuously in the base and peripheral portions of the internode, particularly in the lower portions of epidermis and outer ground-parenchyma. Analysis of change and rates of change in cell number and cell length in relation to stages of morphological development showed that cell division and cell elongation are overlapping processes during early development.

Ebiko (25) used plant height in Triticum as a growth criterion in studying the inheritance of growth curves. His study showed that growth rates are heritable and could lead to genetically controlled differential height expression.

Attempts to simplify the analysis of inheritance of a complex trait such as plant height by studying basic growth rates, or by breaking it down into separate components, are frequently useful because of the complexity of gene action. Genetically, developmental processes may be independent but at the phenotypic level they may interact (30) (32). Sinnott (54) and Duarte (24) have presented evidence of gene action with a geometrically cumulative effect, i.e. their phenotypic expressions are multiplicative in action.

The inheritance of plant height has been shown to resolve itself into two parts: the fairly simply inherited characteristics of dwarf vs. tall and the more complex, continuously inherited height differences of a more subtle nature.

The former has been shown to be mainly under digenic (22) (26) (29) (61) or trigenic (27) (33) (35) (60) (64) control; moreover dwarf types have frequently been shown to be unstable cytologically (29) (60) (65).

Investigations into the inheritance of the more subtle height differences have revealed heterosis (28) partial dominance (20) (62) or no dominance (21) in the F_1, transgressive segregation in the F_2 and greater variability in the F_2 and F_3 generations than in the parents (6), (19) (20) (28) (43) (57) (58) (62). It was generally concluded that the mode of inheritance of plant height is Mendelian but that the number of factors involved is large. Torrie (62) established small, significant relationships between plant height, straw strength and earliness in two crosses.

Carlson (19), in a number of crosses involving the Japanese semidwarf, variety Norin 10, made the following observations: (a) Since transgressive segregation occurred in crosses of Norin 10 with taller varieties, Norin 10 must have some "plus" genes for height. (b) Some or all the factors for height are linked and linkage is mainly in the coupling phase. (c) Some or all the factors show dominance, mainly in the direction of tallness. (d) Dominance and environmental variance should not greatly impede selection for height i.e. heritability is high.

According to the results obtained by Allan et al (6) the heritability of culm length in four winter wheat crosses was high (85 to 92%) and the genetic factors involved, at least in some of the crosses, few.

Merkle and Atkins (43) also obtained high heritability estimates of plant height in wheat. They showed that changes in plant height are positively correlated with changes in length of the third and fourth internodes.

Lebsock (41) transferred genes for shortness from a hexaploid Norin 10 derivative to tetraploid durum wheat types. Short strawed progeny from the crosses stabilized at twenty eight chromosomes, but were apparently more sensitive to environment with respect to reaching optimum yields.

F_2 monosomic analyses carried out by Alan and Vogel (5) indicated that at least eleven chromosomes influenced culm length in winter wheat hybrids incorporating Norin 10. No definite location of dwarfing genes was arrived at; however, monosomic analyses by Hurd and McGinnis (35) and Hermsen (33) indicated that in hexaploid wheat a locus for dwarfing occurs on chromosomes 2A (XIII), 4B (VIII) and 2D (XX).

The studies which will be reported here transgress the fields of morphology, anatomy, histology and genetics of a major economic crop plant. The combined literature is considerable and for this reason it has been impossible to present an exhaustive literature review relevant to the problem. Emphasis therefore has been placed on the selection of the most important papers in each area.

MATERIALS AND METHODS

The winter wheat variety Genesee and two homozygous selections of the pedigree (Norin 10 x (Brevor x Yorkwin)) Genesee^2, which will be designated 1518 and 1328, were used in these studies.

Although of similar genetic background, under most environmental regimes Genesee was tall, 1518 intermediate and 1328 short.

Seeds of the three varieties were sown individually in small peatmoss cups arranged in groups of seventy in wooden flats, allowed to germinate in the greenhouse and then placed in a vernalization chamber for eight weeks at 45°F. During this period the young seedlings were provided with constant low-intensity light from incandescent lamps. After vernalization the seedlings, with peatmoss cups, were planted singly in pots of varying diameter or left to develop and mature in the flats. Whether in soil or in sandculture, plants received applications of a complete nutrient solution (modified Hoagland) twice a week. Plant numbers varied according to space available and limitations of handling individual plants. For investigations carried out in the growth chamber a cycle of 16 hours light at 70°F. and 8 hours dark at 55-60°F. was found to be most satisfactory.

Statistical analysis of the results was carried out as appropriate and statistically significant differences were established using either t or F test. In the discussions to follow plant height and culm length are taken to be synonymous.

The studies were initiated with observations in the three varieties on the gross morphology of the culms, height differences of mature culms and variations in height and culm morphology with subtle environmental changes.

Small populations of the three varieties were grown under the following conditions:

(a) Plants were grown in sandculture in the growth chamber; to simulate conditions of closer spacing and increased competition for rootspace they were planted simply in pots of 4 inch, 3½ inch and 3 inch diameter. Varieties were in a completely random arrangement.

(b) Plants were grown in soil in pots of 4 inch diameter in the growth chamber until a few days before heading (early boot stage), then transferred to a greenhouse kept at a relatively high temperature to induce quick, sudden ripening. This experiment was planned to observe, at the gross morphological level, the effect of a short ripening period on the development and final length of the peduncle, which under most conditions contributes to the total length of the culm as much as all other, lower internodes combined.

(c) Seedlings were kept in the vernalization chamber at 45°F. for six months and then transferred to a greenhouse kept at a relatively high temperature. The plants were left in flats and, although they were watered every day, were not provided with any nutrients.

(d) Plants were grown in flats under constant lighting at a constant temperature of 55°F. At the appearance of the first heads the plants were removed to a greenhouse kept at a higher temperature.

(i) One half of each population was watered regularly with complete nutrient solution.

(ii) The remaining half of each population was only provided with water sufficient to keep the plants from wilting.

Experiments (c) and (d) were designed to accelerate developmental processes within the plants and to reduce actual growth in size to a minimum.

At maturity each plant was removed from its growing medium, roots washed clean and trimmed back to the crown and all the leaves and tillers carefully removed from the main culm. The number and length of internodes of the main culm were recorded for each plant. Where the internodes were short and difficult to determine the culms were split longitudinally to facilitate accurate measurement. Mean culm length and mean internode number and length were calculated with their respective variances. The observations of individual experiments were combined in an analysis of variance in an effort to estimate the effect of environment on the internode pattern and total length of culms.

Having established some of the gross morphological differences in the mature culms of the three varieties under slightly

different environmental conditions, the development of the culm was studied next to relate differences in mature plant height to differential varietal development. Large numbers of plants of each variety were grown in flats in the growth chamber. Five plants from each variety were randomly removed and sacrificed at regular intervals to determine the developing internode pattern and total culm length at various stages throughout development. The plants were removed from the soil, the roots washed and trimmed and the leaves and developing tiller buds removed as far as possible. The remaining axis was then split longitudinally to expose the developing main culm. All macroscopically discernible, extending internodes were counted and measured and the height of the growing point determined. Growth curves of the culm and of individual internodes were constructed from these measurements.

