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THE BREEDING OF CROP IDEOTYPES

C. M. DONALD

Waite Agricultural Research Institute,
The University of Adelaide, South Australia

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SUMMARY

Most plant breeding is based on "defect elimination" or "selection for yield". A valuable additional approach is available through the breeding of crop ideotypes, plants with model characteristics known to influence photosynthesis, growth and (in cereals) grain production. Some instances of the successful use of model characters of this kind are quoted.

It is postulated that a successful crop ideotype will be a weak competitor, relative to its mass. Thus the like plants in the crop community will compete with each other to a minimum degree. This relationship of plant form to the exploitation of the enviroment may lead to two negative relationships among genotypes, namely:

(a) Between the performance of cultivars at low density and at high density respectively, and

(b) Between the competitive ability of cultivars against other genotypes on the one hand, and their capacity for yield in pure culture on the other.

A crop ideotype will make a minimum demand on resources per unit of dry matter produced. Further, in cereals, each unit of dry matter will include such a number of florets as to ensure that the ear has sufficient capacity to accept all photosynthates either from its own green surfaces or from other parts of the plant. These criteria are to be satisfied especially at high fertility, and when the total pressure by the community on environmental resources is intensified by high density of population.

A wheat ideotype is described. It has a short, strong stem; few, small, erect leaves; a large ear (this specifically means many florets per unit of dry matter of the tops); an erect ear; awns; and a single culm.

The design of crop ideotypes is likely to involve concurrent modifications of the environment. The wheat ideotype here described will call for consideration of the density of planting, the fertilizer rate, the plant arrangement and weed control.

Eventually most plant breeding may be based on ideotypes.

INTRODUCTION

Plant breeders have developed an impressive range of techniques in their search for increased yield and better quality in crops. Mutation breeding, polyploidy, the exploitation of hybrid vigour, embryo culture and advanced statistical design and analysis are among the many procedures which have enabled more effective breeding programmes. Yet if we examine the philosophies behind these programmes, we see that they are of but two kinds. In the first group, the purpose is to remedy some known defect in the crop, and this we may call "defect elimination". In the second group, the basic procedure is "selection for yield".

"Defect elimination" is adopted when disease resistance is bred into a susceptible genotype or when earliness is incorporated into a variety prone to water stress late in the season. It may involve the correction of physical imperfections such as weak straw in cereals, or deficiencies within man-made circumstances, such as a fragile skin in tomatoes which are to be mechanically harvested. In yet other projects attention is given to defects in quality, such as weak malting performance in barley or poor flavour in potatoes. These programmes of "defect elimination" have given substantially increased crop yield and quality in a great array of circumstances.

In plant breeding programmes based on "selection for yield", there is no incorporation of a designated physiological or morphological character, but only an intent to improve yield, without consideration of the why or wherefore of that greater yield. In simplest form, such a programme involves hybridisation among "promising parents", (they are defined as "promising" either because they are themselves high yielding or because they have already shown good combining ability for yield), the production of segregating populations, and the selection of high yielding material from among the segregates. This type of breeding has also been highly productive; success has especially depended on the availability of a wide range of material in the programme, the choice of the crosses to be made and the skilful evaluation of the emergent genotypes – together with one's share of good fortune.

When a new variety is produced in this way, the plant breeder may not know why it yields better than its predecessors. A wheat breeder who recently produced a high yielding variety of wheat, was asked what attributes gave it such capacity for yield; he replied, "I do not know... but I will list the characteristics of the variety, and it is for the physiologist to judge whether these may be the reasons for the high yield." Many cereal breeders selecting for yield give a like reply, or state that the new variety has "better adaptation" to the environment. BELL and KIRBY (1966) cite the extension of wheat and barley cultivation into high latitudes in Europe as illustrative of the breeding of cereals for a new environment by selection for yield.

The current remarkable advance in maize yields in the United States is due to higher soil fertility levels, denser plant populations and the use of hybrids able to yield well in these heavily fertilised, crowded communities. In these conditions some hybrids show a substantial proportion of sterility, while others maintain a satisfactory cob on all plants. How are the successful hybrids developed? Basically, by the production of inbred parents of likely value, hybridisation, and the selection of hybrids for high yield in dense, heavily fertilised communities. STRINGFIELD (1964) suggests that breeding for tolerance to crowding at high fertility is potentially the greatest contribution that maize breeders can make in this decade. Little is known of the characters which govern such "tolerance", but hybrids derived from "prolific" inbreds (STRINGFIELD, 1964) or which are themselves 'prolific' (LANG et al., 1956) seem more likely to be successful. ("Prolific" here means a capacity to produce a second ear at wide spacing). Shade tolerance by the whole plant is also a feature of successful hybrids (STINSON AND MOSS, 1960), while HAGEMAN et al. (1967) suggest that the levels of activity of enzymes such as nitrate reductase may ultimately provide breeding criteria. These are as yet but faint and uncertain indices of the attributes of success, and the maize breeding programmes of the United States, other than those aimed at "defect elimination", continue to be based principally on inbreeding, hybridisation, and the selection of F_1's for yield performance.

