AN INVESTIGATION OF DWARF AND WINTER HABIT IN WHEAT USING MONOSOMIC AND CHEMICAL METHODS

by

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ABSTRACT

In the F_1 of crosses between the 21 Redman monosomics and Kenya Farmer, lines VIII and XIII segregated for dwarf and normal growth habit indicating the presence of three complementary dominant genes, one each on chromosomes VIII and XIII of Redman, the other in Kenya Farmer. The normal growth-habit plants in lines VIII and XIII were monosomic and the dwarfs were disomic. A few normal growth plants occurred in lines XV and XVIII and in the F_1 of euploid Redman x Kenya Farmer. These were apparently the result of hetrozygosity for dwarf genes in one of the parents. Backcrosses of lines VIII and XIII to Redman indicated that the Kenya Farmer gene is probably on chromosome XIII but is not allelic or closely linked to the Redman gene on the same chromosome.

Treatments given dwarf F_1's in an attempt to convert them to normals were vernalization and the application of IAA, TIBA, NAA and GA. None was successful but GA did induce heading and the production of a limited amount of seed. GA increased growth in spring and winter wheats to a greater extent under low intensity light and medium to high temperature than under high light intensity and cool temperatures. One spring wheat variety and several winter varieties of wheat, rye and barley, were vernalized 0, 25, 50 and 75 days and one half of each treatment sprayed with 100 ppm of GA. GA had no appreciable value as a replacement for vernalization when applied at 100 ppm, nor did GA reduce the minimum leaf number.

Minimum leaf number, previously reported as seven in rye, was reduced to six in 50-day-vernalized treatments grown under certain conditions of light and temperature. Maximum response to heading was obtained with 50-days vernalization under the test conditions. When vernalization was extended to 75 days heading time increased in 8 of the 10 varieties.

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INTRODUCTION

Wheat is the most widely grown food crop in the world and has received more attention by plant breeders than any other crop. However, geneticists have spent relatively little time working on wheat and those that have worked with this crop have had a disproportionately less amount of success when compared to those who worked with corn or barley. Common wheat, Triticum aestivum L., is a hexaploid. Because of the replication of most genetic material and the consequent complications and inconsistencies in genetic ratios of even the simply inherited characters, the use of conventional genetic methods has not led to chromosome mapping as it has in corn and barley. However, the use of aneuploids and the related newer methods present great promise to wheat geneticists.

The maintenance of rust resistance in varieties of wheat has been a primary problem in most wheat growing areas of the world. The present study was initiated with the object of locating the chromosomes carrying the genes for leaf and stem rust resistance in the variety Kenya Farmer, of common wheat, using the Redman monosomic series. The F_1 from Redman x Kenya Farmer was mostly dwarf and did not set seed. This problem had to be solved before the rust genes could be located.

Although dwarfing in wheat has been studied for over 60 years, its inheritance is still not clearly understood. Since the work of many breeders has been hampered by dwarfing, more information on its inheritance as well as a method of breaking the dwarf habit, or inducing heading in dwarf plants, would be

of infinite value. A portion of the present study reports on the location of genes for dwarf habit in Redman. Some success is also reported on overcoming the dwarf habit by applying gibberellic acid and other chemical growth substances. The delayed heading observed in dwarfs suggested a relationship between dwarfing and winter habit. For this reason and because of the reported successes in inducing earlier heading in other genera, gibberellic acid was applied to winter varieties of wheat, barley and rye in an attempt to determine whether gibberellic acid could be used as a substitute for, or an aid to, standard vernalization.

For the above reasons the original project developed into an investigation of dwarf and winter habit in wheat using monosomic and chemical methods.

LITERATURE REVIEW

Monosomics

Through the process of evolution polyploid organisms have arisen in many wild species and from their domestication, and through plant breeding, they have developed into some of the worlds major crops. Examples of these grown in Canada are wheat, tobacco and oats. The development of aneuploid series opened a new and promising field of research in genetics and plant breeding in polyploid crops. Because of the replication of genetic material polyploids tolerate the deficiency and duplication conditions which would be lethal to organisms with a smaller genetic reserve. Larson (96) points out that it is fortunate that polyploid organisms, whose genetic complexity makes them least amenable to orthodox methods of analysis, are the ones to which the new methods apply. Aneuploids were reported as interesting phenomena (47,128) long before any practical use was made of them. They were first put to use by Blakeslee in Datura (40), McClintock in corn (104) and Clausen and his associates (18,19,89) in tobacco. The present study is more closely related to the development of monosomics in wheat by Sears (112,113,116). The establishment of an original monosomic series in a crop is difficult and time consuming but once a series is set up it is relatively easy to develop additional sets in other varieties of the same crop using this first series (96,134) and this has been done by a number of workers (17,44,133).

Sears' deficient series were numbered I to XXI with those

of the D genome being designated XV to XXI (116). More recently Sears (118) has proposed a system wherein the homoeologous groups are numbered 1 to 7 with the letters A, B and D being added to distinguish the particular group to which each belongs.

Aneuploids have been recognized as having real value in wheat breeding (132) and in making genetic analyses of wheat chromosomes. Several workers (43,80,81,83,91,134) have discussed the difficulties and short-comings of aneuploid use but in spite of objections their use has reached significant proportions.

Unrau and McGinnis (133) in summarizing the important contribution of the genetic studies of cereals in Canada state that in no other country are the Chinese Spring wheat monosomics and related forms, developed by Sears, being so widely used. In addition to Sears in the United States, Sears et al. (119,121), Heyne et al. (41), Wiggins (141), and Nyquist (88) have also used monosomics in the location of genes. Very little use has been made of these series in other countries but interest is now growing. Sears (115), Unrau (131) and Larson (56) have outlined the methods of identifying genes with specific chromosomes. Where nullisomes are available certain characters are readily identified as they are not expressed in the nullisomic condition. Other genes can be located on specific chromosomes through F_1 or F_2 analyses. If the gene in the variety under study is recessive, then the critical chromosome line can be determined in the F_1 of the crosses between the 21 monosomics and the variety. Dominant genes are located by an abnormal

ratio in the critical F_2 line. If a study of a specific character cannot be made in F_2 then selected F_3 populations can be studied. Chromosome substitution is useful in locating the chromosome carrying a gene when classification of segregants is difficult or impossible.

The value of aneuploid series in the determination of major and minor effects of specific chromosomes on complexly inherited characters is well exemplified by the work of Larson (57,58,59, 60,61,62) and Larson and McDonald (63,64) on stem solidness and quality in wheat. These workers found that many of the chromosomes affect stem solidness either as pith promoters or inhibitors. Kuspira and Unrau (50,51) have demonstrated the usefulness of substitution lines in resolving quantitative genetic differences between varieties and how the number of genes and their expression may be determined. They compared the effect of each chromosome in a common background and as an example of the results which were obtained they state that Thatcher appears to have a few major genes for high yield, Hope and Timstein minor genes, mainly, with a few major genes for low yield.

Other uses have been made of aneuploids in assembling a substantial body of genetic knowledge of wheat. One example of their use is in the accumulation of information on the evolution of the TRITICINAE (58,59,116,117,120). Another example of aneuploid use is Unrau's (132) method of mapping chromosomes in wheat. Greater knowledge on the genetics of wheat will facilitate plant breeding. For instance it makes possible the substitution of chromosomes carrying a desirable gene, or

combination of genes, for a less desirable one from another variety or species. This technique promises to form an important part of future plant breeding (23,40,90,51).

Dwarfing

Dwarfing or the grass clump character in wheat has interested workers since the time of Farrer (24) in 1898. Waldron (136) in 1924 made an extensive summary of dwarfing in wheat and other crops, and recently Morrison (82) reviewed the work on the inheritance of dwarfs, semi-lethals and lethals in wheat.

Hayes and Aamodt (39) studying rust resistance in a Marquis x Kota cross in 1923 were the first to find a 13 normal : 3 dwarf ratio indicating one dominant dwarf gene plus an inhibitor. Other workers (29,82,139) substantiated these findings. Pao et al. (90) explained their results by assuming that there were three complementary factors and three duplicate factors with an addition of an inhibiter. Thompson (128) found that an inhibiter to the inhibiter best explained his data. Most studies can be explained on the basis of some combination of these factors, although some data do not seem to fit any simple inheritance pattern. Waldron (136) stated that genes for dwarf habit are labile while Goulden (29) reported lagging chromosomes as the explanation of distorted ratios in his study. Huskins (43) was able to explain Vilmorin's unfixable dwarf on the basis of chromosome numbers; i.e. dwarfs had 43, normals 42 and pigmies 44 chromosomes.

Thompson (128) found the occasional dwarf appearing in

otherwise true breeding tall F_3 families and the occasional tall in dwarf families. He discovered that lagging chromosomes in 20 to 30 percent of the F_1 pollen mother-cells would explain these irregularities. His F_1 in one cross was all dwarf but the F_2 owing to the weakness and death of many dwarfs possessed a relatively large proportion of talls. McMillan (76) who also observed lagging chromosomes, found that they were as frequent in dwarfs as in normals. Morrison, (82) examining root tips of dwarfs and meiotic stages in hybrids carrying dwarf factors, found no cytological irregularities which could account for the occurrence of dwarfs but presumably some irregularities were present which could account for the diverse and inconsistent results obtained. Morrison also states that lethals and semi-lethals are difficult to separate from dwarfs. Classification is difficult because some dwarfs are sterile, others head and produce seed, some die at an early stage, others tiller very profusely and all seem to be subject to modification of the environment. Morrison's summary of the present knowledge of dwarfs states that they do not usually appear in pure lines; nor do all varieties produce dwarfs. Never-the-less, many of those that do, have a common ancestry and many of the crosses involved in producing dwarfs were originally made in an attempt to transfer rust resistance. Dwarfs have occurred within and between spring and winter-wheat-variety crosses and also between T. aestivum and related species.

Vernalisation

History

The original literature pertaining to vernalization appeared

in Russia in 1930 and was made available in English in 1933 (149) and 1934 (70). Lysenko, whose name was associated with the original work, used methods and explained his results in a manner later questioned by most other workers. Whyte (147) gives credit to a German scientist, Klebs, for having begun the research on the developmental physiology of plants which led to vernalization. He and other German researchers found that chilling sometimes initiated flowering. McKinney (73) pointed out that the basic concepts of vernalization were known before 1900 and referred to Klippart's work in Ohio as an example. Lysenko's method of vernalization emphasized the need for commencement of growth before the cold treatment was applied.

Maximov (70) asks: "What is vernalization?" and answers the question by describing it as a practical agricultural method of affecting plant development in such a way that winter plants bear fruit in the first year. Knight's (48) definition agrees with Maximov's but vernalization in this paper refers to cold treatment of germinating seed.

A long series of experiments made by Gregory, Purvis and others of the Research Institute of Plant Physiology, Imperial College of Science and Technology at London, have contributed valuable data on the fundamental biological processes concerned with vernalization. Their work will be discussed later. In America, McKinney and Sando (74) investigated the effect of varying light and temperature on earliness and lateness of sexual reproduction and Lojkin (68) studied varietal effect of vernalization of oats and wheat. Workers in India became enthusiastic about the practical application of vernalization and

thoroughly investigated its use on mustard and rice. In the latter crop it is reported (147) that they decreased the time to flower of the Rupsail variety of winter rice from 133 to 47 days. Except for limited use in India and Russia, vernalization has not been used in commercial grain production. Its main value has been to accelerate the work of plant breeders.

This brief review of the history of vernalization is not intended to be complete nor even to refer to all of the key researches but review papers of Maximov (70), McKinney (73), Murneek and Whyte (84), Whyte (148) and Lang (52) give a comprehensive coverage of the literature.

Developmental Physiology

Although the knowledge of the physiology involved in vernalization is not complete, studies on this subject should start with what is known about the developmental phases and the fundamental processes concerned with plant development and the place of vernalization in the cycle. Lysenko emphasized the fact that growth, increase in size and weight, was a separate process from phasic development. His stages of plant development according to Maximov (70) are: (a) the thermo-stage (vernalization stage) which must be completed before the initials of the reproductive organs are laid down; (b) the photo-stage which requires high temperature and long days (continuous illumination is better); (c) gametogenesis. Klebs noted three stages or phases also in flower production which are not identical to Lysenko's. They were: (1) the production of a condition of "ripeness to flower", (2) the formation of primordia or initiation of flowering and

(3) the development of floral structures and their expansion. Purvis (96) and Hamner (36) accepted this concept of flower production but a recent experiment by Cumming (21) has shown that the general concept of phasic development does not apply to Chenopodium rubrum and thus can no longer be considered a general principle.

Bonnett (9,10,11) contributed to present knowledge by his studies of the morphological development of spikes of barley and wheat and panicles of oats. His papers include photomicrographs of the various stages in each of these cereals. He shows that the barley spike is indeterminate or of indefinite growth. Since the number of spikelets at each joint of the rachis is limited, response to the environment can only be made in varying the number of fertile spikelets at the tip of the spike. Oats and wheat have a determinate inflorescence that is one which has a definite number of flowers resolved by the terminal flower at an early stage. Adjustment to growth conditions in such plants is made in the number of fertile flowers in a spikelet.