To ascertain if differences in size exist before any appreciable growth has occurred, observations were made on embryos and 24-hour old seedlings. Differences between embryos were established on a weight basis. Kernels were harvested in the late dough stage from the heads of ten selected plants from the field. A spikelet was removed from the middle of each spike, care being taken to ensure that the spikelet came from the same position on each spike. The two largest kernels were removed

from each spikelet and the embryos excised and weighed immediately. The average weight of the two embryos was then calculated. Embryos could be dissected from kernels in the late dough stage with a minimum of damage and with far greater ease than from mature, dry kernels. Microscopic examination revealed that the embryos had fully differentiated and little or no difference in size could be detected between embryos dissected from these kernels and those dissected from mature imbibed kernels. The embryos dissected from kernels in the late dough stage still contained a high percentage of moisture and, owing to the very small weight of individual embryos, moisture loss tended to increase the error of the fresh weight determinations. Reasonably accurate results were obtained, however, when each embryo was weighed immediately after dissection.

Observations were repeated using dryweight determinations. Upper and lower spikelets were removed from selected heads leaving the eight central spikelets. Embryos were removed from the two largest kernels of each of these remaining spikelets, bulked in ten groups of 100 embryos for each variety and dried for two days at approximately 106°C. before weighing. Average weights and variances were calculated for the three varieties on both dry- and fresh-weight basis.

To establish differences in size before the onset of extension growth, 24-hour old seedlings were removed from germinating kernels and fixed in a solution of alcohol, water and formalin in the

proportion of 60: 40:4. They were dehydrated in ethyl alcohol and chloroform and embedded in parafin. Median longitudinal sections of 10 micron thickness were cut and triple stained with safranin, crystal violet and orange G. Images of sections of ten seedlings from each variety were projected on a screen with a microprojector and measurements were made of various gross dimensions.

The investigations thus far were designed to establish (a) the relative contribution of internode number and length to differences in mature culm length, (b) the influence of environment on internode pattern and hence total length, (c) differences in development of culms and individual internodes of the three varieties leading to differences in length and (d) the stage of development where size differences related to height differences at maturity first become apparent.

Next, the relationship of cell length and cell number to internode length and culm length was established for the three varieties. Cell size and cell number were estimated in plants grown in sandculture in 4" pots and in soil in flats. Here again the objective was not so much to study the effect of a specific environmental factor on cell size and number as to study the manner in which these two characteristics changed in a slightly varying environment. Approximately 2 weeks after general anthesis i.e. when plants had attained their final

mature height but were still green, four plants of each variety were selected from the plant population in the flats and 6 plants each from the sandculture. The main culms were carefully removed from the plants and stripped of their leaves. After the length of the internodes had been measured, a section 2cm. long was removed from the middle of each internode for estimation of cell size. Cell number was then calculated. Although cell length along the mature internode varies slightly the cell lengths in the middle of the internode give a reasonably accurate estimate of the mean cell length for that internode. The technique that was first used to determine cell length in the collected samples was to split the sections longitudinally, clear the tissues in a mixture of phenolic and chloral hydrate crystals 1 : 1 and then storing and mounting the cleared sections in lactic acid (17). Although the clearing technique was excellent for studying cellular and vascular organization within tissues, it was found to be faster to measure epidermal cells by stripping off small segments of epidermal tissue from the internodes and mounting them in a drop of aceto-carmine. Eventually most observations on cell size were made this way. According to Nilson et al (45) parenchyma cells show less variation and are more constant in demonstrating the changes in cell size and number than epidermal and other cells. However, in the above studies it was found that there was quite a variation

between successive layers of parenchymal tissue of the stem and that it was difficult to select comparable files of cells in the sample sections without bias. Epidermal tissue proved to be quite satisfactory and far easier to observe. Moreover, in developmental studies this tissue is far superior for detailed observation of cell division, elongation, maturation and differentiation. Epidermal long cells, three rows removed from stomatal cell files were used for measurement. Ten samples of 3 cells in succession, selected at random along the 2 cm. long portion were used to calculate the mean cell length and hence the mean cell number per internode. Because of variability of lower internodes only 4 upper internodes were used for comparative studies.

Having established the relationship of cell length and cell number to internode length and total culm length in the three varieties, the next step was to study the histological development of the internodes to relate final differences in internode length to differences in rates and duration of cell division and elongation. Populations of plants were grown in the growth chamber in flats and samples of three plants removed at intervals throughout development. The plants were split longitudinally and the developing culm dissected out and stored in Newcomer's solution (44). The number and length of the

developing internodes was determined and small portions of the various internodes mounted in aceto-carmine and studied microscopically to ascertain cell division and elongation patterns and cell lengths and numbers in the various regions of the developing internode. The number of sample regions of each internode that were studied varied and depended on what was considered to be a reasonable and adequate sample to give a true histological picture of the developing internode.

To conclude this study on plant height (or stem length) an experiment was conducted to elucidate some of the factors involved in the genetical control of plant height. Crosses were made between 1328 (short) and Genesee (tall) to produce populations of reciprocal F_1, F_2 and backcross plants. These populations, together with those of the parents were grown in the growth chamber in $3\frac{1}{2}$ inch pots. The plants were randomly distributed on six tables and to equalize environmental conditions as far as possible the tables were rotated every 2 days in a clockwise direction and each table was rotated through 180 degrees, until the plants reached maturity. Observations made on the populations included internode length, internode number and total length of the main culm.

RESULTS AND DISCUSSION

Height Differences at Maturity

Data on mean culm length, mean internode length and internode pattern have been summarized in Table 1 and Figure 1 (a - h). Statistical analysis of these data is presented in Table 2.

Averaged over all environments Genesee was tall, 1518 intermediate and 1328 short. The environmental influence on height expression was far greater than that of the varietal effect.

Table 1. Variation in mean length (inches) of main culms of Genesee, 1518 and 1328 with different environment.

Environment	Genesee	1518	1328	Mean
Short ripening period	31.09	27.93	23.59	27.54
4 inch pots	27.30	25.57	22.58	25.15
3½ inch pots	19.45	17.70	16.40	17.85
3 inch pots	21.12	19.95	17.40	19.49
55°F. cont. light. High nutr.	18.95	19.25	16.64	18.28
55°F. cont. light. Low nutr.	15.07	13.16	10.47	12.90
6 months vernalization	15.31	13.40	11.55	13.42
Mean	21.18	19.56	16.95	

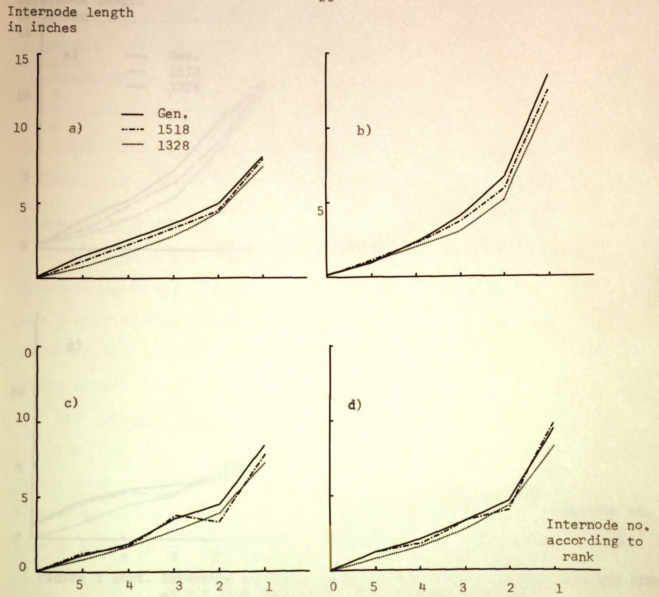

Figure 1. Internode patterns of the main culms of Genesee, 1518 and 1328.
a) Average of seven environments.
b) 4.0 inch pots. Sand culture.
c) 3.5 inch pots. Sand culture.
d) 3.0 inch pots. Sand culture