THE DEVELOPMENT OF MODELS

The bases of crop breeding programmes can be usefully extended by a third philosophy, namely "the breeding of model plants or ideotypes". Man has long used models in his approach to a great range of problems; indeed the process of invention comprises the development of theoretical models based on knowledge, experience and imagination, the construction of the models, their testing and their use. It is the familiar approach in aircraft production, building construction and instrument design, and its validity for these physical purposes is generally accepted. Can this principle be applied to biological needs? We must pose a further question: Is it possible in any defined environmental situation to design a plant which is (i) theoretically capable of greater production than the genotype it is to replace and (ii) of such design as to offer reasonable prospect that it can be bred from the material available? The satisfaction of these criteria lies in the availability of three resources, namely sufficient knowledge, adequate genetic diversity and suitable techniques.

We may not yet have enough understanding of the anatomy and physiology of some crop species to permit the design of new cultivars, but in others, notably the cereals, we may now be able to conceive models of superior productivity. Admittedly, there can be no immediate certainty of success; all agree that models must be tested for performance. But if we can sensibly postulate a model, albeit but a crude attempt at perfection, then we have the opportunity to devise and examine a combination of characters which otherwise may not occur in breeders' plots for centuries. Further, even though the early models produce no immediately useful commercial material, they will provide new bases for the understanding of crop ecology and for the design of progressively more effective models. In contrast, "selection for yield" is unlikely ever to approach the asymptote of yield, since the appropriate combination of plant characters, never being sought, can be attained only by attrition or chance. Selection for yield has all the immediate advantages and all the longer term limitations of a wholly pragmatic procedure.

Those who question the usefulness of designing or breeding model plants do so on a number of grounds. Firstly, they affirm that we do not have sufficient physiological knowledge to devise a model with confidence. In any breeder's plots, high yielding material of diverse growth form may be seen. How, they ask, can one nominate a particular plant form when there seems to be such a wide array of compensating mechanisms or routes towards high yield. Secondly, the definition of a model is potentially hazardous, in that it will narrow the spectrum of a breeding programme, rather than permit the emergence of the highest yielding segregates without prejudice by the breeder as to the most desirable plant form. And thirdly, they add, even if the model plant were to prove high yielding, the unique character of the model would not be established. Any other model could perhaps lead to equally high yields. Only if we breed and test many different models, or a series of models with varying degrees of model-character input, can we determine the advantage, if any, of the preferred model.

LANGER (1967) questions whether the plant breeder can be expected to react to the multiplicity of suggestions currently offered by the physiologist, but he envisages considerable impact on plant breeding objectives as the physiology of yield is further elucidated. MAC KEY (1966) while contributing to the design of models, believes that they cannot be directly applied in practical plant breeding; he considers that their value will lie in providing concepts which permit appropriate decisions within breeding programmes.

While the weight of these arguments and reservations is recognised, they are believed not to invalidate the proposition that cereal models of likely value can be designed and bred at the present time. The very diversity of form among currently successful cultivars may indeed suggest that each variety is deficient in one or several characteristics. The narrower array of material to be used in the breeding of models is implicit in the concepts behind such a programme, just as the aircraft designer chooses materials appropriate to his model.

THORNE (1966) and TANAKA et al. (1966) contribute to thought on models by discussing and evaluating a number of attributes which are believed to influence the grain yield of wheat, barley and rice. Others have taken a further step and have advocated cereal breeding programmes incorporating individual model characters or have actively undertaken such projects (DONALD, 1962; ASANA, 1965; BEACHELL and JENNINGS, 1965; MAC KEY, 1966; TANNER et al., 1966).

Several examples can be given of the use of model characters. Cereal breeders have long laid emphasis on resistance to lodging, based both on the maintenance of grain yield and on the difficulty of harvesting lodged crops. The crop physiologist has established the influence of lodging in terms of its interference with light relationships and photosynthesis. Here then, in a stout stem, is a "model character", a character currently receiving increased recognition because of the extreme resistance to lodging at high fertility of the semi-dwarf wheats of Japan, used so successfully in breeding programmes in Washington State and Mexico.

A second model character of proven value, defined both from physiological studies and through breeders' observations, is the awn on the floret of wheat and barley. But though this character makes a positive contribution to photosynthesis and yield, and is easily incorporated into breeding programmes, there are still many new varieties which do not have this valuable attribute.

A third model character, now gaining recognition by a few cereal breeders, is erect foliage. There is theoretical advantage to be gained in the photosynthesis of various cereals if they have upright leaves (e.g. MONSI and SAEKI, 1953; DUNCAN et al., 1967); it is significant that the modern high yielding rice varieties of Japan and Taiwan, both *japonica* and *indica* types, which yield so much more than do the rice varieties of the tropics, all have this feature in common, together with relatively dwarf stature. TSUNODA (1959a, 1959b, 1960, 1962) has shown that the kinds of rice responsive to high fertility and high density are those with short, sturdy erect stems and short erect dark green leaves. Workers at the International Rice Research Institute in The Philippines have further examined and elaborated the importance of these characters in growth and grain yield (TANAKA et al., 1966; BEACHELL and JENNINGS, 1965; JENNINGS, 1964) and by hybridizing a productive Taiwanese variety (Dee-geo-woogen) of short stature and erect leaf habit with a tall, lax, locally adapted variety (Peta), they have produced a short, erect variety which has given excellent performance under a heavy fertiliser regime both in The Philippines and elsewhere in tropical Asia (I.R.R.I., 1966).