In the developing plant, leaf initials appear as alternate ridges which nearly encircle the growing point. The reproductive stage is initiated by the formation of double ridges. During this stage the spikelet and its parts differentiate from the increase of the upper ridge. Differentiation in wheat begins in the middle of the spike and preceeds toward the top and bottom. The same is true in barley except that the tip, being indeterminate, differentiates later than the base.

Klebs' "ripeness to flower" stage, or stage of "puberty"(30), was not recognizable morphologically but Purvis' discovery of the development of the double ridges on the growing tip is a morphological feature which indicates a change from vegetative to reproductive growth. Purvis and Gregory (97) brought forward a number-of-leaves interpretation which showed that in both spring and fall rye there is a minimum leaf number of seven and a maximum of 25. The primordia between the eighth and the 25th are indeterminate and can produce either leaves or spikelets depending on the external factors such as temperature or length of day. Sharman (122) in studying Agropyron repens and other members of the GRAMINEAE concluded that the initiation of a primordium or a bud is not due to any inherent properties of any layer nor to the cells concerned being derived from any special initial group. He believes their initiation is due to a change in type of metabolism of the particular cells involved such as an increase in rate of protoplasm synthesis or change in rate or direction of division.

Purvis (96) states that winter cereals are annuals since they complete their life in less than 12 months. However, when planted in the spring they continue in the vegetative stage because they are sufficiently slow in passing through the ripeness to flower stage that the ensuing short days inhibit flower development. The Odessa workers (Lysenko and his associates) emphasize the fact that there is no distinct limit clearly dividing winter and spring plants one from the other. All varieties differ in their degree of "winterness". Plant breeders have selected for the extremes which has resulted in two distinct

types.

Temperature and Light Effect

Gregory and Purvis (32,35,98) found that vernalization can be reversed under certain conditions of light and temperature up to 12 weeks of vernalization but sensitivity to reversal diminishes gradually up to that time. They used heat in devernalization of winter cereals but others (110) found that chrysanthemum and mustard could not be devernalized with heat treatment. On the other hand prolonged low-intensity light treatment will cause complete devernalization in chrysanthemum but has apparently little effect on rye. Purvis and Gregory (98) and Lojkin (68) independently reported that even slight drying of seed during vernalization inhibited the process. Friend and Purvis (26) found that long periods of heat (6 weeks) on partially vernalized seed intensified the effect and shortened the time to flower. Vernalization will take place up to 10°C but devernalization does not begin until 15°C and increases to about 40°C. This leaves a neutral temperature range from 10 to 15°C at which no effect of temperature on subsequent flowering exists (98).

Anaerobic conditions brought about by the use of CO_2 by Gregory and Purvis (34) completely prevented vernalization. Nitrogen, on the other hand, reversed vernalization at high temperature but not at low temperature.

Lysenko, according to Maximov (70) considered that the degree of hibernalization (strong preservation of the winter state) was indicated by the duration of low-temperature exposure

required for vernalization. He thought that the vernalization period varied from 15 to 60 days or more and that weak, medium and strong winter types could be distinguished. Bullina's (15) results appear to confirm Lysenko's concept. He reported that weakly winter hardy plants required 46 days chilling, medium 58, and strong at least 70 days. He also concluded from his experiments that all varieties headed more completely and flowered earlier with optimum chilling time than with less and that optimum duration of chilling was proportional to the degree of winter hardiness of the variety.

Saltykovsky and Saprygina, as reviewed by Levitt (66), stated that frost resistance does not depend on length of the vernalization period but no hardy varieties seem to have a short period. Other investigators (3,66,100) also disproved Lysenko's hypothesis. Lojkin (68) found that vernalization did not shorten the vegetative period of either of the spring wheat or oats that she tested. However, McKinney and Sando (74) reported that low temperature treatment retarded earliness in the spring varieties they tested.

Spring wheats such as Marquis complete their life cycle in minimal time when given long days and temperatures of 70°F or more throughout their life cycle and are thus long day - high temperature plants. On the other hand winter wheats such as Turkey complete their life cycle most rapidly when given short days and low temperatures during the early stages of growth and long days and high temperatures during later stages of development. In the light of these investigations McKinney and Sando (75) conclude that winter wheats are really not typical long-day plants

but are "short-day→long day and low-temperature→high temperature plants".

Schwabe (110,111) working with Chrysanthemum showed that a slight alteration of a single factor of the environment can bring about surprising changes in plant reaction. It is thus important to control or keep constant all factors of the environment in conducting plant development studies and also to record these factors so that the results of various experiments may be related.

Flower Forming Substance

Contrary to Lysenko's hypothesis Gregory and Purvis (33) and Gregory (30) concluded that the vernalization effect can spread throughout the plant because it appeared in late tillers which formed after the original stem had been removed. This suggests the presence of a substance which is transmitted through plants and is perhaps formed directly or indirectly (from a precursor) during vernalization. In 1937 Purvis and Gregory (97) postulated the existence of a "flower-forming" substance which affected the labile primordia depending upon the factors of the environment. They suggested that during vernalization a precursor of the "flower-forming" substance accumulated in the embryo and that it was translocated to all growing points. Hamner (36) in his review of the various hypothesis prefers Gregory and Purvis' postulation of flower-forming and leaf-initiating substances in a state of equilibrium, the relative abundance of each depending on the environment. From their investigations Gregory and Purvis (33) reported that

vernalization was localized to the embryo; was entirely independent of changes in the endosperm or aleurone layer and was therefore a synthesis of a hormone. These conclusions conflicted with an early hypothesis of Cholodny which was based upon the existence of large quantities of a substance which he called "blastanin" in the endosperm. Gregory and Purvis (34) showed that the formation of the substance or its precursor was an oxidation reaction since the absence of oxygen caused complete inhibition of the low temperature effect.

Considerable effort has been expended in trying to isolate the "flower-forming" substance. Purvis and Gregory (99) found that chloroform extracts from vernalized grain placed in agar caused non-vernalized embryos to be partially vernalized (equal to 3 weeks vernalization). Certain plant extracts apparently promote earlier flowering as shown by many other experiments. However, all attempts to isolate the flower forming substance or a precursor to it have failed unless the gibberellin-like substances found now in many plants perform this function.

Schwabe (109) discussed the work of Melchers who concluded that the vernalization effect was due to the production of a substance which he called "vernalin" which is transmitted between parts of a plant or from plant to plant by graft. Evidence of the location of the stimulus in the embryo comes from the researches on the pre-ripening effect of cold treatment (33,139). Cold treatment of seeds produced the vernalization effect when applied during the period from the time of anthesis when there was little endosperm or embryo until growth of the forming seed

was complete.

No discussion of plant extracts or hormones would be complete without the mention of auxin. Hatcher (38) studied auxin in relation to vernalization and revealed that in rye auxin is present in the endosperm but could not be found in the embryo. The auxin content of spring and winter rye is the same and none is detectible in the embryo of germinating rye whether vernalized or not. Lang (52) states that auxin appears to be associated with the dark period and thus decreases with the advent of flowering in short-day plants but its role, if any, in the initiation of flowering in long-day plants is in doubt.

Lang (52) in reviewing the physiology of flowering suggests that it is the length of dark period, in long-day plants, during which an inhibitor to floral stimulus is produced, that is critical; not length of day. He found that the leaves played an important part in flower initiation. They either produced the stimulus (or a precursor of it) or were responsible for sufficient growth to permit an autocatalytic substance to develop in newly forming cells. Lang points out that in the initiation of flowering, plants need a continuous supply of some material. This is formed in the leaves in light (or in Hyoscyamus when defoliated, or in the dark at the expense of stored material). Lang (52) found that there were four distinct light-effected processes in long-day plants, two promoting flowering, one inhibiting it and one antagonistic to the inhibitor. Short day plants were found to have at least three processes comparable to the first three for long-day plants.

Harder (37) working with short-day plants concluded that there were at least four groups of chemical processes at work in plants: (1) flower promoting (flowering hormone), (2) flower inhibiting, (3) inducing short-day habit (metaplasin), (4) inducing long-day habit. Lang's discussion of photoperiodic responses was based on the concept that photoinduction resulted in the formation of a transmissible floral stimulus. This stimulus was assumed to be a flower hormone or "florigen".

Thus there appears to be a photo-induced stimulus "florigen" and a cold-induced stimulus "vernalin". Lang discusses experiments which show that where vernalization is required it must be completed before florigen can be formed. Thus vernalin may be a precursor of florigen or it may act as a catalyst in florigen formation. Available evidence at present does not permit a definite conclusion.

Both day-length and low-temperature effects give indications of being self perpetuating. In Xanthium, the photo-induced floral stimulus was transmitted through several generations by means of grafting without any noticeable decrease in effect. The autocatalytic effect in vernalization is also indicated by the success in early cold treatment in cereals. Gregory and Purvis (31,33) and others (Lang 52) showed that low temperature vernalization could be carried out on ripening grain while still in the head. If flower forming stimuli are self-perpetuating, being passed on only in the formation of new cells, then this may explain the difficulty so far encountered in isolating such substances separate from cell tissue. While a great deal has

been learned about photo- and thermoinduction of spring habit in winter cereals the basic action is still not completely understood.

Gibberellins

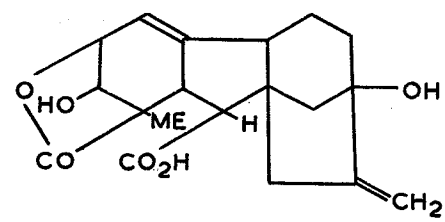
Discovery

Among the long list of biological discoveries none can provide a more fascinating story than that of the Gibberellins. Stodola (126) reviewed the discovery and work on the gibberellins from the earliest reports until the beginning of 1958 by means of 617 abstracts, 70 of which were from early Japanese papers. In addition to his work free use has been made of reviews by Barton (5), Wittwer and Bukovac (146), Brian (12) and Stowe and Yamaki (127).

Gibberellins is the name given to a closely related group of chemical substances which have been found to exert marked effects on plant behavior. The first report on the gibberellins was by Kurosawa (49) who discovered that filtrates from a fungus, Gibberella fujikuroi, which caused plants to grow unusually tall, stimulated the same excessive growth when applied to healthy plants. This disease which occurred first on rice is called "bakanae" or "the foolish seedling disease" because diseased plants grow much taller than normal plants and then usually die. Other than being very tall, diseased plants have long, narrow leaves, retarded root development and are pale yellow-green in color (126). Further investigation continued on the effects of this substance but it remained for Yabuta and Sumiki of the University of Tokyo to first isolate the chemical in 1938 (5,146).

Though the disease had been reported in Japan as early as 1898, British Guiana in 1930, China in 1934, Italy in 1938, Trinidad in 1946 and Africa in 1953 no one outside Japan appeared to be aware of the effect of this chemical substance until Brian et al. (13) published their paper in 1954. Following this paper in English the tempo of investigation increased rapidly. Plant physiologists discovered new and varied effects on a wide variety of crops. Bio-chemists isolated pure gibberellins and discovered that the Japanese had been hampered because their gibberellins were mixtures of more than one active compound (136). Researchers have also discovered that a wide range of plants possess natural gibberellin-like substance (146). This suggests that they have a part in the normal physiological development of plants.

Chemically, Brian (12) states that gibberellins have been characterized as Gibberellic Acid ($C_{19}H_{22}O_6$) or Gibberellin X according to Stodola (136), Gibberellin A_1 ($C_{19}H_{24}O_6$) Gibberellin A_2 ($C_{19}H_{26}O_6$) and Gibberellin A_4 ($C_{19}H_{22}O_5$ or $C_{19}H_{24}O_5$). Cross et al. (20) postulated alternate structures for the gibberellic acid formulae and Brian (12) states that the first one, which is given below, was the correct one.



Stodola (126) summarizing assay methods for gibberellins stated that most of those used were bioassay in type. For the most part rice seedlings were used in Japan, wheat seedlings in England and corn mutants (85) and oat coleoptiles in the United States. Peas and Beans have also been tried (72,123). Because plant bioassays are slow, manufacturers have developed chemical and physical methods including deuterium tracer assay, a fluorescence assay and a hydroxylamine assay. Assays are used in the commercial manufacture of gibberellins and in research.

Effect on Plants

The following summary of the most important effects of gibberellins on plants is based primarily on the reviews because to review the many hundreds of papers published in the last five years would be undesireable in this treatise.

Practically every application of gibberellin, where penetration to the growing parts has been accomplished, results in rapid growth and elongation. The amount of chemical required to initiate, or give maximum response, is not critical though some considerable variation occurs between species and within species (13). Amounts varying from 1/1000 to 300 micrograms per plant are needed to produce noticeable effects in specific plants. Application is usually made in water solutions sprayed on the plants or dropped in axils of leaves but the use of hypodermic-needle injections has also given positive applications. Results are noticeable within hours with certain plants but not for weeks with others of the woody-plant group (85,146). The chemical is systemic and highly mobile but its effect is only temporary

necessitating repeated applications (79,143). Both cell elongation and cell division (107) is promoted in the above ground parts and in some reports root growth has been shown to be retarded (13,87). New growth is usually a pale yellow-green color, a condition which can be corrected to some extent by maintaining a high level of fertility or by optimum growing conditions (2,79,144).

Speed of germination and height of seedlings have been increased with seed treatment. Special effects on dwarf plants and the induction of flowering have been reported and are discussed later. Miscellaneous effects of gibberellins and their association with other plant growth substances are also included in succeeding pages.