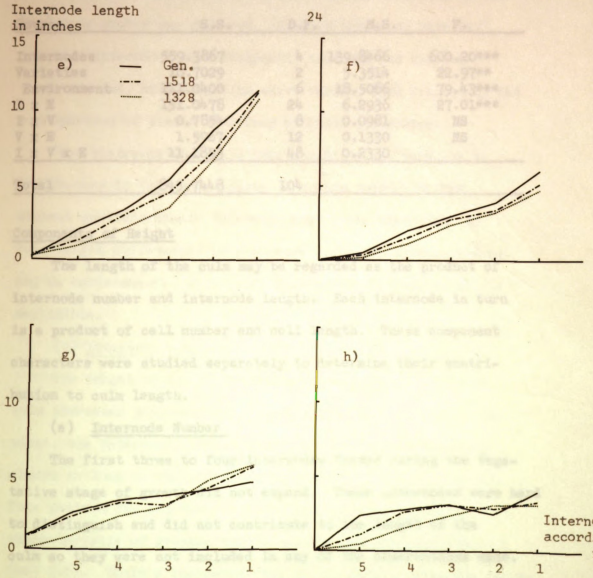

Figure 1 cont. Internode patterns of the main culms of Genesee, 1518 and 1328.
e) 4.0 inch pots. Soil. Short ripening period.
f) Seedlings kept 6 months at 45°F.
g) Continual light. Constant 55°F. High water and nutrition.
h) Continual light. Constant 55°F. Low water and nutrition.

Table 2. Analysis of variance of internodal pattern of main culms of Genesee, 1518 and 1328 under different environmental conditions.

Source	S.S.	D.F.	M.S.	F.
Internodes	559.3867	4	139.8466	600.20***
Varieties	10.7029	2	5.3514	22.97**
Environment	111.0400	6	18.5066	79.43***
I x E	151.0478	24	6.2936	27.01***
I x V	0.7854	8	0.0981	NS
V x E	1.5967	12	0.1330	NS
I x V x E	11.1853	48	0.2330	
Total	845.7448	104		

Components of Height

The length of the culm may be regarded as the product of internode number and internode length. Each internode in turn is a product of cell number and cell length. These component characters were studied separately to determine their contribution to culm length.

(a) Internode Number

The first three to four internodes formed during the vegetative stage of growth did not expand. These internodes were hard to distinguish and did not contribute to the length of the culm so they were not included in any of the observations made. As the number of extended internodes depends on the lowest internode to expand first, internodes have been numbered according to rank from the top of the plant down, the peduncle being designated internode 1.

The number of extended internodes varied from four to six,

between and within varieties, but averaged five under most environmental conditions. Some differential variation in the internode number was observed. Genesee tended to have six extended internodes more frequently than the two shorter varieties and, similarly, the short variety 1328 frequently had a proportion of plants with four extended internodes.

The statement that culm length differences were due to differences in internode length therefore cannot be made without qualification. Internode number did contribute to culm length differences to a greater or lesser extent, depending on environment. As a rule, however, its contribution was negligible.

(b) Internode Length

The length of the five extended internodes in the main culm increased progressively from the base to the apex of the plant, the uppermost internode or peduncle frequently being almost as long as all the other internodes combined (Fig. 1). This pattern did not vary with variety and appears to be characteristic of grasses and cereals in general (13) (38) (46) (48). Table 2 indicates that the variety x internode interaction was not significant, suggesting that the internodal pattern is the same in all varieties. In all cases, the variation due to internodes within plants was somewhat greater than that due to plants indicating a certain amount of compensation between internodes.

In the tall variety Genesee, the lower extended internodes contributed proportionally more to total stem length than in the shorter varieties. Averaging the internode measurements of plants in the seven environments studied (Figure 1 (a)), 62.8% of the total stem length of Genesee was due to the upper internodes whereas the three lower internodes contributed 37.2%. For 1518 and 1328 comparable figures were 64.1% and 35.9%, 69.1% and 30.9%.

Proportionally the difference between comparable internodes of the three varieties tended to increase down the culm. However, as the internode lengths decreased sharply the contribution to the difference in absolute terms was not so great. The proportional increase in internode difference was not evident under all conditions.

Maturity differences were very slight, but were observed in a good many cases. Earliness was always correlated with reduced height. The peduncle contributed progressively more to total length in the shorter varieties. In T. vulgare the peduncle is frequently out of phase with the other internodes especially in short and early varieties.

A definite association with maturity was observed by Prat (48) in both cereals and other grasses. He was able to demonstrate that, as the plant became earlier in maturity, the lower extending internodes became proportionally less and less important in the length of the culm. In the very short lived

ephemeral types of grasses the culm is made up almost entirely of peduncle.

Internode length contributes far more to plant height differences than internode number. Differences in total length of culm between varieties are due to differences in length of all individual internodes (Figure 1). Changes in internode length must be due to alteration in cell number, cell size or both. The evidence obtained from the observation of the three closely related varieties indicated that indeed both are involved and, moreover, that they are independent.

(i) Cell Number

Within each variety, cell number per internode increased from the lower to upper internodes. Thus, the greater length of each successive internode was due to a greater number of cells. This was not a simple relationship because cell size decreased in progressively higher internodes and so cell number increased almost exponentially.

Figure 2 (a) and (b) shows the distribution of cell length and number in the four upper internodes of each variety, under two different environmental regimes. The great variability which generally occurs is clearly demonstrated when these results are compared.

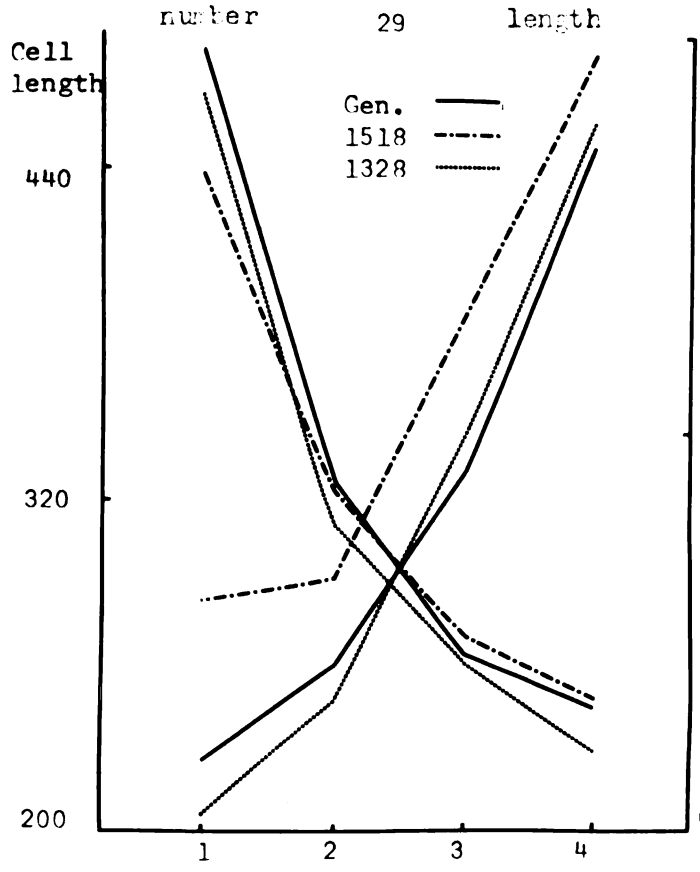

Figure 2 (a). Cell length and number in four upper internodes of Genesee, 1518 and 1328 plants grown in soil in 1 3/4 inch square peatmoss pots in flats.