Thus we see growing evidence that "model characters", especially those emerging from physiological studies, are now influencing the approach by a few plant breeders. Perhaps model plants will in fact develop in this way, by the progressive adoption of individual model characters until, in the aggregate, these characters constitute a total model in the mind of breeders. If this were so, then the development of models might evolve from "defect elimination" but in the positive sense of "character incorporation".

Whether there has been an incorporation of one or many "model characters", there will remain other attributes which, according to local circumstances, must be incorporated into the new variety, such as disease resistance and maturity. Because of this, and also because of the unpredictability with which "model-character genes" may affect other characters, any intended cultivars produced to model specifications must finally be subjected to rigorous selection for yield. Further this testing must include examination of the adaptability of the cultivar and its capacity for yield over a sufficient range of environmental situations. Yet if the model is successful, the whole level of testing will be at higher yields than those of existing cultivars.

The term "ideotype", literally "a form denoting an idea", is here proposed for biological models. In its broadest sense, an ideotype is a biological model which is expected to perform or behave in a predictable manner within a defined environment. More specifically, a crop ideotype is a plant model which is expected to yield a greater quantity or quality of grain, oil or other useful product when developed as a cultivar.

Principles of design of cereal ideotypes

Concepts of cereal plants with high yield based on more culms, more ears, spikelets or grains are derived from considerations of the isolated plant. Here such criteria are valid. But the performance of a plant growing in isolation may have little relationship to its potential for yield as a community. The principles of plant design here enunciated are based on experimental findings and theoretical concepts related specifically to capacity for high grain yield when grown as a crop.

In a field crop each plant suffers intense competition from its neighbours, with its yield reduced to 20% or 10% or less of the yield of an isolated plant, and it is in this crowded community that any ideotype has to succeed. This capacity of a genotype to yield well in a community can be analysed in terms of two parameters, namely (a) the yield per plant in the absence of competition from neighbours, and (b) its response to crowding among other plants of like genotype. The response by wheat cultivars to crowding is almost unexplored. In no wheat environment do we know how much of the success of leading cultivars is due to their capacity to yield well at wide spacing and to maintain that margin over other cultivars when sown as a dense crop, or alternatively the degree to which a successful cultivar may be a low producer under very wide spacing, but with a capacity to maintain its yield per plant *relatively* well within a crop. In rice it is the latter attribute which gives success under crop conditions (TANAKA et al., 1964), and a similar situation may be indicated for wheat (WIEBE et al., 1963). It is because of these relationships that much of the work on the physiology and yield of the isolated plant may have but limited relevance to the crop situation.

Clearly the individual plant within the community will express its potential for yield most fully if it suffers minimum interference from its neighbours. Thus its neighbours should be weak competitors. And since, for the purpose of this discussion, all plants in the crop are of like genotype, then the ideotype itself must be of low competitive ability.

This may seem a paradox – that a successful crop plant should be other than an aggressive competitor for those factors needed for growth. But this seems to be so. While strong competitive ability is advantageous against other species such as weeds, it will lead in a monoculture to intensified competition and heavy mutual depression among the crowded plants. For example, a genotype which shows effective interception of light through expansive leaf display by the isolated plant, may show less efficient utilization of light within a community of that genotype, because of mutual shading by neighbours.

The efficient production of dry matter by a monotypic community will depend on the ability of the individual plant to make maximum use of the resources of the limited environment in which it grows, and to encroach to a minimum degree on the environment of its like neighbours. For example, if an erect leaf can photosynthesize effectively within a less horizontal area than a drooping leaf of like size, it is operating with a less demand on the light resources. Similarly a genotype of high net assimilation rate or with a particular pattern of deployment of photosynthates may be efficient in terms of its demand on resources within the community. But some of these same attributes may be disadvantageous among widely spaced plants.

Though the individual plant in a crop should have a low demand on resources relative to its production, the community as a whole must press on total resources to a maximum degree, for only then can full production be envisaged. The means towards this end does not lie in the aggressiveness of the individual plant but in a high density of plants resistant to crowding (i.e. of low competitive ability against each other), each making efficient use of its limited environment, yet each ultimately in intense competition with its neighbours because of dense planting.

It is submitted that the successful crop plant will be of low competitive ability relative to its mass and of high efficiency relative to its environmental resources.

This low competitive ability of the successful crop plant means that as well as the negative relationship already indicated (performance at low and high density respectively), there may be a second negative relationship; this is the relationship of (a) the competitive ability of a particular cultivar within a mixture of different cultivars with (b) the yield of that same cultivar in pure culture. This has been demonstrated with barley (SUNESON, 1949), and dramatically for rice (JENNINGS and DE JESUS, 1968), where it has been shown that high yielding cultivars are suppressed and even totally eliminated in mixtures[1].