Many of the effects of gibberellins were discovered first in cereals and grass research because the early work originated in studying a cereal disease. Increase in length of stem and leaf area in cereals and grasses suggest increase in vegetative yield though promotion of apical dominance and thus decreased tillering may offset the former. However, increases in branching have been reported (69) as well as increases in dry weight (13,69,103). The commercial value in spraying grass is to prolong the season in the fall and to induce growth earlier in the spring at which times the temperature is too low to promote growth (5,79). The economic advantage results in improved pastures at both ends of the season with little detrimental effect during mid season if the fertility level is kept up. Other advantages have been cited such as early turf for lawns

and sports fields.

Considerable emphasis has been placed on the economic value of the gibberellins especially by the Michigan group (16,77,142, 143,144,145,146). These substances have real value for some crops, limited value for others and are detrimental to a third group. Caution must be exercised since favorable effects must be balanced against deleterious ones. Wittwer and Bukovac (145) and McVey and Wittwer (77) report that gibberellin has value in celery production, in seed production in radish, for early fruiting and increased vigor in determinate tomatoe varieties, for increase in terminal growth without aesthetic loss in woody plants, in increase in aesthetic and shade value of other woody ornamentals by greater lateral bud growth, in causing death to the terminal meristem in some shrubs and thus eliminating pruning and in increasing flower size (77).

Effect on Dwarfs

The reversal of genetic, physiological or disease produced dwarfs in various plant groups has attracted considerable attention (1,9,12,92,146). Some treated dwarfs in corn have attained normal height when sprayed with gibberellins and thus suggest a biochemical basis for heritable characteristics (127,146). While the reversal of genetic dwarfs may not have any practical value the reversal of physiological dwarfism in apple (4), peach (25) and probably in other fruit, may be useful in reducing after ripening procedures (146).

Brian (12) mentions that the "physiological dwarfs" produced in Malus spp. by sowing non-after-ripened seed and the

pathological dwarfing associated with certain virus infections can be reversed by gibberellins. He suggests that these dwarfs and some genetic dwarfs have a common biochemical background. The first report on the reversal of dwarfism was made by Brian and Hemming (14) working with peas. Phinney and his co-workers have investigated corn mutant dwarfs and shown that four of the known single-gene mutants are reversed by gibberellin while one other is only partially reversed and one not at all (83,93,95). Stowe and Yamaki (127) postulated that dwarfness in corn can be interpreted as due to individual blocks in a biosynthetic pathway that eventually ends in the production of a gibberellin-like compound. In their work with peas, however, they found that dwarfness was polygenic and thus the same simple explanation used for corn did not fit the pea data. Allan et al. (1) in studying the effects of gibberellin on dwarfing in winter wheat found that dwarf and semi-dwarf varieties did not grow to normal size when treated, but that standard height varieties responded more than the dwarfs. Their tests showed that tall varieties headed earlier and that the greater stimulation occurred when 100 ppm of gibberellic acid was applied than with 1, 10 or 1000 ppm. Their treatments were applied by injection of vernalized plants.

Replacement of Day Length and Vernalization Requirement

Some of the most striking effects of the gibberellins on flowering were not discovered until 1956 when the growth substance was applied to plants grown under non-inductive conditions. Lang (53) for example found that gibberellin almost

completely replaced the cold requirement of Hyoscyamus niger but did not replace the need for long days. Many other workers got similar results using a wide variety of long day plants (7,103,146).

Moore et al. (78) working with telephone peas found that gibberellic acid reversed vernalization when applied after 20 - 30 days cold treatment and inhibited vernalization when applied previous to cold treatment. Wittwer and Bukovac (142,143) later showed that a large number of long day plants could be induced to elongate and flower in short days by applying only one application of gibberellic acid. Lang (54) induced considerable stem elongation especially at high concentrations of gibberellin in the Petkus variety of winter rye but obtained no significant effect on heading time or number of leaves produced.

Barton and Chandler (6) replaced the need for cold pretreatment of dormant apicotyls of tree peony with gibberellic acid. This is the first chemical shown to bring about the after-ripening effect usually accomplished by low temperature. Brian (12) emphasizes the need for high doses of chemical to replace vernalization. He also states that gibberellins do not induce flowering in short-day plants grown under long-day conditions: in fact, treated Kalanchoe plants kept under inductive short-day conditions were prevented from flowering.

The Michigan group (16,67,146) point to the commercial value of earlier flowering, flowering in non-inductive day lengths or as annuals rather than biennials. Other uses which they discuss are improved flower quality and better methods of variety improvement. For example gibberellin treatment makes it possible to

rogue plants, from nurseries, which are susceptible to bolting. Wittwer and Bukovac (146) in summarizing flowering effects state that in no crop has gibberellin been able to replace both the cold and long-day requirements. They discuss the use of gibberellins in a wide variety of crops including tomatoes, cucumbers, potatoes, grapes, tree fruits, citrus and flowering plants.

Natural Occurrence of Gibberellin-like Substances

Brian (12) suggests that a gibberellin-like hormone should be expected in plants since the application of gibberellin simply induces a natural physiological response which will eventually take place when the environment is suitable. Other reasons point even more forcibly to the same conclusion. Auxin metabolism does not explain the sudden bolting of plants from the rosette plant to a plant with a long flower stock. As previously mentioned blocks apparently occur in the biosynthesis of a gibberellin-like hormone causing dwarfing. This also suggests the natural occurrence of such substances. This hypothesis has been confirmed by a large number of researchers working on a wide variety of crops (55,72,94,101,102,105,140) including wheat (123). Nickell (86) in tissue culture studies concluded that gibberellin-like substances are universal in the plant kingdom and might play a vital role in the control of plant growth. Some of the natural gibberellins have been shown to be identical with the previously established gibberellins (94). Bean factor I is identical to gibberellin A_1 but bean factor II and a pea-seed factor are different from known gibberellins thus suggesting the presence of a more extensive range of such hormones.

Brian (12) concludes that evidence of gibberellins in primitive plants such as algae and ferns indicated that a gibberellin growth regulator evolved early in the history of green plants. He also concludes from the discovery of bean factor II by Phinney and Neely (94) that gibberellins in higher plants may be far more specific than the fungal gibberellins.

Since gibberellins were first discovered in a fungus it was natural to expect that other fungi would produce the same kind of stimulus. Curtis (22) made a survey of about 1000 fungi and 600 actinomycetes but not one produced filtrates which stimulated growth on the dwarf corn seedlings.

Cytological Effects

Cytological examination of plant sections whose growth rate had been accelerated by gibberellin were first made in 1949 by Wada (137). His studies of the stamen hairs of Tradescantia reflexa revealed no effect on mitosis except that the rate was slightly increased. Sachs et al. (106,107,108) and Kato (45) found that increased growth was mainly due to cell elongation rather than increased division. Leivonen (63) reported that gibberellins do not effect the course of mitosis, nor do they give rise to either changes in the chromosomes or to polyploidy. Berger's (8) study was more extensive. He found no cells undergoing C-mitosis, no polyploidy and no stimulation for resting cells to enter mitosis. His finding substantiated those given above as he noted increased cell division in meristematic tissue. Notable changes in the appearance of the chromosomes especially at metaphase were also reported by Berger. At prophase the

chromosomes were longer and the spindle structures were evident. He photographed and discussed segmentation in chromosomes at metaphase in which extreme examples resembled salivary-gland chromosomes of the Diptera. Apparently the treatment caused the matrix to swell and the coiled chromonema to break at many points giving rise to banding and finally segmentation. He concluded that the clear places represent breaks in the chromonema because he could focus through these regions. They may have been a non-stainable substance with the same refractive index as the cytoplasm. Such chromosomes completed their normal division as some banded chromosomes could be seen in anaphase. Abnormalities were rare and probably not due to the gibberellin.

Relation of Auxins and Hormones

Gibberellin is a hormone which influences the regulation of vegetative growth, flowering and dormancy of plants (12,55,95). It closely simulates effects usually induced in nature by light or vernalization. Brian (12) postulates a scheme to explain their regulatory function. In response to light gibberellin-like hormones are formed in leaves with a precursor P acting as an intermediary step. In darkness the hormone is converted back to P but is reversed if placed again in red light. In long days increasing concentrations of hormone are built up. If high levels of the hormone induce flowering in long-day plants and inhibit it in short-day plants then the effect of application of exogenous gibberellin and light can be accounted for in both types of plants. If low temperature treatments tend to increase synthesis of this hormone then the scheme does not conflict with the known

thermo-responses. More work must be done to varify such an hypothesis.

Many investigators have studied the interaction of gibberellins with indolacetic acid, IAA, (46,65,135,136). Brian (12) summarized the comparisons of these two plant regulators as they effect various parts and processes. Gibberellins are similar to auxins in their light response and in their stimulation of cell extension but apparently they are not active in the absence of IAA. In other words GA enhances the effect of IAA. van Overbeek (135) points out that in respect to flowering the two are antagonistic in reaction as gibberelline promote flowering and IAA inhibits it. Auxin inhibits lateral bud development but gibberellin stimulates their growth. IAA does not show the gibberellin effect on the corn dwarfs (92); but it strongly inhibits root growth while gibberellin does not (12). van Overbeek concludes his discussion by saying that "the IA inhibition of GA is a general principle of great significance in the process of growth regulation".

MATERIAL AND METHODS

Location of Genes for Dwarfing

Kenya Farmer (Kenya 338. A. C. 2. E.2) is a variety introduced from Kenya to provide a new source of stem rust resistance in the Canadian wheat breeding program. A project was instituted to determine the location of the genes for rust resistance in the variety by utilizing the 21 different Redman monosomics developed in 1955 by Campbell and McGinnis (141). Redman is a hard red spring wheat variety derived from the cross Regent x Canus, that is, (H-44-24 x Reward) x (Marquis x Kanred). In the fall of 1957 crosses were made between the 21 Redman monosomics and Kenya Farmer as well as between disomic Redman and Kenya Farmer. The Redman monosomics x Kenya Farmer crosses were made and the F_1s grown in one of the Coldstream Plant Growth Cabinets (Plate 1, Figure 2 and 3) at the Cereal Breeding Laboratory, Canada Department of Agriculture, Winnipeg. Since most of the F_1 plants were dwarf, a study of the inheritance of this character and possible methods of inducing seed set in dwarfs was undertaken thus replacing the original project.

Six seeds of each of the 21 Redman monosomic lines were sown and the monosomics cytologically identified by pollen mother-cell analysis using Smith's (124) method. Cytological equipment used is shown in Plate 1, Figure 1. Wherever possible at least two stable monosomic plants ($20^{II}\ 1^{I}$) were emasculated and pollinated with pollen from Kenya Farmer. Between 20 and 24 seeds obtained from each line were used in the project. Additional monosomic material of certain lines had to be grown

to obtain this number. Eight seeds from each monosomic line and 50 seeds from the euploid cross were planted for F_1 studies.

Some monosomics were late and crosses could not be made early enough to produce mature seed for the second winter crop. Embryos of 28 seeds from such crosses were cultured on orchid agar 14 to 20 days after pollination following the method outlined by Melnyk (71). Embryo cultures were kept under continuous light at 65°F and were transferred to pots and placed in the growth cabinet when the first leaf was 1½-2 inches long.

Since some of the F_1 seed was dormant the growth cabinet was cooled to 4°C for two days. As a result all but 15 seeds germinated after seven days. These 15 were placed outside for 48 hours during which time the temperature went down to -4°C. The pots containing the seed in frozen soil were brought into the greenhouse. Ten of these seeds grew and six of them produced plants of normal growth habit (hereafter referred to as "talls" in contrast to dwarfs). The other F_1 plants were all dwarfs except some plants in lines VIII and XIII. The growth cabinet containing these plants was cooled to 0°C for one week in an attempt to induce more of the plants to head.

These results suggested that seed which would normally produce dwarf plants could be induced to produce talls with cold treatment in a similar manner to converting winter annuals to spring habit. For this reason a new set of F_1 seed from monosomic crosses was vernalized at 3°C for six weeks. This vernalized F_1 seed was sent air express to Regina in May, 1958, and was planted in the field six hours after removal from the refrigerator. In the fall all available F_2 seed was sown in

the greenhouse at Winnipeg and a great many of the resulting plants were examined cytologically by PMC or root tip analysis. Tsunewaki's (130) root tip procedure was used. Since lines VIII and XIII segregated for dwarfs and talls in F_1 they were backcrossed to Redman in an attempt to determine how many genes for dwarfing were present in Kenya Farmer and if either chromosome VIII or XIII possessed such a gene.

Through the entire study four inch pots were used and one or two seeds were sown in each pot. Whenever the growth cabinet was used it was kept at 16±1°C for six weeks to induce tillering and then raised to 20°C until crossing was complete. The temperature was then raised to 21°C and later to 24°C to speed up maturity. One half teaspoon of 16-20-0 fertilizer was applied to each pot twice during the growing period, once after emergence and once about heading time. Temperatures in the greenhouse at Winnipeg or at Regina could not be controlled as desired for this particular study because of sharing space with other projects and the general limitations in greenhouse control. The specific growing conditions used will be cited for each test.