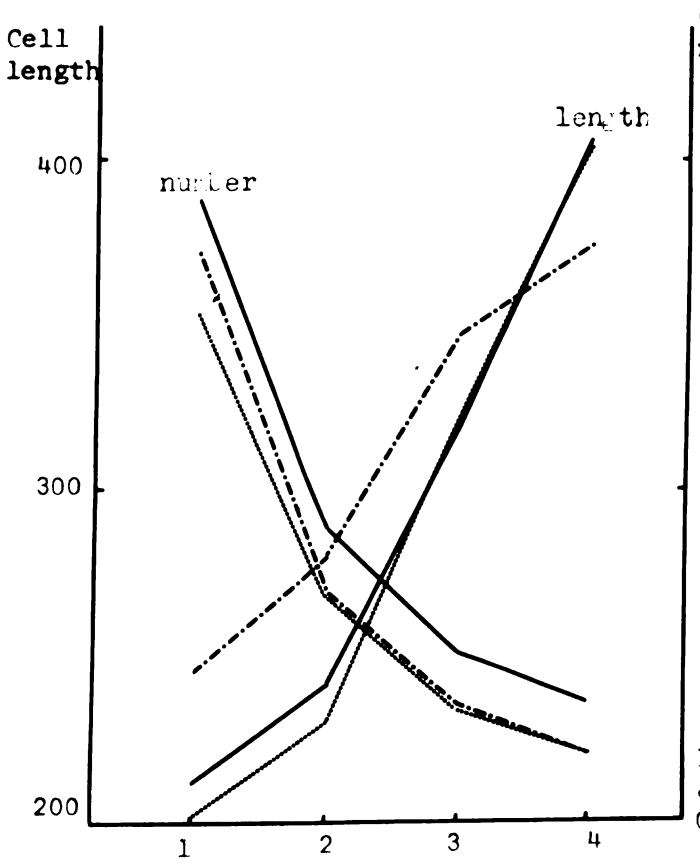

Figure 2 (b). Cell length and number in four upper internodes of Genesee, 1518 and 1328 plants grown in sandculture in 4 inch pots.

Statistical analyses of cell number are presented in Tables 3 and 4. Cell numbers are significantly different between varieties and internodes. Because of the fairly great variability between plants the interaction varieties x internodes only just reaches significance (Table 4). The interaction is due to the fact that the cell number of the Genesee and 1518 peduncle decreases more rapidly than that of 1328 (Figure 2 (b)). Although differences existed between all three varieties, Genesee had a considerably greater cell number than 1518 or 1328.

Table 3. Analysis of variance of cell numbers in internodes of plants of Genesee, 1518 and 1328 in Figure 2 (a).

Source	S.S.	D.F.	M.S.	F
Varieties	23048.0417	2	11524.0208	NS
Internodes	6134284.2292	3	2044761.4097	**
V x I	75125.9583	6	12520.9930	NS
Subtotal	6232458.2292	11		
Within	361652.7500	36	10045.9000	
Total	6594110.9792	47		

Table 4. Analysis of variance of cell numbers in internodes of plants of Genesee, 1518 and 1328 in Figure 2 (b).

Source	S.S.	D.F.	M.S.	F
Varieties	629168.44	2	314584.22	19.37**
Internodes	23435365.04	3	7811788.34	481.18***
V x I	97407.34	6	16234.55	2.54*
Subtotal	24161940.82	11		
Within	383291.17	60	6388.18	
Total	24545231.99	71		

(ii) Cell Length

The change in cell length between internodes is not a gradual one. Above each node cell length changes abruptly but stays fairly constant within each internode, although at maturity the lower cells of each internode are slightly larger than those towards the top.

Cell length is inversely related to internode length within each variety. Cell length decreased almost linearly from the lowest internode up, except for the peduncle. In this internode there was a sharply decreased reduction in cell size in all varieties (Figure 2 (a) and (b)). It is interesting to compare this with the data obtained by Athanassoff (13) which showed that cell length in T. turgidum was directly proportional to internode length, except in the peduncle in which cells were considerably smaller.

Each internode is a fairly distinct entity, the elements of which are of a constant size at maturity. As a rule its length, cell size and cell number are intermediate to its neighboring internodes, but a great deal of variation occurs and the remarkably constant expression of final height appears to be the result of a compensating relationship among its components. Statistical analysis of cell length data confirmed that Genesee and 1328 have similar average cell length while the average cell of 1518 was significantly longer (Tables 5 and 6).

Table 5. Analysis of variance of cell lengths in internodes of plants of Genesee, 1518 and 1328 in Figure 2(a).

Source	S.S.	D.F.	M.S.	F
Varieties	167.3721	2	83.6860	3.42*
Internodes	2526.4402	3	842.1467	34.43**
V x I	26.3183	6	4.3863	
Subtotal	2720.1306	11	247.2846	
Within	1001.0055	36	27.8057	
Total	3721.1361	47		

Table 6. Analysis of variance of cell lengths in internodes of plants of Genesee, 1518 and 1328 in Figure 2(b).

Source	S.S.	D.F.	M.S.	F
Varieties	6655.66	2	3327.83	1.23 NS
Internodes	341316.69	3	113772.23	45.21***
V x I	15098.98	6	2516.49	9.33**
Subtotal	363071.33	11		
Within	16177.29	60	269.62	
Total	379248.62	71		

In the analysis shown in Table 6, the great combined effect of internodes and interaction variety x internodes obscured the true differences between varieties. When the results were reanalyzed with the effects of internodes and variety x internodes removed (Table 7) only in the fourth internode did the difference not reach significance.

Table 7. Analysis of variance of separate internodes to remove the effect of internodes and variety x internode interaction.

	Source	S.S.	D.F.	M.S.	F.
Internode 1	Varieties	6226.54	2	3113.27	36.76***
	Within	1269.35	15	84.62	
Internode 2	Varieties	8739.94	2	4369.97	23.20***
	Within	2825.27	15	188.35	
Internode 3	Varieties	2901.63	2	1450.81	5.79*
	Within	3758.24	15	250.54	
Internode 4	Varieties	3886.53	2	1943.26	3.50NS
	Within	8324.45	15	554.96	

The results in Figure 2 (a) were obtained under conditions of growth that produced internode lengths more variable than normally encountered under more favorable conditions. 1518, the intermediate variety, actually grew taller than Genesee. The particular environment also affected the expression of internode numbers (Table 8). It appears that in this instance the difference in height between Genesee and 1328 was not only due to internode length but also to the fact that 1328 consistently formed only four internodes. Plants of Genesee had at least five internodes.

Table 8. Mean internode number and length and total culm length of plants used for estimation of cell lengths and numbers presented in Figure 2 (a). Plants were in flats.

Variety	Internode						Total Length	Internode Number
	1	2	3	4	5	6		
Genesee	26.0	12.9	8.2	7.6	3.3	0.6	58.6	5.25
1518	26.5	13.8	10.6	8.6	4.1	---	63.6	4.50
1328	22.9	11.0	8.1	4.7	---	---	46.8	4.00

Height differences observed were not due to the multiplicative effect of cell lengths and cell numbers, but to a variable and often compensatory expression of internode number, cell number and length. However, it would appear that cell number and length characteristic for each variety, and for internodes within each variety, have considerable stability.

Combining the data presented on cell number and size, and keeping in mind the great variation encountered throughout these studies, it can be stated that both cell number and cell length contribute to plant height differences. Between Genesee and 1328 it is mainly cell number, whereas between 1518 and 1328 it is cell size. Both are involved in the difference between Genesee and 1518.