[1] The results of JENSEN and FEDERER (1965) at first appear to sustain contrary relationships to those postulated above. They found the same ranking of four wheat cultivars "in the absence of neighbours" and "under more competitive conditions". However the mean relative yield per row in the two situations was only 1.75/1 and thus the two intensities of competition were not very different. Secondly, they found that the cultivar which was highest yielding in pure culture was also dominant

Because of these relationships, selection for yield in heterozygous communities may be an erratic means of advance. WIEBE et al. (1963), studying mixtures of parental and heterozygous barley to simulate successive filial generations, concluded that because of competitive effects between genotypes, "where high yield is the criterion selected for, say in the F_6, and the selection is intended for use in pure stands, the instructions from the present study are that one should save the poorest plants from the F_6 rather than the good ones". JENNINGS and AQUINO (1968) advocates the hand rogueing of F_2 populations of rice to eliminate tall, leafy and spreading types, which would otherwise shade and depress the potentially more productive segregates.

Thus the successful crop ideotype, despite its potential for high yield as a monotypic community, may not emerge from mixed or segregating populations. The development of ideotypes must depend on the active recognition of their attributes and not on their ability to compete with other genotypes.

The foregoing relationships will apply especially to total dry matter production. However NICHIPOROVIC (1954) and many others have emphasized that total production (biological yield) is an insufficient criterion of crop yield when the economic yield comprises only a part of the plant, such as its grain, fibre or oil. Assuming that the model is capable of heavy dry matter production (net photosynthesis), a further feature must be its capacity to render a maximum part of that yield as the useful product. Nichiporovic terms this ratio of 'economic yield' to 'biological yield', the 'coefficient of effectiveness of formation of the economic part of the total yield'; DONALD (1962) has suggested the term 'harvest index'. The translation of a 'high harvest index' into meaningful morphological and physiological plant characteristics is a specific and major need in the design of any model. It is not enough that a model plant have many large ears or bolls, but that the weight of these organs be high relative to its dry matter production. This is a critical aspect of plant design.

In some species the 'economic part' clearly forms a sink for photosynthates during the later part of the plant's growth. The cereal grain and the potato tuber are such organs; thus ear production and ear characteristics in cereals will have high relevance to grain yields. Here lies further opportunity to define characteristics of an effective ideotype.

The design of a cereal ideotype will thus depend heavily on theoretical knowledge and experimental evidence in three areas, namely photosynthesis in cereal communities, the role of the cereal ear as an available or limiting sink for photosynthates and the operation of plant competition in crop communities.

The question arises whether any of these principles of design can have substantial constancy of expression over a wide range of environments. Though the principles be valid, their application may conceivably lead to such a range of models as to make plant design both difficult and profitless.

It is suggested that two considerations should influence the approach to plant ideotypes in relation to environments. Firstly, it seems reasonable that the designer should initially seek to cater for the simplest environmental situation, and, further,

in the mixtures. This finding is subject to the reservation that the mixture was not of intimate kind, but consisted of dense rows of the respective pure cultivars, spaced one foot apart. Competition from like neighbours within the row seems likely to have been much greater than that from plants in the contiguous rows.

one which can readily be defined. In general this will be the situation in which the factors needed for growth and development approach maximal needs. In particular, water and nutrients should be in non-limiting supply, with emphasis centred on the efficiency of the crop community as a photosynthesizing system. Here then will be a basic ideotype designed to give maximum production in a highly favourable or idealised environment. If such an ideotype is developed, then the effect of any curtailment of resources, as by a decrease in nutrient or water supply, can be examined in terms of the progressive modification of the basic ideotype. This approach promises a more rational array of variants than could be achieved by a series of ideotypes independently conceived for each major environmental situation.

The second point pertaining to environment is that the production of a crop ideotype may call for the concurrent creation of a new environment. HUTCHINSON et al. (1947) wrote, "Successful evolutionary change depends on a fortunate coincidence of the emergence of a new character with the occurrence of an environmental change which makes it advantageous." Similarly the conscious development of an ideotype may need to be accompanied by conscious change of the environment. Though we are concerned in this instance with a potential to yield well as a pure culture rather than with a potential to compete successfully with other genotypes, the concept of the relationship to the environment is basically the same. Model building need not, therefore, be exclusively associated with existing environments, but may involve the concurrent design of new environments, including such man-made components of the plant environment as the crop density, planting arrangement and nutrient level.

A WHEAT IDEOTYPE

The feasibility of designing a wheat ideotype is best examined by attempting such a design. In accordance with the foregoing discussion, the ideotype here presented is conceived as potentially capable of high grain yield when grown as a crop community in an environment favourably endowed for water and nutrient supply, though most of the characters are believed also to be of ubiquitous value. This basic ideotype is submitted therefore as suited to well-fertilized, well-watered lands as of irrigation areas or of northern Europe.