Induction of Seed Set in Dwarfs

A preliminary attempt was made to induce dwarf plants to set seed. The following chemical treatments were applied to replicates of four plants each from the disomic Redman x Kenya Farmer cross:

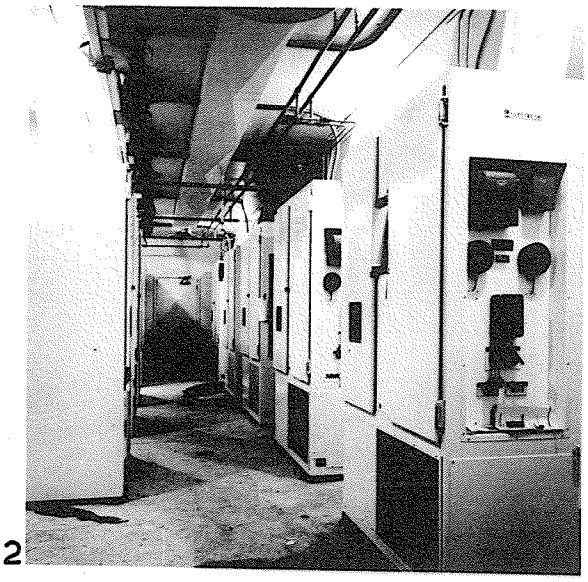
1	-	Indoleacetic acid (IAA)	- 5ppm
2	-	2,3,5 triiodobenzoic acid (TIBA)	- 5ppm
3	-	Naphthalene acetic acid (NAA)	- 5ppm
4	-	Gibberellic acid (GA)	- 10ppm
5, 6	-	" "	- 100ppm

All treatments were applied by spraying the plants in two applications at three day intervals except No. 6 which was applied by placing drops in the axils of leaves nine times at two day intervals. Plants receiving drops remained on the greenhouse bench but plants receiving spray treatment were placed in a plastic walled cabinet (Plate 1, Figure 4) over night. The humidity was kept high enough so that the droplets of the spray remained on the leaves for 8 to 10 hours. Two height measurements i.e. average height of leaf auricle and average length of leaf were taken on each plant at the time of application and at three succeeding times.

Because gibberellic acid gave the most promising results it was used in succeeding tests. All dwarf F_1 monosomics still growing in the growth cabinet were reduced in number of tillers and sprayed with 50 ppm of gibberellic acid. This application was repeated in one week. These plants had been sown 75 days previously and had produced from 25 to 30 tillers each. The number of tillers was reduced to 4,5 or 6 in the hope that stronger culms and more vigorous heads would result in less

Plate 1


1


2


3


4

Figure 1. Cytological equipment used in PMC and root tip studies.

Figure 2. Growth Cabinets of the type used in making crosses and growing the F_1.

Figure 3. Redman Monosomic plants crossed or selfed in the growth cabinet.

Figure 4. Plastic covered incubation chamber in which humidity can be kept high for many hours.

sterility. Soil fertility was maintained by two applications of nutrient solution prior to heading. Since these plants did set some seed in spite of their age at time of treatment a new set of Redman monosomics x Kenya Farmer F_1's were subjected to a number of treatments as follows:

1. Seeds germinated in water, planted and the plants sprayed with 100 ppm of gibberellic acid weekly from emergence to heading.

2. Seeds germinated for 24 hours in gibberellic acid, transferred to water for completion of germination, planted and sprayed as in 1.

3. Seeds germinated as in 2, subjected to temperatures of -2 to -6°C for 10 hours, planted and sprayed as in 1.

4. Seeds germinated in water and cold treated as in 3. (no gibberellic acid).

One easy- and one difficult-to-vernalize winter wheat was obtained from Dr. R.G. Anderson and added to check the effect of the various treatments on winter wheat. The easy-to-vernalize variety, I.B.C. 1533 (WG 57566), was introduced from Italy and had been vernalized readily and planted in 1957 at Winnipeg. The other winter wheat variety, Zanda (WG 57562), was introduced from Belgium and had not been vernalized with the normal six week vernalization at 3°C. Because of the large number of plants in this experiment, spray was applied to plants on the greenhouse bench. High humidity was maintained by spraying the floor and walls with water at the time of application and again two hours later.

Treatment of Winter Cereals

Several varieties of cereals were vernalized 0,25,50 and 75 days and one half of each treatment sprayed with 100 ppm of GA at weekly intervals from emergence to heading in an attempt

to determine how extensively this chemical could be used to replace the cold treatment in vernalization.

The procedure used in vernalization was first to clean the seed by shaking for one minute in each of three rinses, one of alcohol and two of distilled water: then to germinate it on filter paper in petri dishes. As soon as germination occurred (definite growth of root and sheet) lots of 20 seeds each were placed flush with the top of a one quarter inch layer of washed sand in a standard petri dish. The sand was moistened with 13 cc. of distilled water. Sterilized dishes and aseptic forceps were used throughout. The plates were placed in the refrigerator at 1±1°C for the required time. None of the plates dried out though an additional 4 cc. of distilled water was added to some plates of the 75 day vernalization set when condensation on the lid decreased. Vernalization of successive sets was initiated at 25 day intervals and all treatments were planted in the greenhouse the same day. The varieties which were sprayed and their crop classification were as follows:

I.B.C. 1535	-	soft red winter wheat
Zenda	-	soft white winter wheat
Minhardi	-	soft red winter wheat
Kharkov MC22	-	hard red winter wheat
Kenate	-	winter barley
Hudson	-	winter barley
Wong	-	winter barley
Antelope	-	fall rye
Sanosate	-	fall rye
Tetra Pethus	-	fall rye
Redman	-	hard red spring wheat

These varieties were chosen in an attempt to test a wide range of cold temperature requirements. Vernalized seed and the non-vernalized checks were planted in the greenhouse at Regina on the fourth day of December, 1959. For the first 18 days they recieved only the reduced natural light available in December. By the 18th day when the first application of spray

was made most plants were in the early three-leaf stage. At this time all plants were placed under approximately 300 foot candles of continuous florescent light. One week later when stronger lights became available the intensity was increased to approximately 1000 foot candles. The temperature was kept at 16°C for 90 days and then raised 2°. Three lapses in the temperature occurred during this period in which it went down to 10°C twice and up to 22°C once. The average date of heading (Plate 2, Figure 1) and the number of leaves at heading time were recorded. A more restricted group of varieties which included only Redman, Kharkov, Hudson and Antelope were given the same vernalization and spray treatments and grown under the same temperature and light conditions. These were to be dissected as suggested by Purvis (97) to determine the time of initiation of flower primordia.

Only a portion of the plants were dissected as it soon became evident that many plants would be wasted in becoming familiar with the time of collection. Too few plants would be left to enable any definite conclusion. In addition dissection was very time consuming. Plants were collected in the four leaf stage (fourth leaf emerged) unless procumbent. Plate 2, Figures 2,3 and 4 show plants which have been carefully removed from the soil for dissection. Commencing at the first true leaf, which was brown and dried up, and progressing upward, each leaf was pealed back and removed from the base of the plant. Plants with four leaves evident have three or four additional leaves within the leaf sheath of the next older leaf. They became smaller as the dissection progressed until in some instances the

Plate 2

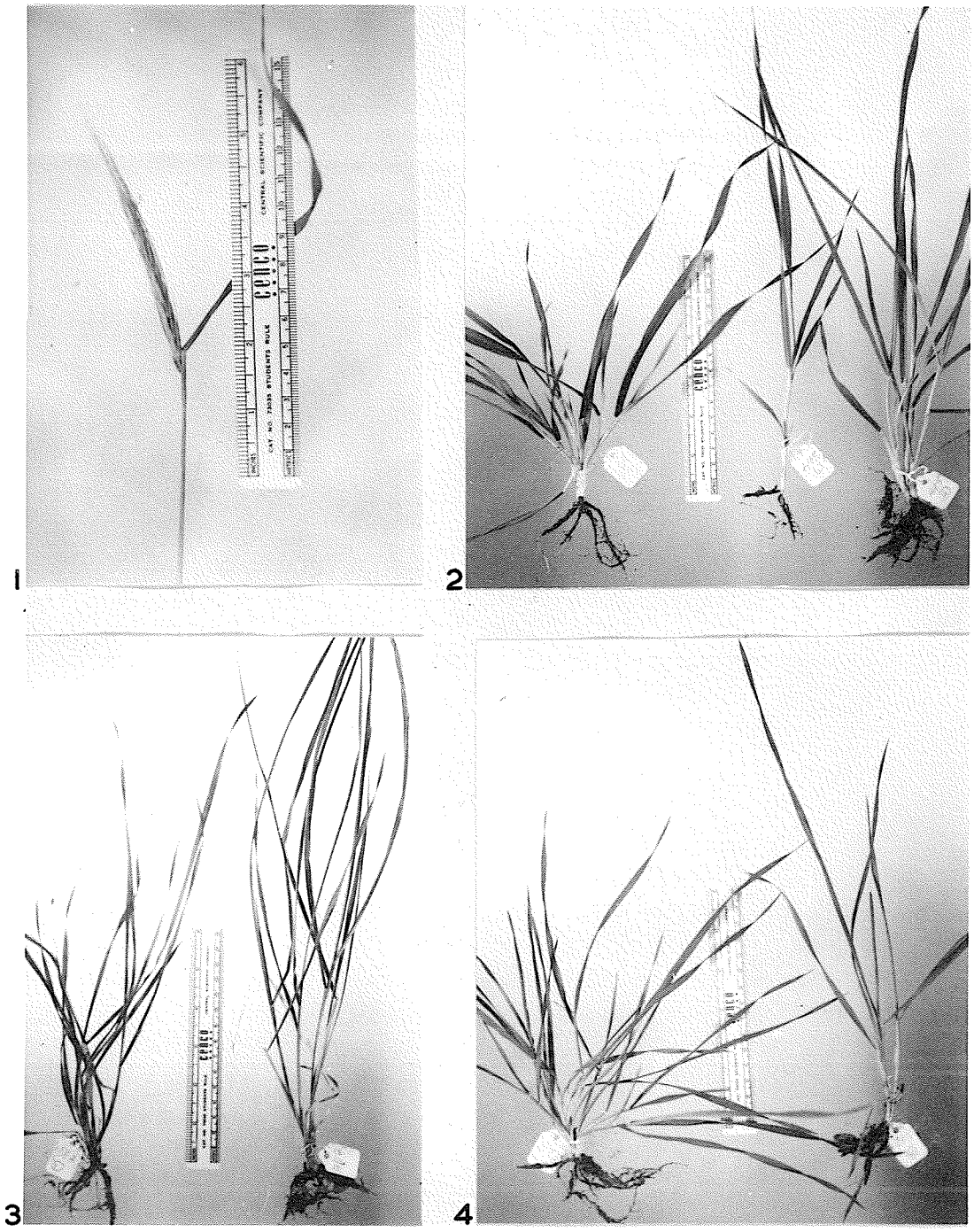


Figure 1. Rye plant at the stage referred to as heading.

Figure 2. Winter barley; check plant left, GA-treated plants right, showing elongation and range of tillering.

Figure 3. Winter wheat; check left, GA-treated plant right (elongation).

Figure 4. Fall rye; check left, GA-treated plant right (reduced tillering).

leaf simply enclosed the growing tip (Plate 3, Figure 1) and the last leaves were only alternate primordia below the growing tip (Plate 3, Figure 2).

Dissected plants were classified in five stages starting with the earliest appearance of the double ridge condition as stage one. The distinct enlargement of the upper of each pair of ridges was classed as stage two (Plate 3, Figure 3). Plants were at stage three when the upper ridges commenced to form spikelets (Plate 3, Figure 4). Stage four began when signs of differentiation into various parts of the spikelet appeared (Plate 3, Figure 5) and plants were said to be in stage five when the developing spike began to enlarge and the differentiation of parts of the spikelets was quite prominent. The spike at stage 5 had just started to move up the leaf sheath. Plants dissected which had progressed past this stage were classified as past stage five (Plate 3, Figure 6).

Statistical analyses were made wherever they assisted in the evaluation of the data. Chi-square analyses were carried out on genetic ratios (Table 1). Analyses of variance were applied to the data obtained in preliminary tests to induce heading in dwarfs by chemical means. Analyses of variance were also attempted on the days-to-head and number-of-leaves data obtained in the vernalization and gibberellic acid combination treatments. A non-paired comparison "t" test proved a greater value in assessing the effect of GA in this latter test.