The Effect of Environment on Height

The tall variety appeared to be more influenced by environment than the two shorter ones. With decreasingly favorable environment, the absolute height of all varieties decreased, the height differences between the three lines were reduced, but their relative positions remained the same, except on one occasion when 1518 exceeded Genesee in height.

One exception to the reduction in culms length with increasing stress occurred when plants were grown in 3 inch pots. The mean length of all lines was greater than that observed in the $3\frac{1}{2}$ inch pots, presumably a more favorable environment. Plants in the $3\frac{1}{2}$ inch pots produced 2 to 3 tillers while those in the 3 inch pots generally had only one culm. Possibly the lower light

intensity, owing to smaller spacing, and the greater nutritional stress significantly reduced tillering at this point and all the nutrition available went into the main culm.

The Effect of Environment on Components of Height

(a) Internode Length and Number

Statistical analysis of internode length shows that all varieties are similarly affected by environment, which, within varieties, has a differential effect on individual internodes. It deserves special note that the interaction, internode x environment, contributes more to the overall variance than the effects of varieties and environment combined (Table 2).

The internode pattern of plants grown under optimum conditions was nearly exponential. With increasing environmental stress the pattern changed progressively from an exponential to a linear one. Eventually, the upper internodes formed were shorter than the lower ones (Figure 1, b-h).

The lower internodes were more resistant to change with environment than the upper ones. The internodal patterns as plotted in Figure 1 (b-h) show this very clearly. These graphs, called internode diagrams by Anderson and Schregardus (9) not only show the change in length of successive internodes but also the rate of change of their respective lengths. This rate of change, especially in the lower internodes, was less in the shorter- than in the tall varieties. Environment greatly influenced it, particularly in the upper internodes. Thus,

whereas genetic differences in length were evident in all internodes, environmental changes were reflected more in the upper internodes.

Generally the upper internodes of Genesee were more affected by environmental stress than those of the shorter varieties (Figure 1). This accounted for the fact that, with increasingly severe environment, the average difference in culm length between varieties was reduced. The intermediate variety appeared to be more variable in its behavior than the other two.

The length of an internode is determined by its sequential position on the culm, i.e. it is probably influenced by the internode above and below it, and by environment. Because the development of internodes is separated in time, minor fluctuations in environment result in variation in internode pattern of individual plants. The mean internode pattern, however, is remarkably consistent and the general trend of environmental effect on the final expression of internode- and culm length is broadly predictable. Conditions of increasing stress and competition result in progressively decreased length of internodes and total length.

The effect of environment on internode number could not be determined with certainty. It appeared that unfavorable conditions tended to decrease the internode number. Observations indicated, however, that this did not occur in all cases (See Figure 1 (g)).

(b) Cell Length and Number

Environmentally induced variation tended to obscure the differences in cell numbers between comparable internodes of varieties. But, as in internode number, no general pattern could be detected in environmental influence on cell number.

It has been reported that the decrease in culm length as growing conditions move away from the optimum is due to a reduction in cell size rather than cell number (66). Observations made here indicated that both were affected. Plants that were grown under less favorable conditions were found to have smaller cell numbers, but cell size was actually increased compared to those grown under more favorable conditions (Figure 2 (a) and (b)). The greater height of the latter plants, therefore, was actually due to increased cell numbers.

Culm Development

Primarily for convenience and simplicity, the developing culm was studied in a number of more or less arbitrary growth periods in order to determine where, when and how plant height differences are first expressed and how they consolidate throughout development. The periods of growth studied were (1) before germination (2) germination to three-leaf stage (3) three-leaf stage to period of rapid elongation (4) period of rapid elongation through maximum extension. Growth periods (2) and (3) were separated by vernalization treatment and thus the

critical transition from the vegetative to the reproductive phase occurred there.

(1) Before Germination

Embryos of Genesee weighed significantly more than those of 1518 and 1328. No difference could be detected at all between the latter two (Table 9).

Table 9. Fresh- and dry-weights of embryos excised from kernels, in the late dough stage, of Genesee, 1518 and 1328. (gms. x 100,000)

	Fresh weight	S.D.	Dry weight	S.D.
Genesee	210	2.05	158	2.66
1518	194	0.97	131	3.32
1328	193	0.95	133	3.82

Bigger seeds have bigger embryos as a rule. Hence the greater "initial capital" frequently leads to increased size at maturity. This has been established, although results do not always agree. Bindloss (15) mentioned the conflicting reports of the effect of seed weight on plant height and made sure that both the tall and dwarf plants she studied had similar seeds. Nevertheless, she found that height differences may be evident throughout development, or manifest themselves only at a later stage of development. The seed weight of Genesee, 1518 and 1328 decreased progressively in direct relation to height, as did kernel volume and specific

gravity of the kernel (Table 10). Thus, there appeared to be a positive correlation between height and seed weight of the three varieties.

Table 10. Weight, volume and specific gravity of kernels of Genesee, 1518 and 1328.

	Mean Kernel weight mgs.	Mean kernel volume ml. x 10^{-3}	Spec. Grav. of kernel
Genesee	37.66	31.05	1.2133
1518	33.55	28.25	1.1881
1328	29.58	25.55	1.1581

The F value for varieties was significant at the .01 percent level.

Equal seed weight is no guarantee that plants start growth with the same "initial capital." Correlation of seed weight and plant height is affected by (a) the relative contribution of embryo and endosperm to total seed weight and (b) the stage of development that size (or height) differences are initiated. Bindloss found dwarf types with cells that matured earlier and elongated for a longer period than those of tall types, resulting in dwarf plants with fewer but larger cells. The difference between Genesee and 1518 would appear to approach this situation. However, the difference between these varieties was already evident in the embryos, something which Bindloss attempted to avoid, although she did not actually verify that this had been accomplished, other than on the basis of seed weight.

(2) Germination to Three-Leaf Stage

As representative of this period 24-hour-old seedlings were used. These seedlings had just germinated and the three foliage leaves, although present, had not yet unfolded. Estimates of various gross dimensions of the young seedlings showed again that 1518 and 1328 were similar, although the seedlings of 1518 were somewhat more slender. Genesee was larger than the other two but did not appear to be more advanced in development (Figure 3, Table 11). Owing to the difficulties involved in obtaining comparable longisections for microscopic examination, estimates of cell size and number showed a great deal of variation. However, the size of the meristematic cells in the apical regions appeared to be the same for all three lines.

Figure 3. Diagramatic representation of a median longisection of a 24-hour-old seedling indicating the various gross measurements made as listed in Table 11.

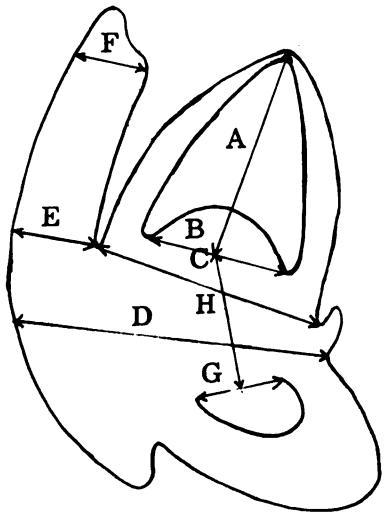

Table 11. Mean measurements in inches made of various gross dimensions of projected images of ten 24-hour-old seedlings of Genesee, 1518 and 1328, as indicated in Figure 4.