All the attributes of the ideotype are morphological characters, but all are based on physiological considerations. It is believed that the model may offer levels of yield appreciably greater than those available from genotypes of currently prevalent plant form. The features of the model are:

1. *A short, strong stem.* As already discussed, the advantage of a short stout stem in reducing the likelihood of lodging, is well established. The need for a strong stem increases as fertility is raised, since the modulus due to wind becomes greater as the weight of the ear increases.

A secondary effect of height will be to change leaf disposition, in particular the vertical interval between successive leaves on the stem. If the leaves are very closely spaced, as on an extremely short stem, there may be serious shading of all but the top leaves, especially because of the two-ranked arrangement of grass leaves. This seems to be a possible explanation for the lack of sorghum cultivars with all four of the known dwarf genes, and it suggests a disability of excessive dwarfness. (This relates also to the 'leaf area density' (KASANAGA and MONSI, 1954), discussed under leaf size).

It is possible that shortness of stem may make a small contribution by reducing the investment of photosynthates into stem production, but this proposition is doubtful in wheat because the stem is itself covered with photosynthesising tissues.

If we weigh these points it seems that a relatively short stout stem, though not excessively so, is essential as a safeguard against lodging, while still providing a sufficient dispersal of leaves in the canopy.

2. *Erect leaves*. Reference has been made to this aspect of plant form in rice breeding programmes. It is based on the concept that in a dense community, near-vertical leaves will permit adequate illumination of a greater area of leaf surface than will occur in a canopy of long, horizontal or drooping leaves, in which the upper leaves will be overlit and the lower leaves harmfully shaded. This relationship will apply to any species in which the leaf is nearly saturated for photosynthesis at a light intensity substantially below that of the ambient light. Such is the case for rice (e.g. MURATA, 1961) and wheat (e.g. WARDLAW, 1967).

A direct demonstration of the effect of leaf angle in rice was made by MATSUSHIMA et al. in 1964. They grew an erect-leaved rice variety at wide and at close spacing; half the plants were treated by dropping the leaf angle with paper fasteners attached at the leaf tips. Carbon assimilation was unaffected in the widely spaced plants, but was depressed by 35% in plants at close spacing. HAYASHI and ITO (1962) similarly showed in a collection of rice varieties that the steeper the leaf angle the greater was the light penetration (lower coefficient of extinction), and the greater the crop growth rate[1].

GARDENER (1966), working at Guelph, Canada, compared three barleys known to be high yielding for grain with three known low-yielding barleys. The high yielders had narrow, upright leaves and showed deep light penetration into the leaf canopy, while the low yielders characteristically had long wide drooping leaves and showed strong light interception by the upper leaves of the canopy. TANNER et al. (1966) classified 300 varieties of wheat, oats and barley at Guelph into high, medium and low yielders purely on the basis of their leaf angle and leaf width. They found that they had correctly selected all but two of the 50 high yielding varieties, and they consider leaf habit to be a valuable criterion in selecting for cereal yield in Ontario.

Vertical foliage accords with the concept of greater production per unit of environmental factor and with low competitive ability. Plants (or culms) with vertical leaves can be crowded with less mutual competition than would occur among crowded plants with floppy leaves, and this potentially permits a greater population of ears per unit area. (Varieties of rice with large floppy leaves give low production, but become dominant in mixtures; they are characteristic of much tropical village agriculture because of their ability to suppress both weeds and other rice genotypes (JENNINGS, 1966).

3. *Few small leaves*. The postulated advantage of small leaves is mainly based on

[1] Increased yields of maize were gained at Urbana, Illinois, U.S.A. in 1967 by mechanically raising the leaves to a more vertical position (PENDLETON, 1968).

theoretical considerations. KASANAGA and MONSI (1954) showed that a scattered leaf arrangement (a low leaf area within each 'leaf plane' of the canopy) is potentially advantageous in plant communities under high illumination, i.e. in crops, in contrast to shade communities. WILSON (1960) similarly calculated that the more uniform the dispersion of leaves in each leaf layer, the greater will be the crop growth rate. Each of these theoretical considerations indicates an advantage of many small leaves over a few larger leaves. In support of this hypothesis, TSUNODA (1959b) reported that in both rice and soybean the varieties adapted to heavy fertiliser application (we may regard this as applicable also to high density situations) tend to have smaller-sized leaves. In wheat, small leaves and more especially shorter leaves, tend also to be erect leaves, while longer leaves are more likely to be floppy and downward curving.

The number of leaves on the main shoot of wheat ranges from 7 to 20 or more. The axils of the lower leaves are the sites of origin of the primary tillers, but in a uniculm plant (see below) this role disappears, and we are concerned with leaves mainly as photosynthetic, respiring and evaporating surfaces. If we assume that each leaf produces net photosynthates exceeding the sum of its own dry weight and the contribution it makes to later leaves, stems and roots, then the greater the number of leaves, the greater will be the culm's potential to produce a large ear. But this will be true only as long as each additional leaf permits a more complete exploitation of the environment. If, for example, the leaves in the crop are already sufficient to intercept all light then there can be no advantage in more leaves (DONALD, 1963; PUCKRIDGE