Plate 3

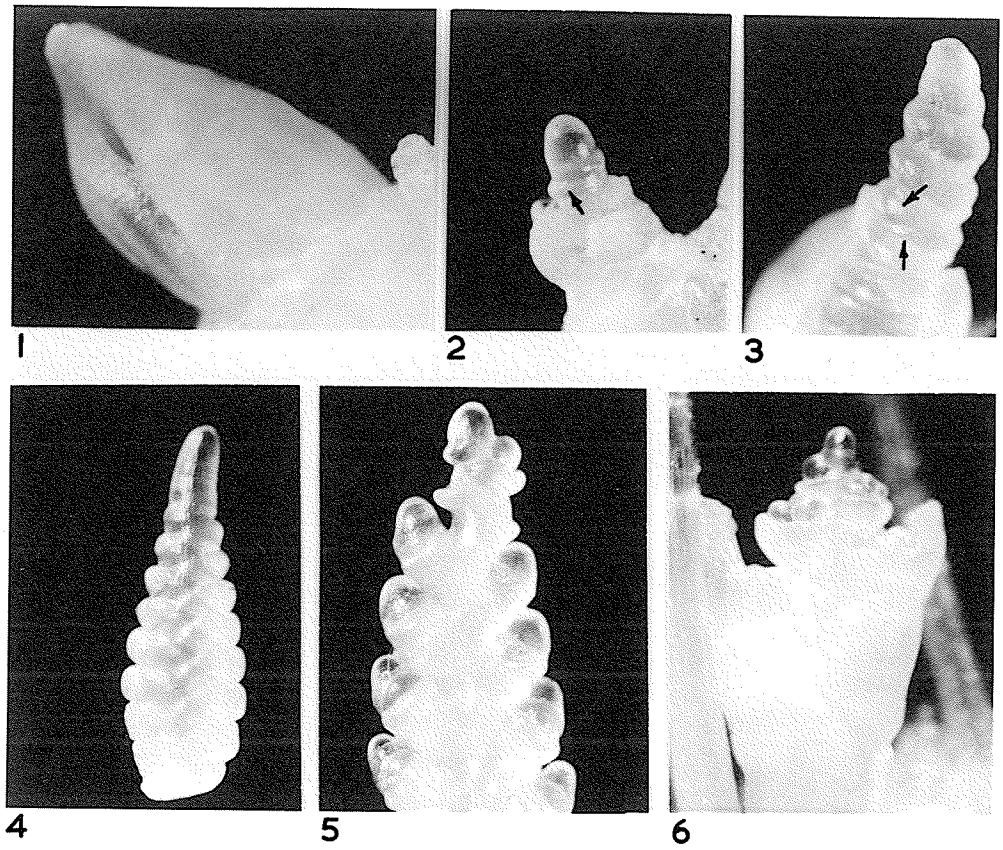


Figure 1. Last leaf covering primordia in a wheat plant. Five previous leaves removed (X44).

Figure 2. Primordia of Figure 1 with sixth leaf removed showing new leaf primordia as alternate ridges below the apical meristem (X44).

Figure 3. Wheat spike primordia showing slightly enlarged upper ridge and smaller lower ridge (X44).

Figure 4. Wheat spike primordia showing commencement of differentiation of spikelet parts from the centre (X36).

Figure 5. Barley spike primordia showing commencement of differentiation of spikelets from the tip downward (X44).

Figure 6. Differentiation of the upper spikelet in a barley plant showing primordia for the various parts (X44).

RESULTS AND DISCUSSION

Inheritance of Dwarfing in the Redman and Kenya Farmer Varieties of Spring Wheat

Dwarf F_1 plants resulted from crosses between the 21 Redman monosomic lines and Kenya Farmer (RM x KF). Segregation for dwarfs and talls (normal growth habit) occurred within lines VIII and XIII (Plate 4, Figure 1) and with few exceptions the remaining 19 lines produced dwarf plants. Two plants in line XV and one in line XVIII were tall and produced only tall plants in F_2. Of the 12 F_1 plants grown from each of the segregating lines VIII and XIII, seven were tall and five were dwarf in line VIII, while from line XIII there were six tall and six dwarf. Chromosome counts made on root tips revealed that dwarf plants in these two lines had 42 chromosomes (Plate 4, Figure 2). Analysis of pollen mother cells of tall plants showed that they were monosomic (Plate 4, Figure 3). Root tip analysis of 50 dwarf plants sampled from other F_1 lines showed that both monosomic and disomic plants were present. In the additional set of F_1 plants segregation for talls : dwarfs was 7 : 2 in line VIII and 2 : 1 in line XIII. No chromosome counts were made on these plants.

From the segregation in lines VIII and XIII it was concluded that at least three complementary dominant genes condition dwarfing in the Redman x Kenya Farmer (R x KF) cross. The absence of any one of these genes results in tall plants. The data indicate that Redman possesses two genes for dwarfing located on chromosomes VIII and XIII respectively. The other complementary and non-allelic gene (or genes) must be carried by Kenya Farmer since dwarfing is only expressed in hybrids of

Plate 4

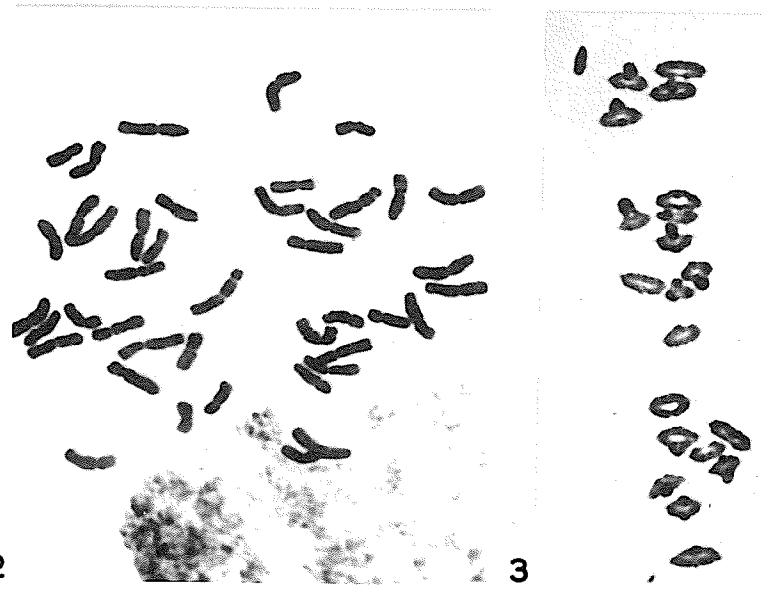


Figure 1. Dwarf and normal F_1 plants from the cross Redman monosomic XIII X Kenya Farmer.

Figure 2. Root tip cell with 42 chromosomes (disomic) from a dwarf plant shown in Figure 1.

Figure 3. Pollen mother-cell with $20^{II}1^{I}$ (monosomic) from a plant with normal growth shown in Figure 1.

the two varieties. These findings are consistent with Morrison's (32) summary and with Hsu et al. (42) who reported one complementary dominant gene in Kenya Farmer.

F_1 plants from R x KF were mostly dwarf but from one set of 41 F_1 plants seven were tall and produced seed which gave all tall plants in F_2. Tall plants that should have been dwarf according to this hypothesis were probably tall because one of the parents was heterozygous for at least one of the dwarfing genes. Thus the tall plants in lines XV and XVIII and in the R x KF F_1, failed to receive one of the three genes necessary for dwarf expression. Cytological analysis of the chromosome numbers of plants in lines XV and XVIII revealed both monosomics and disomics in both talls and dwarfs. Since there was no selection for homozygosity of genes for dwarfing in the development of either parent variety it is not surprising to find at least one of them segregating for this character.

F_2 plants from tall F_1's of both lines VIII and XIII segregated for chromosome number but none was dwarf. Segregation of the F_2 plants from dwarf plants of other lines and from R x KF appeared to give a satisfactory fit to a 27 : 37 ratio (Table 1) indicating the presence of three complementary factors and thus a single gene for dwarfing in Kenya Farmer. Back-crossing line VIII to Redman gave 16 dwarf to 16 tall and back-crossing line XIII gave three dwarf to 15 tall (Table 1). Since the two lines did not give the same segregation one would suspect that the gene in Kenya Farmer was on either chromosome VIII or XIII. If this gene is on chromosome XIII then the back-cross of line VIII should give a 1 : 1 ratio and of line XIII should give a

Table 1 - Observed and theoretical ratios of dwarf : tall plants from F_2 and backcross populations.

	Observed dwarf : tall	Theoretical dwarf : tall	χ^2	P
F_2 from dwarf F_1 of RM x KF*	17 : 23	16.9 : 23.1 (27 : 37)	.01	.90 - .95
F_2 from dwarf F_1 of R x KF	29 : 44	30.8 : 42.2 (27 : 37)	.18	.50 - .70
Backcross of line VIII (RM x KF) to Redman	16 : 16	16 : 16 (1 : 1)	0	1.00
Backcross of line XIII (RM x KF) to Redman	3 : 15	4.5 : 13.5 (1 : 3)	.67	.30 - .50

* seed from lines V, XII, XIV, XVI, XVII and XIX of Redman macrosomics x Kenya Farmer.

1 dwarf : 3 tall ratio. The calculation of these ratios is presented in Table 2 and are based on small populations. The observed ratios gave a satisfactory fit to the ratios suggested by this hypothesis (Table 1). Therefore it appears that chromosome XIII of Kenya Farmer carries a gene for dwarfing which is non-allelic and not closely linked to the gene carried in the same chromosome in Redman. The element of doubt exists because of the small number of plants and because the expected ratio is based on Sears' (113) female gamete ratio of three deficient to one normal which was established for the variety Chinese Spring.

Table 2 - Possible gametes and their frequencies* from F_2 monosomic plants of VIII and XIII and Redman with the expected backcross phenotypic segregations. A and B represent genes on chromosome VIII and XIII respectively in Redman and C on chromosome XIII of Kenya Farmer.

	Functional gametes and their relative frequencies	Redman gamete	Phenotype of offspring of backcross dwarf	tall
Line VIII	1 a BC	A Bc	1	-
	1 a Bc	"	-	1
	1 a bC	"	1	-
	1 a bc	"	-	1
	3 - BC	"	3	-
	3 - Bc	"	-	3
	3 - bC	"	3	-
	3 - bc	"	-	3
		Total	8	8
Line XIII	1 A bC	A Bc	1	
	1 a bC	"	1	
	3 A --	"		3
	3 a --	"		3
		Total	2	6

* based on the work of Sears (113).

Since this ratio is attributed to the loss of the unpaired monosome during reduction division some variation from variety to variety might be expected. Of the 110 F_2 plants from RM x KF examined in the present study 61 were monosomic and 47 disomic, while one was nullisomic and one had 36 chromosomes. This indicates that the loss of univalents in the Redman series is lower than in Chinese Spring.

Induction of Seed Setting in Dwarfs

In a preliminary experiment gibberellic acid (GA) had a much greater influence on dwarf wheat than indoleacetic acid (IAA), 2,3,5 triiodobenzoic acid (TIBA) or naphthalene acetic acid (NAA). Leaves on GA treated plants grew much more rapidly than those of the check plants (Plate 5). The other three chemicals appeared to stimulate leaf growth with one application, but not with subsequent treatments. The growth of the check plants soon caught up to those treated with IAA and TIBA but the NAA treated plants maintained their lead in growth. The 100 ppm spray application of GA gave only a very slight increase over GA applied at 10 ppm. The application of drops in the axils of leaves was slightly less effective than the foliage spray. This was probably because the drops soon evaporated and in spite of the more frequent treatment probably less GA was actually taken into the plant. Treatments were applied to dormant tillers as illustrated by the check plants in Plate 6, Figures 1 and 5. Dwarf plants at this stage had reached maximum height and were continuing to produce new tillers. These tillers grew taller when sprayed than the original tillers and it is the average height of the later tillers which is graphically represented in Plate 5.

Analyses of variance of the data on leaf and auricle height indicated that the differences were nearly significant at the 5% probability level three days after the first GA treatment while at seven and 20 days they were significant at the 1% level.

The dwarf F_1 lines from RM x KF sprayed with GA when 75 days old produced 34 seeds (Table 3). GA applied to a much