	A	B	C	D	E	F	G	H
Genesee	9.89	5.10	8.56	10.57	2.47	3.47	5.20	6.06
1518	8.87	4.07	6.66	8.14	1.77	2.73	4.03	4.83
1328	8.58	4.22	6.62	9.23	1.70	3.10	5.03	5.00
S.E.	0.445	0.121	0.268	0.283	0.184	0.283	0.346	0.245

The F value for varieties was significant at the .01 percent level for all measurements.

At this early stage, therefore, the difference between Genesee on the one hand and 1518 and 1328 on the other appeared to be due to cell number. Recalling that the difference in culm length between Genesee and 1328 is due to cell number and that between 1518 and 1328 to cell length, it appears that height differences based on cell number originate at some stage during embryogenesis while the capacity for greater cell elongation is expressed at a later stage of development, after germination. Thus, clearly, two fundamentally different developmental processes must be involved in causing the respective differences in height, making apparent independence understandable.

(3) Three-Leaf Stage to Period of Rapid Elongation

This relatively short period began when the vernalized plants were brought into a favorable environment for growth and ended with the beginning of rapid elongation. Although growth was slight, differences in the height of the growing point became observable under a dissecting microscope as soon as the plants had adapted themselves to their new environment, after a few days at the most. During this period the first evidence of greater cell size in the stem of 1518 became visible. Varietal differences in extension were far greater at this stage than any environmentally induced variations. Genesee was at all times more advanced in development than the two shorter varieties. Development was more rapid in all varieties when kept at low temperature and low levels of nutrition, but this was not so striking in Genesee as in the shorter lines. Figure 4 indicates the differences in culm extension and development that could be detected just prior to the beginning of rapid elongation.

(4) Period of Rapid Elongation Through Maximum Extension

Growth curves of the three varieties and the relative chronological development of their internodes are presented in Figures 5 and 6. It is evident that the difference in culm length between the three varieties is manifested at a very early stage.

In terms of relative growth during this period, the observed

Figure 4. Tracings of projected images of longisections of shoots of Genesee, 1518 and 1328 at the beginning of rapid elongation.

(a) Genesee; high nutrition and moisture

(b) Genesee; low nutrition and moisture

(c) 1328; high nutrition and moisture

(d) 1328; low nutrition and moisture

differences in length of mature culms could be explained by both differential duration and rates of growth. Genesee elongated over a longer period than either 1518 or 1328 but its rate of growth was similar to that of 1518. The rate of growth of 1328 however, was distinctly lower than that of the other two.

Genesee did not always start elongation much earlier than the other two varieties, but in such cases maturity differences at the end were more pronounced with Genesee always being the last to fully expand and mature. The total effect appeared to be one of shifting the growth curve of Genesee slightly to the right of 1518, (Figure 5), in such a way that the curves of these two varieties cut across each other. Especially under crowded conditions with high nutrition 1518 was frequently found to be taller in the early stages of development. At a later stage, however, Genesee would overtake it to mature at a greater length.

The pattern of internode elongation is basipetal, the upper internode being the last to elongate. Elongation does not begin until the plant has entered the reproductive phase and flowering primordia are visible at the apex. The number of internodes has therefore been determined at the time of first elongation.

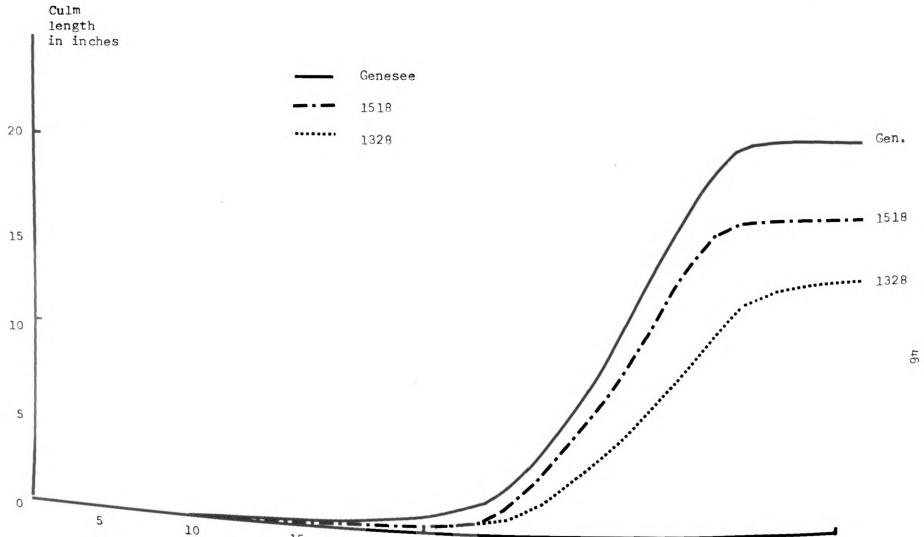

Figure 5. Relative growth rates of main culms of Genesee, 1518 and 1328 in growth chamber 1963, as expressed by total length. Plants were grown in flats in peatmoss cups.

Three consecutive internodes elongate simultaneously at any one time: the upper one starting, the middle one extending rapidly and the lower internode just completing expansion. The most rapid increase in total length takes place during the elongation period of the first and second internodes from the top. These two internodes combined make up a large percentage of the total length at maturity and during their "grand phase" of expansion the increase of the total length of the culm is extremely rapid.

The growth curve of the entire stem is, in effect, the sum total of the growth curves of its internodes. Differences in the rates of growth of comparable internodes of the three varieties were difficult to define. However, both duration and time of initiation of elongation of comparable internodes differed greatly. The length advantage of Genesee is primarily due to the fact that its lower extending internodes generally elongate over a much longer period. The internodes of 1518 and 1328 elongate to an almost identical pattern except that the lower internodes of 1518 elongate for a slightly longer period (Figure 6).

The actual duration of extension appears to be the more important contributing factor to mature length differences. Johnson (38) studying the development of three wheat varieties of different inherent height also found the difference to be due to duration rather than rate of growth. This may explain