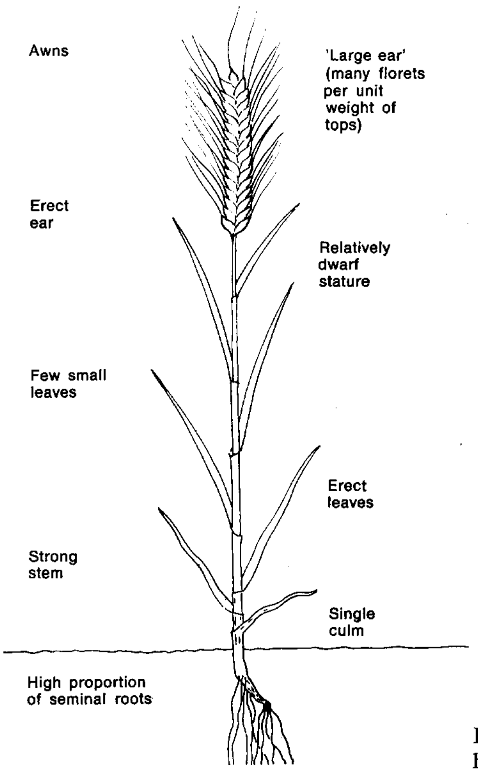

Fig. 1. A basic wheat ideotype, designed to give a high grain yield as a crop community

and Donald, 1967). The same general considerations would be true if water or nitrogen were limiting. Though our understanding of the significance of leaf number is very incomplete, it seems that a high density of culms offers better prospects of a heavy grain yield than does a high number of leaves per culm; for any given leaf area index it permits greater potential sink size relative to vegetative growth.

4. *A large ear.* (Many florets per unit of dry matter). There is much circumstantial evidence that the wheat ear is normally a limiting sink for photosynthates. In brief, this evidence is of two kinds. Firstly, when various individual parts of the photosynthetic surface responsible for grain filling (flag leaf, upper stem, ear) are removed or shaded, the remaining parts can partially compensate for the loss of the part that has been removed or shaded (e.g. Buttrose and May, 1959; Thorne, 1963). Thus none of these organs normally operates at full capacity. Secondly when the grain number in a wheat ear is reduced from the full complement, the weight per grain may show no increase (Buttrose, 1962). This indicates that in the control ear, the number and potential size of the grains, rather than the supply of assimilates, may govern the total weight of grain produced.

Thus at least up to the time of fertilisation, the wheat plant may be said to re-act 'conservatively', in the sense that its number of tillers, its number of surviving spikelets per ear or its number of fertilised florets show such reduction, relative to past and current environmental conditions, as to offer high probability that the load of developing grain will lie within the photosynthetic capacity of the plant to bring it to maturity. This means that a limitation to yield may occur in existing cultivars in the pre-anthesis period simply because of the genotype-environment interaction. (There is probably survival value in 'conservative' grain production by annual grasses in natural communities. In very adverse seasons a smaller number of fully formed seeds is advantageous over a greater number of seeds which are imperfectly formed).

Thorne (1966) points out that any limitation to yield imposed by the capacity of the ear is at present supported only by indirect evidence. Nevertheless the reasonable deduction from a considerable array of data is that the receptive capacity of the grains of the wheat ear is usually less than the post-anthesis photosynthetic capacity of the shoot that bears them.

If the proposition of sink limitation be accepted, then clearly the model wheat plant must have large ears. We have yet to learn whether the spikelet number or the floret number per spikelet is per se of the greater consequence, but by 'large ears' we certainly mean ears with many fertile florets. In particular the attribute of high floret number, relative to that of other genotypes, must be expressed under the acute competitive stress of a crop community.

It may be thought that all this is but a truism – that the number of fertile florets in the cereal ear is not only related to yield but is indeed synonymous with it. But this is not necessarily so. The wheat breeder has long been familiar with argument on the relative advantage of a large number of ears on the one hand or of many grains per ear on the other. The rice breeders of Japan are similarly divided into devotees of 'panicle number' and 'panicle weight'. Further, it is recognised that these attributes are usually negatively correlated, and that pursuit of size of ears commonly leads to a decline in ear number.

The proposition that the ideotype should have a 'large ear' is therefore interdependent with other points. 'Large ears' must specifically mean a large number of florets per unit of dry matter of the whole of the plant tops. (If one uses weight of grain instead of florets, the ratio to total dry matter is then the 'harvest index'). It is of interest that the increased grain yield by the varieties of oats currently in use in Australia is associated with a higher harvest index, without increase in the total dry matter production (SIMS, 1963). Compared with earlier varieties the index has risen from about 0.32 to about 0.40. The meaning of 'large ears' in a wheat crop is thus a sufficient number of florets per unit of total dry matter to ensure that their aggregate capacity will impose no sink limitation for photosynthates. No cereal breeding programme can be wholly effective without measurement of the total yield of dry matter as well as of grain.

A further model character critically related to the ear size of the model plant is a single-culm habit of growth, discussed below (Item 7).

5. *An erect ear.* This is adopted in the belief that the best mean illumination of all sides of all ears will be attained in a community of erect ears. This is the common ear disposition in wheat, though drooping ears are to be seen in some commercial varieties.