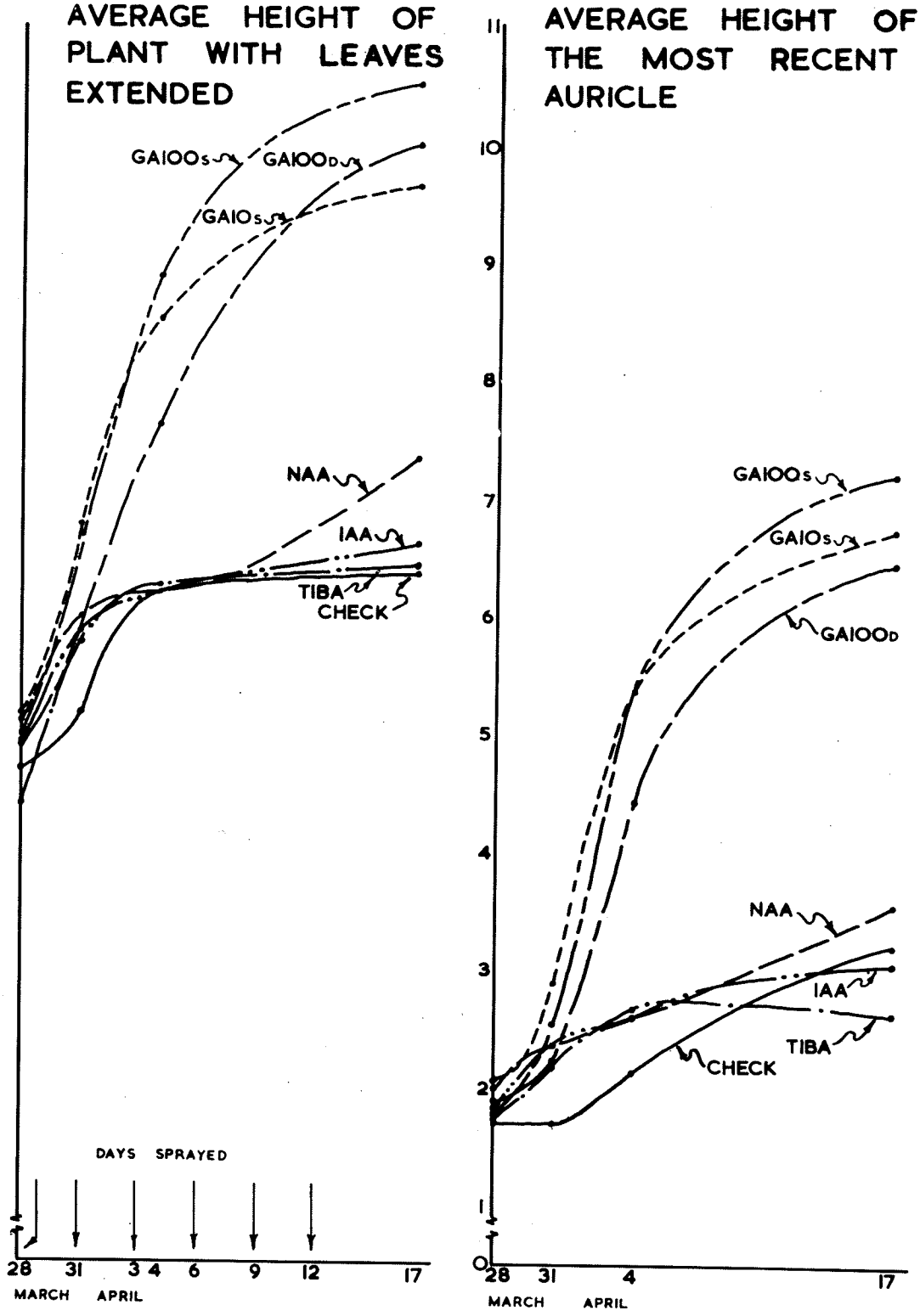


Plate 5 - Plant heights at various stages following treatment with GA at 10 and 100 ppm applied by spraying plants (GA10S and GA100S), at 100 ppm applied by placing drops in leaf axils (GA100D), and NAA, IAA and TIBA sprayed on plants at 5 ppm. Arrows indicate dates for spray application. Measurements were made in inches from soil surface.

Table 3 - Number of heads and seeds produced by F_1 dwarfs when treated with chemicals.

Material Treated	Treatment	No. of Plants Treated	No. of Heads	No. of Seeds
RM x KF 75-day-old plants	GA 50 ppm sprayed	81	9	34
R x KF 46-day-old plants	GA 10 ppm sprayed	4	2	8
	GA 100 ppm sprayed	4	4	19
	GA 100 ppm drops	4	2	26
	IAA 5 ppm sprayed	4	1	19
	NAA 5 ppm sprayed	4	0	0
	TIBA 5 ppm sprayed	4	0	0
	check	4	0	0

smaller number of plants at a slightly earlier stage produced 53 seeds. One tiller on a dwarf plant treated with IAA produced a large head with 19 seeds. Perhaps a particularly heavy dose of IAA contacted this tiller or possibly some other factor triggered the development of this spike. Because GA induced 75-day-old dwarfs to produce heads (Plate 6, Figure 2) and to set seed (Table 3) it was concluded that this treatment could be used to induce heading in dwarf wheat and that the next step was to learn the best technique to use. Since gibberellin-like material has been discovered in wheat (123) and GA has been used successfully to reverse dwarf habit of growth in corn and other

crops (65) these conclusions are not startling. Many of the spikes had a high percentage of sterile florets but pollen mother-cell analyses revealed no abnormalities. Sterility appeared to be physiological in these plants as stems and spikes were spindly and weak in spite of adequate soil fertility. It was thought at this stage of the project that, since GA treatment of late tillers caused dwarf plants to elongate, such a treatment applied to seedlings would probably break dwarf habit and produce tall plants.

Mortality was high when cold-shock treatment was applied to germinating seed but this treatment only induced heading in six of the 25 F_1 plants from the RM x KF cross and in neither of the two R x KF F_1 plants which survived the treatment (Table 4). Kenya Farmer and I.B.C. 1535 were more resistant to cold, but treated Kenya Farmer was later heading than the Kenya Farmer check. The cold-shock treatment vernalized I.B.C. 1535 as all plants headed in an average of 56 days. Cold treatment in combination with GA seed treatments and foliage applications appeared to speed up head development by four or five days over the same GA applications with no cold treatment.

GA as a foliage spray applied weekly from emergence to heading induced almost all dwarf plants to head but did not break the dwarf habit (Plate 6, Figure 4). This treatment did not shorten the time to head for Redman but did decrease by five days the time required for I.B.C. 1535 to head when compared with cold treated plants. Germination of seeds in GA solution caused many subsequent plant deformities and appeared, as a result, to decrease the number of dwarfs producing heads

Table 4 - Heading induction effects of GA as a seed treatment and as a foliage spray with and without cold-shock treatment of germinating seed in the dwarf F_1 of RM x KF and R x KF and in Redman (R), Kenya Farmer (KF), Zands (Z) and I.B.O. 1535 (IBO).

Materials / Treatment		Dwarf F_1		Parents		Winter Wheat	
		RM x KF	R x KF	R	KF	Z	IBO
Cold Treatment	No. of Seeds	38	10	4	4	12	12
	No. of Plants	25	2	0	4	2	10
	No. Headed	6	0	-	4	-	10
	Days to Head	85	-	-	61	-	56
GA 100 ppm Spray	No. of Seeds	57	10	4	4	12	12
	No. of Plants	49	10	4	0	7	9
	No. Headed	44	10	4	-	-	8
	Days to Head	75	74	50	-	-	51
GA Seed Treatment, GA Spray	No. of Seeds	54	10	0	0	0	0
	No. of Plants	43	10	-	-	-	-
	No. Headed	21	9	-	-	-	-
	Days to Head	76	76	-	-	-	-
GA Seed Treatment, GA Spray, Shock Cold Treatment	No. of Seeds	57	10	4	4	12	12
	No. of Plants	29	8	4	2	6	6
	No. Headed	11	5	4	2	-	6
	Days to Head	71	69	40	44	-	51
Check (no treatment)	No. of Seeds	0	19	4	4	0	0
	No. of Plants	-	19	4	2	-	-
	No. Headed	-	0	4	2	-	-
	Days to Head	-	-	47	53	-	-

Plate 6

Figure 1. Dwarf and tall F_1 plants from Redman x Kenya Farmer showing stages when sprayed with gibberellic acid.

Figure 2. Deformities caused by GA in 2 Redman (buckling of stem) and 2 F_1s from RM x KF (crown roots at 2 nodes one inch apart and branching).

Figure 3. Zanda check and GA treated when 30 days old.

Figure 4. GA induced heading in dwarf plant.

Figure 5. Two dwarf checks and 3 GA-treated plants (branching).

Figure 6. A GA-sprayed-winter-wheat plant which has established a second crown.

Figure 7. I.B.O. 1535 check and GA-treated when 30 days old. Plants headed in 56 and 51 days respectively.

in the RM x KF cross (Table 4).

Deformities included branching and an attempt to form crown roots at nodes above the ground. In several plants the stems apparently grew very rapidly after GA application and were spindly with "needle-like" internodes ranging from one to four inches long. These needle-like sections of the stems supported considerable growth and branching in one plant (Plate 6, Figure 2,3). Sometimes this section buckled as it grew and forced its way through the leaf sheath to form a semi-circular bow in the stem. When this happened the leaf sheath supported the plant. Neither the high mortality nor the deformities occurred in the R x KF cross which suggests that the monosomic dwarfs were less resistant to the GA seed treatment. GA replaced the cold requirement of I.B.C. 1535, the easy to vernalize winter wheat, but 86 days from planting treatment Zands showed no signs of heading.

In spite of the many heads which were produced in the dwarfs very little seed development occurred. This was not surprising because the parent plants and the talls from line VIII produced only five or six seeds on plants with two and three heads. The reason for poor seed set was likely due to high day temperatures during seed setting time. Dwarf plants which produce weak, spindly heads under good growing conditions would not be expected to set seed under adverse conditions.

In the first experiment plants elongating due to GA treatment turned a pale yellow-green color. Fertilizer restored the natural color and thus in addition to the two applications of 16-20-0 fertilizer a nutrient solution was applied to each pot at two dates. This overcame the yellowing but did not seem to

correct the spindly stem and spike characteristic of GA treated plants. Perhaps under more ideal temperature and light conditions, high soil fertility would produce stronger tillers and more seed.

Effect of Gibberellic Acid and Vernalization on Winter Cereals

Vernalization and GA treatments resulted in greater variability between varieties within T. aestivum than between species. Graphs in Plates 7 and 8 present the results on number of days to head and number of leaves of plants at four periods of vernalization sprayed and not sprayed with GA. In general the varieties follow a similar pattern of heading. Non-vernalized material headed in 90 days or more. The optimum period of vernalization varied from 30 to 60 days, the differences being mainly varietal. Beyond this period heading time increased as vernalization increased. GA did not change this general pattern appreciably but caused slight variations in the number of days to head depending on the length of vernalization and the variety. In general the number of leaves decreased with increase in vernalization time regardless of GA application.

For the varieties which had not headed in 100 days, at the time the graphs were prepared, it was assumed that heading would take place between 130 and 160 days. Since the line on the graph would be altered very little regardless of the time of heading within this range an 'expected-result line' was drawn in an attempt to present a more complete picture of the results. Statistical analyses were considered but due to the wide variability in numbers of plants receiving the treatments only a few of the differences in number of days to head were shown to be significant.

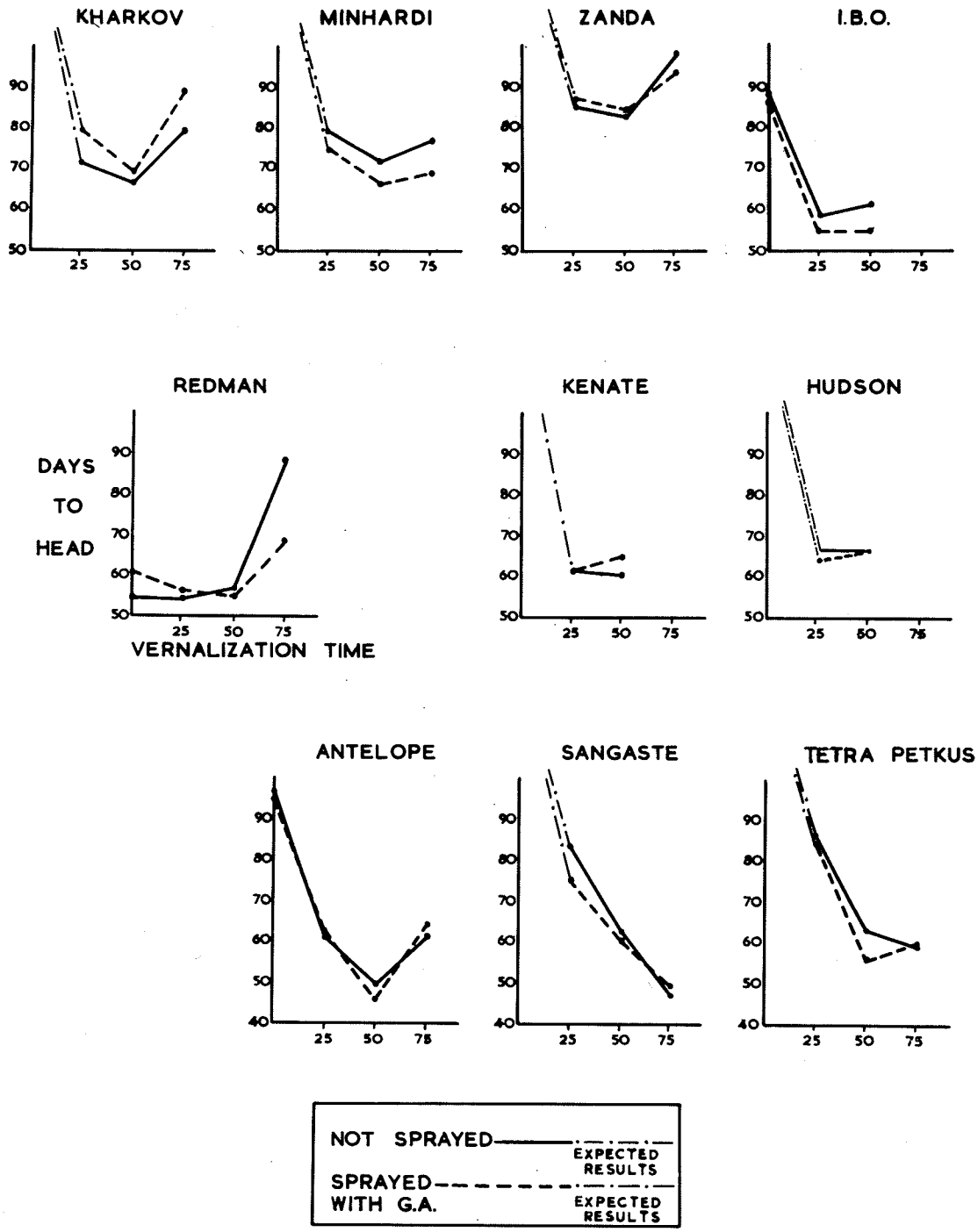


Plate 7 - Effects of various periods of vernalization (GA-sprayed and unsprayed) on number of days to head of selected varieties of wheat, barley and rye.