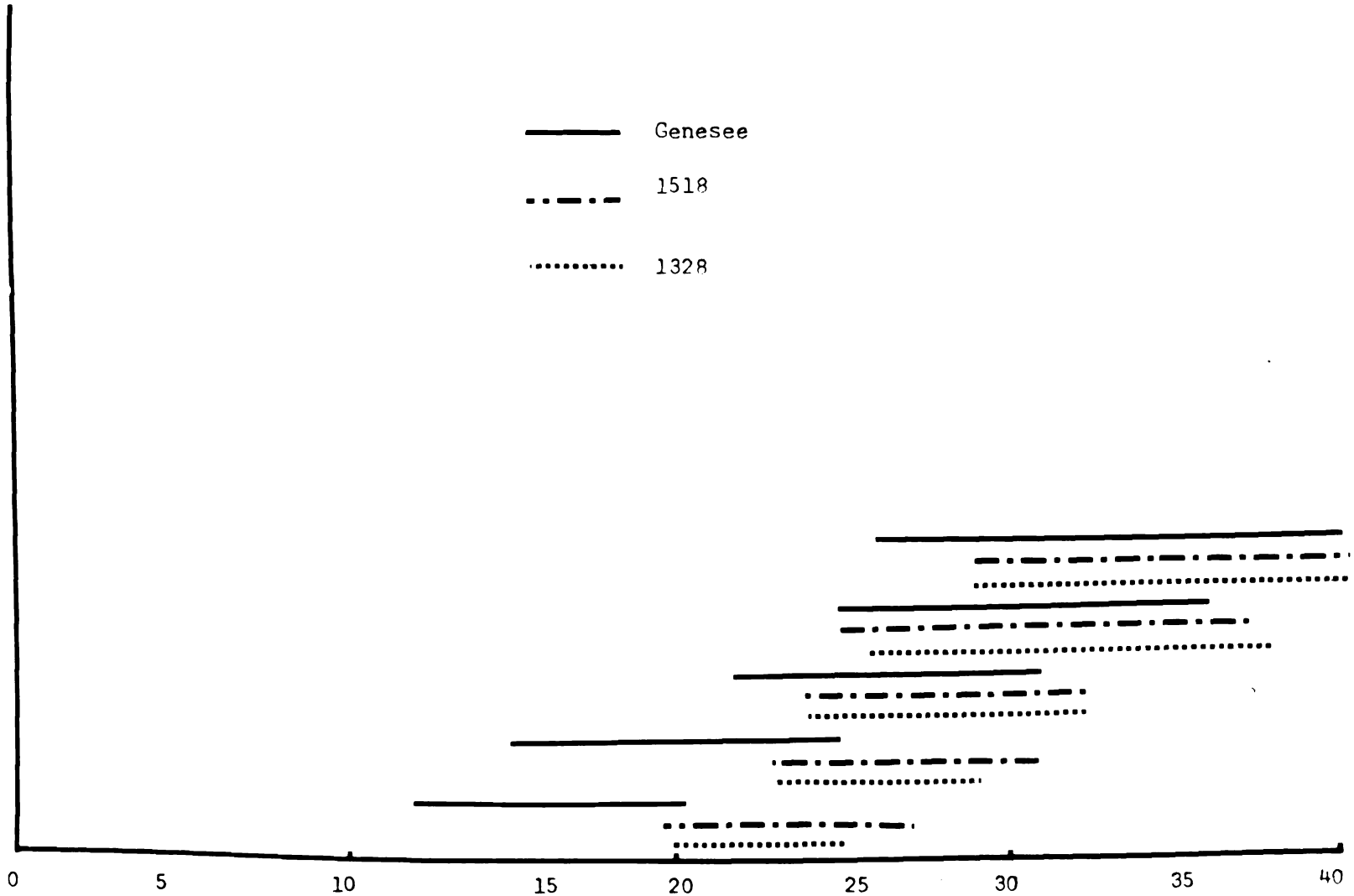

Figure 6. Approximate pattern of internode elongation of Genesee, 1518 and 1328. Growth chamber 1963.

the definite association with maturity found here, by Johnson (38), Prat (48) and others. The results here, however, indicate that differential growth rates are also involved. These growth rates are heritable as was shown by Ebiko (25).

The data suggest that the greater culm length of Genesee is due to a greater "initial capital" and longer duration of growth. Ashby (11) postulated that increases in growth due to heterosis were no more than the maintenance of a greater initial size caused by physiological stimulation during embryogenesis. The greater embryo size of Genesee must also be due to increased physiological activity during the development of the embryo.

In trying to account for the heterotic effects, Ashby could find no differences in growth rates so they must have been due to greater duration of growth activities. Stein (56) found that in reciprocal hybrids between inbreds of Zea mays, scutellum development and leaf initiation appeared to start earlier, giving hybrids an advantage. As no difference could be detected between the rates of development in hybrids and inbreds it seemed to be the longer duration of growth processes that lead to eventual greater plant size. Since the greater height of Genesee seems to be due, in no small part, to longer periods of development of its internodes as compared to those of the shorter varieties, it is easy to surmise, considering this and the above evidence, that the larger size

of the Genesee embryo is possibly also due to a longer duration of development. Duration of growth is therefore more important than growth rate in the expression of culm length.

In Figure 7 the cell numbers of the developing peduncle of Genesee, 1518 and 1328 are plotted against the length of this internode at the various stages of development. This gives some indication of the relative importance of cell division and elongation in the extension of an internode and differences which exist between varieties in this respect.

Homeostatic Systems in Plant Height Expression

The influence of environment on culm length is great. Even greater variability exists at the internodal and cellular levels due to environmental influence. For example, in one of the experiments (Figure 1 (d)), the internodes of Genesee had coefficients of variability of 19.9%, 13.1%, 20.3%, 18.8% and 50.3%. The C.V. of total height, however, was only 10.6%. These results are typical for all varieties under all environmental conditions. Similarly, average cell size and cell number, characteristic for each internode of a variety, are fairly constant. However, a tremendous amount of variability exists within internodes.

Considering the influence of light, temperature and other factors on both cell division and cell elongation this is perhaps not surprising (18). Variation is induced at this "micro level" (16) and compensating mechanisms, which are due to nothing more

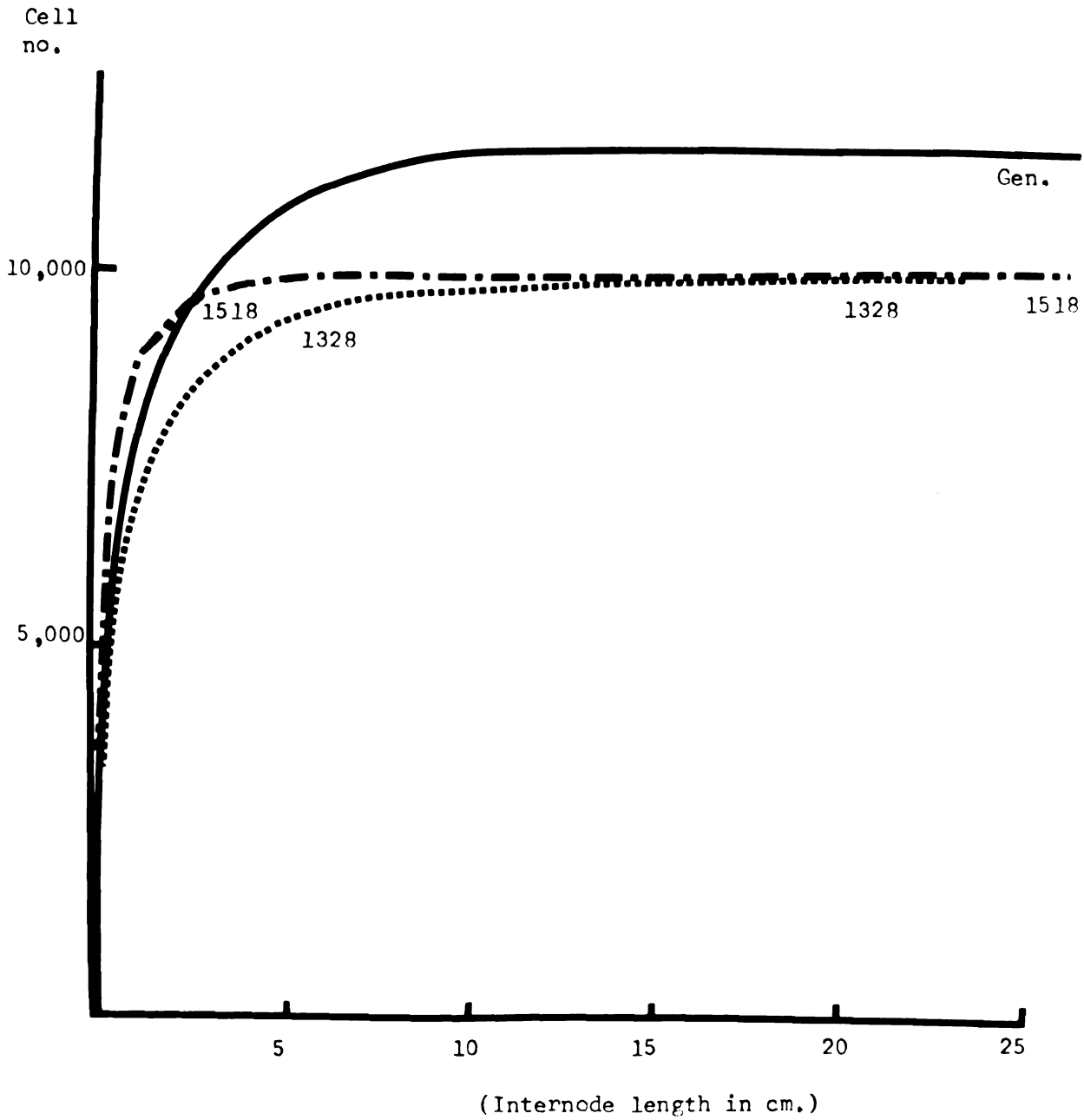

Figure 7. Cell number of the peduncle of Genesee, 1518 and 1328 during development.