6. *The presence of awns.* There is evidence dating back to 1920 (HARLAN and ANTHONY, 1920) that the additional surface provided by awns will contribute significantly to photosynthesis by the cereal ear. GRUNDBACHER (1963), who has reviewed the literature on this topic, considers that as assimilating organs they may contribute more than ten percent of the total grain dry weight. The contribution seems to be greater under semi-arid conditions, supposedly because of the xeromorphic structure of awns compared to that of cereal leaves. This contribution to yield by the awns has been recognised in many plant breeding programmes (e.g. VOGEL et al., 1963).

Perhaps there is a limitation to the advantage of awns, in that very heavy awns or branched awns may shade the photosynthetic surface of the glumes to a significant degree. But of the value of simple awns there can be no doubt.

7. *A single culm.* It is important to appreciate that the number of culms per plant (main stem plus tillers) in any cereal community is not characteristic of the species, but is a consequence of the selection of a genotype to fit the local climate and more particularly the local agronomic practices. For example under crop conditions, rice in Japan has more than 20 fertile culms, while wheat in the United Kingdom has 2 or 3. This is no indication of any interspecific difference between rice and wheat in respect to tillering. Rice plants in Japan are normally spaced at about 24 cm $\times$ 24 cm. Any closer spacing would intensify the enormous annual task of hand planting some six hundred thousand million individual rice seedlings. And so a genotype has been selected which will occupy the 24 cm $\times$ 24 cm environment – one which tillers freely. The number of tillers on wheat in England is similarly a consequence of agronomic practice – of the selection of a seeding rate in the days of hand broadcasting on unfertilised fields and of the subsequent transfer of that seed rate to 18 cm rows. No new variety is accepted into the system unless it produces well when sown at the

usual rate in these rows, and this includes having the appropriate number of fertile tillers per plant.

If this viewpoint is accepted, then the desirability of a low or high tillering capacity in any cereal can be re-considered without prejudice invoked by past or current practice. In this context it is now proposed that a community of wheat plants with a single culm – that is, with a main stem and no tillers – will give greater production per unit area than is given by a variety which tillers freely or even sparsely.

The wheat plant is potentially capable of indefinite perennation through culms successively developed from buds on the primary, secondary, tertiary and succeeding orders of tillers – a sustained production of 'daughter' vegetative organs. But at a later stage, because of competition between the ears and the younger tillers for nutrients, and because of the suppression of tiller buds through the apical dominance of the ear bearing tillers, the younger tillers produce no ears and die, or are even totally suppressed (ASPINALL with barley, 1961, 1963; RAWSON with wheat, 1967).

The growth of the wheat plant can thus be regarded as beginning with a period of perennation, followed by a period of active competition between perennial and annual attributes, and finally by a period in which the annual habit prevails. Seed is produced and the plant dies. To the extent that 'unsuccessful' sterile tillers are produced, wheat has not yet evolved to become a fully efficient annual plant.

On the other hand, a wheat plant comprising only a main stem and no tillers will have no remnant of perenniality. There can be no internal competition between developing ears and young tillers, but only a uni-directional organisation towards ear and grain formation.

Though the sterile tillers in wheat crops are considerably smaller than those which produce an ear, they nevertheless use a part of the environment. Some of these environmental resources, notably part of the nitrogen and minerals, are passed to the fertile tillers as the sterile tillers senesce, but there is a net 'loss' in the sterile tillers even of these nutrients. When we turn to water and light, the competition by the sterile tillers is essentially irreversible. The loss of water through sterile tillers may be particularly significant in the drier environments in which most of the wheat of the world is grown.

Reference has been made to the inverse relationship between the number of ears per plant and the size of the ear in multi-culm plants, either in comparisons of genotypes or due to environmental or density differences. As a result there is no control of ear number per plant or per unit area when the density of multi-culm plants is varied. On the other hand if a uni-culm plant is used, the ear number per plant will be constant at unity (except at excessively high densities), and the numbers of ears per unit area will be controllable; it will be feasible to achieve an optimum density/ear size relationship. Similarly, in plant breeding programmes with uniculm material, there can be positive pursuit of ear size as a character of the ideotype, because of the non-plasticity of the culm number.

If the seed rate of a normally multi-culm wheat variety is heavily increased, then eventually a density is attained at which all plants will have a single culm. At such a seed rate, the plants will be extremely depauperate, and the yield per unit area will be less than at a lower seed rate (PUCKRIDGE and DONALD, 1967). This single culm community attained by crowding multi-culm plants is thus not comparable with a crop of genetically single-culm plants. The latter will of course be plastic as density rises, at first in ear size, then by total ear failure and finally by plant mortality. But the uniculm habit will prevail at the optimum density for grain yield and not only at excessive densities.