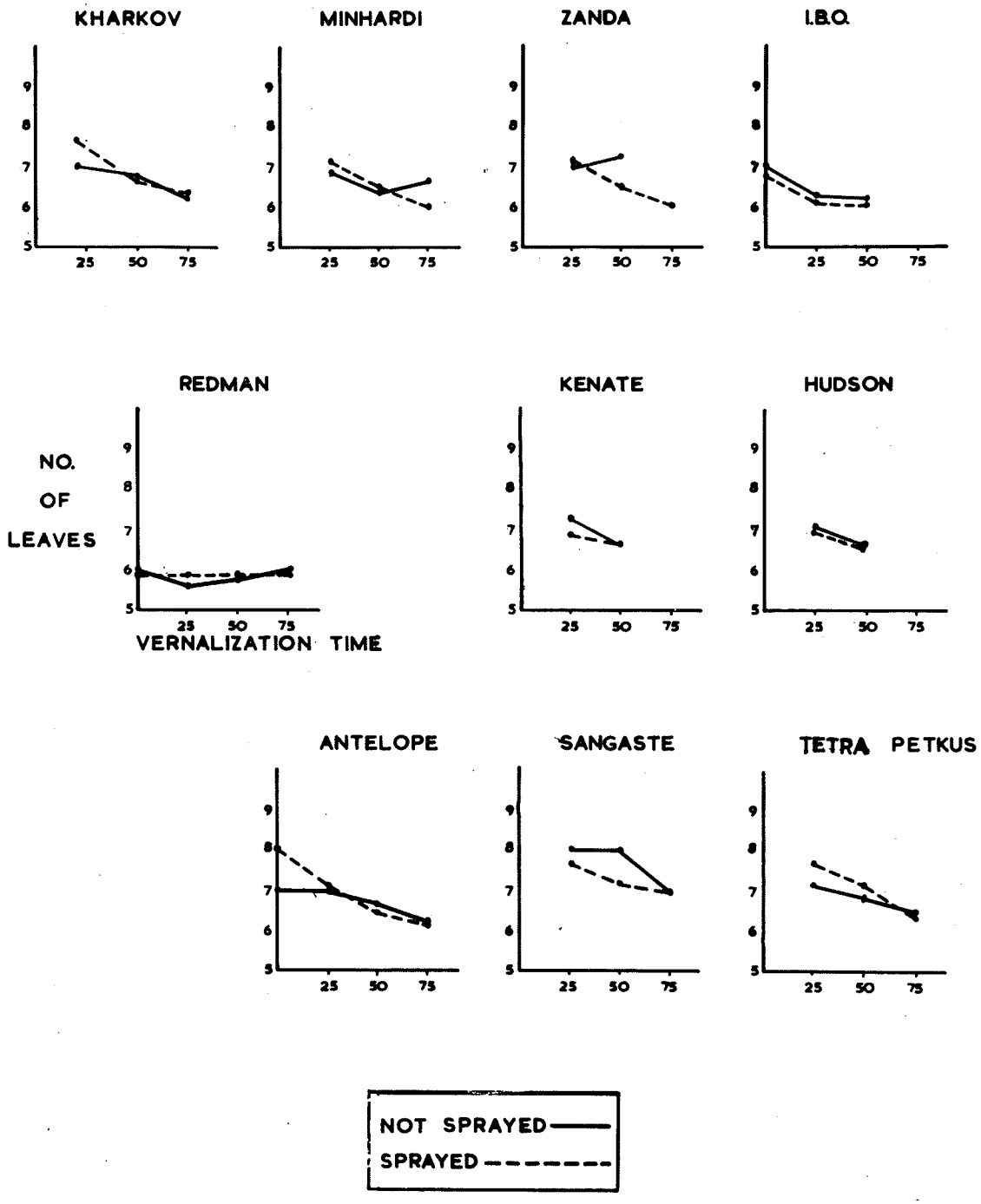


Plate 8 - Effect of various periods of vernalization (GA-sprayed and unsprayed) on number of leaves produced by selected varieties of wheat, barley and rye.

The numbers of plants surviving all of the vernalization treatments averaged 10 but some of the varieties had less than five plants in the 75-day-vernalization class. In spite of the fact that significant differences could not be shown for all varieties there was a uniform pattern which showed a surprising but distinct increase in the number of days to head when vernalization was extended to 75 days.

Redman

Redman, which was used as a spring wheat check in testing the winter cereals, showed no response to vernalization or GA treatment in the number of leaves produced. There were only six leaves. In this variety GA retarded heading in the absence of vernalization but showed no retarding effect in the combined treatment. The difference in the number of days to head with GA treatment only was nearly significant at the 5% probability level in an unpaired "t" test. On the other hand, when vernalized for 75 days, the six plants which survived the treatment were retarded an average of 32 days. GA reduced this delay in heading to 12 days. The average number of days to head for the two vernalization periods of 50 and 75 days was 56 and 79 respectively. This difference was highly significant (P less than .01). Redman headed in 54 days without vernalization and none of the treatments applied reduced this number whereas Redman headed in 40 days in an earlier test when treated with GA. Plants in the earlier test received a much lower intensity of light for an 18 hour day length as contrasted with high intensity continuous light. The manipulation of the light and dark periods throughout

the life of the plant no doubt had a considerable influence on its development.

Kharkov

Heading time was reduced to 67 days in Kharkov by a vernalization period of 50 days. The average number of days to head for the two vernalization periods of 50 and 75 days was 66 and 69 respectively. This difference was highly significant. GA increased the days to head by five when vernalization was 25 days and by ten when it was 75 days. This is a reversal of the effect which was expected. GA increased the number of leaves when vernalization was 25 days but had no effect when the time was increased to 50 and 75 days. The average number of leaves was reduced to 6.4 in Kharkov.

Minhardi

The number of days to head for Minhardi was reduced to 72 at the vernalization time of 50 days, however, with the same vernalization period GA spray reduced the heading time to 65 days. A seven day reduction was maintained with 75 days vernalization but these differences were not shown to be significant in a "t" test. GA also reduced the number of leaves from an average of 6.7 to 6.0 with 75 days of vernalization.

Zanda

The results of vernalization tests with Zanda show why Dr. R.G. Anderson (c.f. Materials and Methods) was unable to vernalize this variety. Its optimum vernalization time would probably coincide with the 42 days Dr. Anderson used but the

least number of days required to head was above 80. The induction of heading would probably be even later with cool spring weather and in general less favourable growing conditions in the field so that the day length would be too short to induce heading. GA treatment showed no effect on the number of days to head. The vernalization time which gave the greatest reduction in leaf number was 25 for Zanda when not sprayed with GA and 75 days when GA was applied. Since these data are based on average heading time and leaf numbers taken on only three to six plants its reliability is doubtful. Vernalization alone reduced the number of leaves to seven while the combination of vernalization and GA reduced the number of leaves to six.

I.B.O. 1535

I.B.O. 1535 is a European variety which is in between the North American winter and spring wheat groups in degree of "winterness". It headed in just under 90 days when not vernalized whereas unvernalized Canadian winter varieties head between 130 and 160 days. Vernalization reduced heading time to 56 days which equals that of spring wheat. The optimum vernalization time appeared to be between 25 and 50 days while in Kharkov and Minhardi it appeared to be near 50 days. GA consistently reduced the time to head and the number of leaves regardless of the length of vernalization time. As mentioned previously under certain conditions I.B.O. 1535 headed in 51 days when GA was applied and in 56 days with cold-shock treatment. This is in contrast to heading in 87 and 88 days respectively when sprayed and not sprayed under continuous light and cool temperatures.

As suggested for Redman, the difference in the manipulation of light and temperature is the most likely explanation for these results.

Antelope

Similar to I.B.C. 1535 wheat, Antelope rye headed in about 90 days without vernalization. This period was rapidly reduced with a vernalization period of 25 days and at 50 days vernalization Antelope required less than 50 days to head. Increase in vernalization time to 75 days resulted in a highly significant increase in the number of days to head (P less than .01). GA sprayed plants headed in an average time of 46 rather than 49 days when vernalized for a period of 50 days. GA treatment increased the minimum number of leaves from seven to eight in Antelope when not vernalized.

Sangaste

Only three Sangaste plants survived 75 days vernalization. Two were sprayed and one was not. The 47 and 48 days required to head which are plotted on the graph are thus not as reliable as the other figures. The vernalization time which increases heading most in Antelope may be at or past 75 days. A longer vernalization period than this, on plants which survived the treatment, might reverse the vernalization effect as in the other varieties. GA reduced the number of leaves from eight to seven with 50 days vernalization but did not have any appreciable effect at 25 or 75 days. The minimum leaf number for Sangaste was seven whereas Antelope produced as few as six at 75 days vernalization.

Tetra Petkus

The number of days to head was not decreased by vernalization nearly as much with Tetra Petkus as with Antelope and Sangaste and the optimum vernalization time appears to be between 50 and 75 days which is intermediate between the other two rye varieties. GA decreased the number of days to head but increased the number of leaves with 25 and 50 days vernalization.

Winter Barleys

Kenate and Hudson gave a very uniform response to the treatments but none of the Wong plants survived 50 days of vernalization and no barley plants of any variety survived 75 day vernalization. Kenate headed in less than 60 days with an optimum vernalization time apparently between 25 and 50 days whereas Hudson's heading time was reduced to 64 days with a vernalization time near optimum at about 50 days. GA increased the number of days to head especially with longer periods of vernalization but caused a slight decrease in minimum number of leaves. The number of days for Wong to head after 25 days vernalization was 79 when sprayed with GA and 71 when not sprayed. Thus the pattern for Wong was similar to that of the other two winter barleys.

Dissection to determine time of Flower Initiation

Results of dissections to determine the exact time of floral initiation were inconclusive but supported the heading and leaf number data already reported. Under ideal growing conditions plants passed from vegetative to beyond stage 5 (Plate 3, Figure 6) in six or seven days. To determine the exact number of days ex

to be able to choose plants for dissection within developmental stages 1 to 5 would require many more plants and much more time than was available.

It was evident that the leaf number of Hudsen barley, Antelope rye and particularly Kharkov wheat was increased with delayed heading. GA treatment increased the length of the growing tip substantially over that of non-treated plants. This was particularly evident in the vegetative stage as well as stages 1 and 2 of flower induction. However, foliar application of GA had comparatively little effect upon the rate of development of flower primordia under the conditions of this experiment.

The Influence of Light and Temperature on results of GA Treatment

One other result worthy of special mention was the influence that the growing conditions had on treatment with GA. For example, varieties I.S.C. 1535 and Zanda when grown in the greenhouse at Winnipeg produced very vigorous growth with leaves measuring 40 to 50 inches in length (see Plate 6, Figures 3 and 7). In the greenhouse at Regina I.S.C. 1535 headed at 10 - 14 inches and none of the leaf tips were more than 16 inches from the surface of the pot. Zanda at Regina grew slightly taller than I.S.C. 1535 but showed no more than half of the extension of Zanda under the Winnipeg conditions. The amount of GA applied and the method of application were the same in both cases but growing conditions were different. Restricted light for an 18 hour day and moderately high temperatures were used in Winnipeg, while lights were on continuously at high intensity and temperatures were cool in the Regina greenhouse. Under these same

conditions I.B.C. 1535 headed in about 55 days at Winnipeg and in 67 days at Regina. It would be interesting to test the effects of GA at both high light intensity and temperature and low light intensity and temperature.

GA has been reported to decrease root growth (13,146), to have no effect on it (13) and to increase it but to a lesser extent than corresponding increases in top growth (12,65). While no measurements of root growth were made in this study many plants were dug up for dissection (Plate 2, Figures 2,3 and 4). Observation on these plants did not detect any decrease in development in the roots of sprayed plants.

GENERAL DISCUSSION

In 1926 Goulden (29) suggested that there was real value in combining the genetic and cytological methods of attack in inheritance studies, especially when the experimental results do not seem to fit a direct explanation. The value of this advice is evident in the close association which has developed between genetics and cytology; in fact the general usage of the term 'cytogenetics' unites the two in the minds of investigators. The use of chromosome counts has become an important supplement in genetic analyses, especially since the advent of aneuploid work. Improved techniques and methods have increased the scope of genetic work considerably. The present study, involving hundreds of PMC and root-tip-chromosome counts, re-emphasizes the value of monosomics in the location of specific chromosomes carrying particular genes. This is the first report which associates genes for dwarf habit in wheat with specific chromosomes.

In the study of dwarfing Redman and Kenya Farmer headed in 47 and 53 days, respectively, from time of planting germinated seed. Seeds germinated in GA headed in 44 and 40 days, respectively, when subsequent treatments were or were not applied. These results are presented in Table 4. However, in a later experiment (Plate 7) Redman headed in 55 days but when GA was applied heading time was increased to 60 days rather than decreased. Temperatures for plant growth in the former experiment were kept high, especially during the day, whereas in the second experiment they

remained low. Light intensity in the former experiment was comparatively low and plants were given a six hour dark period every day whereas in the latter experiment the light was stronger and continuously applied after the first three weeks. Apparently GA is either not effective in decreasing time to head in the absence of a dark period or in strong light, or some other factor brought on by the environment reversed the effect of GA. The cooler temperature would more than offset the increased light and delay heading as much as the seven days reported here (30).