than the influence of one developing part on another become evident. If the development of one part is altered by a change in environment, presumably its correlative effect on that of another is also changed giving a compensating effect. Compensatory mechanisms are evident at both the cellular and component levels.

This raises the question of how far down does one set the micro- or component level in attempting to explain the heritable behavior of a complex character. In research, the explanation of any biological phenomemon is normally procured by breaking it down into smaller and smaller components and by developing a "micro-theory" (16). However, in heredity, the variation at this microlevel may be so great that this, and the very large number of interacting genetic and physiological components which may be involved, lead to a situation where the complex, integrated trait may be more stable and predictable in its behavior than any of its individual components.

Plant height in cereals, although a complex character, normally has a fairly high heritability. Its expression within any one environment is stable owing to compensation of its components, which themselves can display a great deal of variation. This would suggest that, from an applied point of view at least, it may be more meaningful to remain at higher levels and

in more complex categories when manipulating quantitative traits such as plant height in heredity. Studies, under rigidly controlled environments, of components at the micro-level may provide some of the answers as to basic mechanisms, but from a practical plant breeding point of view the interactions at higher levels are more important. Other complex systems, however, may be amenable to the component approach.

In the final issue one is only concerned with interactions: nucleus x cytoplasm, gene x gene, cell x cell, cell x external environment, and one can only arrive at sensible explanations by specifying all known relative conditions. In morphogenetic development of a quantitative trait this can be exceedingly complex.

In crosses between Genesee and 1328, heterosis was evident in the F_1. The variance of the segregating F_2 population was only little greater than that of the tall, homozygous parent. Under field conditions, the variance of the F_2 population was actually smaller than that of the homozygous, tall parent. Means and variances of culm length of Genesee, 1328 and their hybrid are presented in Table 12.

Table 12. Means (cm.) and variances of culm length of Genesee and 1328 and the hybrid Genesee x 1328.

	Growth chamber			Field	
	$\bar{x}$	σ^2		$\bar{x}$	σ^2
Genesee	62.84	30.58	Genesee	75.57	100.95
1328	52.26	22.73	1328	54.27	16.79
F_1	65.23	38.18	F_2	62.57	55.01
F_2	62.04	36.66			

It will be recalled from the results of earlier experiments that the tall variety Genesee was less resistant to environmental changes with respect to height than the short 1328. Other experiments in the growth chamber and in the field confirmed this. It would thus appear that in the interaction with the micro-environment a homeostatic or buffering element is present which masks the expression of quantitative characters. This could take the form of compensatory interaction, which was evident at the component and at the cellular levels.

Homeostasis is usually associated with heterozygosity, the developmental paths of heterozygotes being better buffered against environmental fluctuations than those of homozygotes (23). Tebb and Thoday (59), however, found that heterozygosity does not necessarily promote homeostasis. Moreover, others (4), (7), (36), (51) have presented evidence that differential

buffering exists amongst homozygous genotypes. At first glance it would therefore appear from the results in Table 12 that differential buffering capacity may have been responsible for differences in variability in the varieties, and that plants in the F_2 populations especially in the field segregate for these properties of homeostasis and environmental interaction. One must be careful in drawing conclusions, however, because most of the difference in variability observed is due to variance associated with height (Table 13).

Table 13. Regression of variance on height in Genesee and 1328.

	Source	DF	S.S.	M.S.	F
Genesee	Regression	1	174.21	174.21	20.96**
	Deviations from regression	5	41.56	8.31	
1328	Regression	1	80.62	80.62	4.93 NS
	Deviations from regression	5	81.79	16.36	

Previously presented evidence showed that the greater variability of Genesee was mainly associated with the greater sensitivity of its upper internode to environmental fluctuations. Table 13 indicates that when the variability dependent on plant height has been allowed for, Genesee is actually less variable than 1328 i.e. more homeostatic. This one would expect, as Genesee is a commercial variety of long standing, probably more highly adapted than 1328, a selection of recent breeding.

The great difficulty of obtaining and interpreting valid data in inheritance studies of continuously variable traits is emphasized by the above evidence. Differential homeostasis of homozygous parents and heterozygous hybrid populations and variability dependent on height will tend to obscure segregation. In the particular case reported here both of the parental lines were adapted lines, in harmony with their particular environment, and had probably evolved an efficient buffering system to maintain phenotypic stability. For full expression of genotypic variation the F_2 should probably have been grown and observed outside their adaptive environment. Rigid control of environmental conditions in the growth chamber only seemed to enhance the buffering effect, most of the observed variation being environmental.

Study of the character at the component- or even the cellular level does not seem to be the answer, as the great variability and compensatory interaction here leads one to the conclusion that little can be gained from such studies.

Athanassoff (13) states in his concluding remarks: "Dans le chaume de blé en question, il n'y a pas deux tranches qui soient identique. Pourtant, chaque coupe a ses analogues, plus bas et plus haut." Herein lies the whole problem of quantitative biological variation in heredity. On the one hand the great constancy of phenotypic expression, on the other the great variability, more often than not of a compensatory nature, of all the characters associated with it. This constant

correlative interaction of character with character, component with component and each with environment is a criterion of biological phenomena and so prevalent in all studies of morphogenesis, including this one.

The variation in characters, and in components of that character, which occurred between plants are indicative of the extraordinary variability that occurs with subtle differences in environment, both in space and time, and probably also with subtle differences in genotypes.

This has mitigated against the presentation of clear cut results. However, the evidence presented here has led to a somewhat better understanding of the nature of plant height differences in cereals and difficulties involved in the genetic study of this complex trait.

SUMMARY

The nature of height differences was investigated in three closely related, homozygous lines of wheat: Genesee (tall), 1518 (intermediate) and 1328 (short).

Differences in culm length were generally due to internode length, both within and between varieties. The contribution of internode number was negligible.

Differences in length of comparable internodes of Genesee and 1328 were due to cell number, whereas in 1518 and 1328 cell size was responsible. Both were involved in the difference between Genesee and 1518.

It appeared that height differences based on cell number originate during embryogenesis while those based on cell length arise after germination. Thus, two independent developmental processes are involved.

Although the varieties differed slightly in their growth rates, the actual duration of extension growth appeared to be the more important contributing factor to mature length differences.

Compensatory mechanisms were evident at both cellular and component levels. The variability encountered at these levels was greater than that of the complex trait.

A strong positive relationship existed between variance and height, especially in the tall variety, and there was some evidence of differential homeostasis of homozygous parents. Such properties tend to obscure genetic segregation.

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