Whyte (147) reported that Indian workers reduced the time to head of a rice variety from 133 to 47 days with vernalization. Heading time of Antelope rye was reduced to as few days as the rice variety by vernalization but unvernalized Antelope headed in about 95 days. Sangaste rye might equal the reduction of time to head of the rice variety when final heading of non-vernalized plants is complete. However, Tetra Petkus rye and the winter wheats and barleys tested which are expected to head in 130 days or more were not induced to head in less than 58 days. One winter wheat variety could not be induced to head in less than 80 days under the conditions of the test.

The results of this experiment support Lysenko's statement that there is no distinct limit clearly dividing winter and spring plants. Plant breeders in most of the cereal growing countries have selected plants from the extremes of a heterogeneous mixture including a complete range of maturities. From this selection has developed two distinct types. The Italian variety in this test, which, because of growing conditions in that country, was not selected at the extremes, headed in 88 days

when not vernalized which is similar to the minimum heading time of Zanda when vernalized. I.B.O. 1535 was also intermediate in that it did not behave as a late spring wheat as it responded to vernalization in the same manner as other winter cereals.

Other data presented here conflict with Lysenko's ideas (70). He described the first stage in winter wheat development as the 'therme-stage' or vernalization stage which must be completed before the initials of the reproductive organs are laid down. However, in the present study Antelope rye and I.B.O. 1535 wheat headed without any cold treatment and several of the other varieties have initiated flower primordia. Purvis (96) and others have also shown that fall rye will flower 130 to 160 days after planting if given sufficient day length.

The double ridge condition in the primordia was found to indicate the initiation of flowering in Antelope rye, Kharkov wheat and Hudson barley. While the double-ridge state is a critical indication of floral initiation and provides a more accurate comparison of varieties and species, it is not practicable where data on several varieties at various treatments are required. The time involved in micro-dissection for large populations is prohibitive. On the other hand, investigators who use heading time as their criterion should remember that varieties and species differ in the time required from flower initiation to heading.

The minimum number of leaves required for flower initiation was below seven in all varieties except Wong barley and most of the plants in this variety did not withstand vernalization. Gregory and Purvis (97) reported that seven leaves was the

minimum number below which rye plants could not be induced to head. A few workers (3,74) reported that winter wheat was induced to head with less than seven leaves by vernalization. Sprent and Barber (125) leached a flower inhibitor from Pisum sativum and by doing so were able to induce heading at an earlier node. Cumming (21) has shown that certain Chenopodium species can be induced to flower without going through a "puberty stage". This is in direct conflict with Gregory's (30) report which states: "Before ripeness to flower has been attained no change in external factors can induce flower initiation; this thus corresponds with the stage of puberty". The results of this study indicates a minimum-leaf number of six in rye which conflicts with the minimum number suggested by Gregory (30) for this species. Short days and restricted light for the first 20 days after emergence followed by continuous light at 1000 foot candles in addition to the day light available in January and February appeared to be sufficient to induce heading one leaf earlier than the conditions used by Gregory and Purvis (97). Similar results reported here for winter wheat corroborate McKinney and Sando's (74) findings.

Lysenko considered that the time required for vernalization of a variety was an indication of its winter hardiness (70) and Bullina's (15)results confirmed this concept. The results of the present experiment are contradictory to these reports. Antelope rye is much hardier than Tetra Petkus but its optimum vernalization time is less. Several other workers have previously disproved Lysenko's hypothesis (3,66,68,100). McKinney and Sando (74) reported that vernalization retarded spring wheat.

This was not true for Redman when vernalized for 25 or 50 days but the number of days to head increased significantly with 75 days vernalization.

Retardation in heading time, when vernalization was increased to 75 days, occurred not only with the spring wheat but with all of the winter varieties on which data was obtained. The delay in heading time in plants vernalized 75 days as compared to those vernalized for 50 days was highly significant in Kharkov winter wheat and Antelope fall rye as well as in Redman spring wheat. In attempting to account for these results some of the most obvious explanations can be discarded first. If the seed during the long period of vernalization had become dry for even a short time devernalization would have occurred (66,98). However, the sand in the dishes was moist throughout the vernalization period and the humidity in the dishes was sufficiently high that there was always condensation on the lid. Most dishes were free of fungal growth and only the occasional seed showed any sign of disease.

Another possible explanation was that anaerobic conditions (34) developed in the dishes between the 50 and 75 days vernalization and so caused devernalization. If condensation sealed the dishes and prevented air from entering then the respiration of the growing seeds may have used up all of the oxygen. While this explanation cannot be discarded completely several reasons can be given as to why it is unlikely that this is the correct explanation. Very little growth occurred especially in the wheat varieties because they were placed in the refrigerator as soon as both shoot and root showed signs of growth and were no more than one half inch long when planted. Some of the rye seedlings

had sheets which were two inches long and roots which were longer when they were planted. No more than 20 seeds were placed in one dish and at least one half of the dishes in the 75-day-vernalization class were opened to add water.

One additional explanation for these results could be that the temperature was so low in the 75-day class that no growth occurred and thus no vernalization took place. This explanation is also unlikely as all dishes were held in the same refrigerator and were on the same shelves as the 50- and 25-day classes. Several times during the period plates were shuffled around to avoid any differential treatment. The thermometers used in the refrigerator were not checked and could have been in error but the low temperature would have had a similar effect on the shorter vernalization classes.

Notes on the stage of growth of each plant were taken 18 days after planting and these notes re-affirmed at 25 days. Most of the plants from the non-vernalized class were in the 2- to 3-leaf stage and those in the 25-day-vernalization class were in the 3- to 4-leaf stage. The 50-day-vernalization class varied from 1 to 4 with most of them at the 3-leaf stage. The 75-day-vernalization class varied from 1 to 4 also but the majority were in the 1 and 2 leaf stage and were marked as "stunted". Some plants in the other classes especially in the 50-day class were also classed as stunted. "Stunted" plants which were growing very slowly were of two types having either short broad leaves or fine-grass-like-seedling leaves. Many of the seeds which had not emerged were dug up. Some were alive but not growing much and apparently could not push through the soil. Others had grown

some, and then died.

The stunting may have been the result of injury. A sudden reduction in the temperature during the first 25 days of vernalization may have occurred resulting in slight frost injury. On the other hand prolonged cold treatment weakens seedlings so that even a reduction in temperature of one or two degrees might injure the 75-day-vernalization class and not the other classes.

One possible source of error in the test which could have been corrected by larger populations is the genetic variability present in wheat and barley and particularly rye varieties. All varieties possess variability but winter varieties have more than spring varieties because selection is made in earlier generations due to their biennial habit of growth. Because of the small populations used in these tests genetic variability could have disrupted the general heading pattern. Purvis (96) used rye in many of her studies but overcame the extreme variability of this crop by working with very large classes. She reported an increase in time of anthesis with increasing periods of vernalization when the time was recorded from the start of vernalization. Banting (3) found an increase of 10 days in Thatcher spring wheat with increase in vernalization time from 60 to 90 days. The heading time of Minhardi, one of the varieties used in this study, increased with increase in vernalization period from 60 to 70 days, then decreased from 70 to 80 and again increased with vernalization of 90 days. Such fluctuations were common to other varieties when the vernalization period increased from 60 to 90 days.

It is possible that during the latter 25 days of

vernalization that a growth inhibiter had developed in the seedlings. Perhaps it inhibited the gibberellin-like substance present in seedlings. In Redman and Minhardi exogenous GA overcame the inhibitory effect to some extent and in the other varieties there was an insufficient number of plants in one or other of the GA treated or untreated class to support or contradict these findings. It appears that the extension of the vernalization period may not directly effect the initiation of flowering but retards vegetative growth and this indirectly results in an increase in the number of days to head.

These findings do not conflict with the schematic explanation of vernalization and photoperiodism in plants proposed by Purvis and Gregory (30,97) but is also compatible with Melchers' explanation of inhibitory-promoter balance reported by Lang (32). Lang states that the effect of day length consists not in the formation of flower promoting substances under the inductive conditions, but in the formation of flower-inhibiting substances under the non-inductive conditions. If flower-inhibiting substances are present in plants, and such substances are autocatalytic in their production, then some condition present in the vernalization procedure used in this study may have promoted the development of such a substance. Thus a longer inductive period was necessary to overcome the inhibitive effect and flowering was delayed.

This explanation is purely speculative as the limitations of the data and the lack of control of certain conditions do not permit definite conclusions. The vernalization experiment should be repeated with larger numbers of plants in each class

and with greater control of vernalization and growing conditions.

In studying the effect of gibberellin on dwarfing in winter wheat Allan et al. (1) found that dwarf and semi-dwarf varieties showed some growth response to the chemical but were shorter than normal. They found that normal plants responded more than dwarf plants. Results of the present study agree with those of Allan et al. However, light intensity appeared to influence response to GA. With low intensity light the total length of leaves of GA-sprayed winter wheat varieties Zanda and I.B.O. 1535 was 45 to 50 inches while still in vegetative growth (Plate 6, Figures 3 and 7). However, under high light intensity the leaves of Zanda were only 20-24 inches long while I.B.O. 1535 actually headed at a height of 14 inches. Redman spring wheat responded in a similar though less pronounced manner. Measurements of GA-sprayed Redman grown under low and high light intensity were 32 and 20 inches, respectively. Temperature of the plants exposed to high light intensity was 5 to 10 degrees cooler than plants grown under low light intensity. I.B.O. 1535 grown under low light headed in 56 days when sprayed with GA while under high light intensity it took 87 days. Several workers (142,143) have replaced the need for long days with GA and others (6) have replaced the need for cold treatment but no one has found that GA replaced both (146). In the present study GA appears to be effective in increasing elongation in the absence of high-intensity light. It is probable that the reason grasses respond to GA in the spring and fall and not in the summer may be because of shorter days and lower light intensity rather than because of lower temperatures as has been suggested (5,79).

Some GA-treated dwarfs in corn have been converted to normals, others have not been affected. Probably the dwarfs which are affected are dwarf because of the lack of ability to produce the gibberellin-like substance whereas those which do not respond are dwarfs because of a block at another stage in the metabolic process.

In a similar manner a gibberellin-like hormone may be necessary at one stage in the development from vegetative to floral initiation and if GA is applied at this stage it will induce flowering. However, if there is no lack of a gibberellin-like substance then no beneficial effect would occur. It may also be, as suggested by Phinney and Neely (94), that higher plants may be more specific in their gibberellin requirement. To test this hypothesis a gibberellin extract from a normal plant of the same variety or species should be used in an attempt to change dwarfs to normals.

If, as Brian (12) suggests, gibberellin-like substances are built up in long days, then it should be expected that plants grown under continuous light would have sufficient, and that adding GA would not speed up development. Brian (12) also believes that the replacement of vernalization requires high doses of GA. Results of the present study indicate that frequent application of 100 ppm of GA had little or no value as a replacement for vernalization under the specific conditions used. Much higher rates should be tried under a variety of light intensities, day lengths and temperatures before GA is discarded as ineffective in the vernalization process. The author has preliminary studies of this nature underway. Some measure of

success is assured because GA completely replaced vernalization in I.B.C. 1535 under one set of conditions.

CONCLUSIONS

1. Redman possesses two complementary dominant genes for dwarf habit on chromosomes VIII and XIII. These are only effective when in combination with a third gene from another variety.
2. Kenya Farmer possesses one complementary dominant gene for dwarf habit which appears to be on chromosome XIII but is not allelic to, or closely linked with the dwarfing gene on chromosome XIII of Redman. The dominant expression of this gene is only effective in producing dwarf plants in crosses with Redman when both of the dominant-dwarf genes of Redman are present.
3. Indole acetic acid, 2,3,5 triiodobenzoic acid and naphthalene acetic acid were ineffective in increasing stem and leaf length or inducing heading when applied to plants at 5 ppm.
4. Gibberellic acid was effective in increasing leaf and stem length at 10 and 100 ppm. Only slight increases in growth occurred at higher rates of application.
5. Gibberellic-acid action in inducing extension of growth was greatly enhanced by low light intensity and high temperatures, whereas, this gibberellic-acid action, with continuous high-light intensity and cool temperatures, was relatively moderate.
6. Gibberellic acid did not affect the course of meiosis or give rise to chromosome changes or polyploidy in *T. aestivum*.

7. Gibberellic acid induced heading and the production of a limited amount of seed in dwarf wheat although it did not alter the dwarf habit of growth.
8. Application of fertilizer to dwarf spring wheat overcame yellowing in gibberellic-acid-treated plants but did not overcome the spindly growth which occurred.
9. Gibberellic acid induced branching at the nodes and caused other abnormalities in wheat plants especially those derived from seed germinated in gibberellic acid solution.
10. Gibberellic acid had no appreciable value as a replacement for vernalization when applied at 100 ppm under continuous strong light intensity and cool temperatures but did replace the need for vernalization in an easily-vernalized-winter variety under low light and high temperature.
11. Gibberellic acid did not appreciably affect the minimum leaf number when plants were given optimum vernalization time.
12. The minimum number of leaves were reduced below seven in all species tested by vernalization under certain conditions of light and temperature.
13. Extension of the vernalization time to 75 days reversed the vernalization effect. Applications of gibberellic acid offset this reversal to some extent.

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