We can examine as a separate point the question of whether the main stem, as a single culm, has any advantage over any other tiller, also as a single culm. The greater grain production by the main stem than by any tiller of a wheat plant in a crop is not proof that a community wholly of main stems will produce more grain than a community made up of both main stems and tillers. If the main stem in the latter situation uses environmental resources proportional to its greater production, then obviously its yield may be correspondingly depressed when it competes only with other main stems. Nevertheless the main stem may truly have a greater potential for production within a defined and finite environment than has any other single tiller. In the first place it has the principal benefit of the early water and nutrient uptake by the seminal root system (KRASSOVSKY, 1926). Secondly the early development of the main stem gives a much longer interval for the development of ears than in later culms. It has a far longer period to double ridge formation (RAWSON, 1967) and this may be the factor leading to its greater number of spikelets. Similarly it has a longer period in which to initiate florets. This time factor could give additional advantage to a community of main stems compared with a mixed community of main stems and tillers.

It may be noted that the non-tillering character has appeared in barley (e.g. as a mutant cv. Kindred, and also as chemical mutants, SWAMINATHAN et al., 1962). Meanwhile there is already a trend in wheat varieties in N.W. Europe towards decreased tillering, larger heads and larger seeds (MAC KEY, 1966).

8. *Other characters*. The ideotype here formulated does not permit the nomination of particular parents solely because of their strong display of desired characters. There may be various routes towards a variety conforming to the general pattern of the model; further it has already been emphasized that the ideotype must meet local requirements for disease resistance and so on. Thus the parental material must include high yielding, locally adapted cultivars, and indeed the extent to which this is needed is an index of the limit to our knowledge of the desirable attributes of our ideotype.

The features of the ideotype here described do not, for example, designate any specific maturity nor do they show the pattern of leaf area duration after anthesis. In general, early flowering, relative to the environment, may be indicated as a means of gaining a maximum number of florets per unit of dry matter at flowering and a lengthened period of grain filling. And similarly the finding by WELBANK et al. (1966) that leaf area duration (area of green leaf integrated with time) above the flag leaf node after anthesis is related to grain yield, suggests the desirability of strong persistence of the uppermost photosynthetic tissue. (May it be however that the persistence of these green surfaces is in part an effect rather than a cause of high yield? If an ear fills quickly because it is small, may the leaves then die early?)

Another character that could perhaps be developed to advantage is the heavy accumulation of sugar in the stem, followed by a maximum transfer to the growing grain; the transfer of these substances may again depend on ears of such capacity as to be non-limiting sinks (BUNTING and DRENNAN, 1966). Residual carbohydrates in the base of the cereal stem at maturity may, like tillering, be an undesirable vestige of perenniality, corresponding to the swollen lower internodes which serve as inter-seasonal survival organs in many perennial grasses.

Brief reference has been made to the influence of the singleculm habit on the root system. In a community of uniculm plants the seminal root system will retain far greater importance relative to the adventitious roots, and because the seminal roots are the oldest they will potentially be more deeply penetrating. Beyond this, no model characters of the root system are here specified.

The extent to which the ideotype is defined will be a matter of judgement by the designer. Those characters which are left unspecified must be cared for in the final selection for yield.

9. In summary the wheat ideotype will be of such form that it is a weak competitor relative to its mass, and thus will be less affected by crowding among like neighbours. It will make a minimum demand on resources per unit of dry matter produced, but each unit of dry matter will include a sufficient number of florets. The ear is to have a capacity to accept all photosynthates either from its own green surfaces or from other parts of the plant. These criteria are to be satisfied especially at high fertility, and when the total pressure by the community on the environmental resources is intensified by high density of population.

AGRONOMIC CONSIDERATIONS

The wheat ideotype here described calls for a number of modifications in the environment or in the agronomic practices relating to the crop; we can also consider some of the possible variants from the basic ideotype which may be needed in less favourable situations than those for which the ideotype is primarily designed.

1. *Density of planting*. Since each plant will produce only one ear, the rate of planting must be increased by a factor about equal to the mean number of ears per plant in existing varieties. The factor will however need to be greater than this, because the ideotype is specifically intended to 'tolerate' a high density of ears per unit area. (Here we see certain disabilities of the model, associated with its single culm habit. First, its yield as a crop must more than compensate the heavier seed rate. Secondly any partial failure of establishment or any winter killing will not be compensated by an increased rate of tillering by the surviving plants.)

2. *Rate of fertiliser application*. The whole philosophy behind the ideotype and especially its strong stem and small erect leaves is that it will produce well at high density and high fertility, with maximum utilization of light, minimum lodging and minimum sterility. A heavy nutrient supply is a cardinal feature of the environment of the proposed ideotype. When the fertility level is lower, small erect leaves or a 'large ear' become progressively less advantageous.

3. *Plant spacing*. When wheat is sown in narrower rows instead of the standard 18–20 cm rows, it commonly gives a slightly increased yield (HOLLIDAY, 1963), an

effect almost certainly due to the closer approximation to square planting, and thus to improved illumination of the foliage and more efficient soil exploration by the roots. The small and erratic nature of the increases so gained in wheat is presumably due in part to the multi-culm units involved, and the consequent 'aggregation' of the culms, particularly in the earlier growth stages, irrespective of the planting arrangement.

If a uni-culm plant is used, the benefits of square planting can be realised to the fullest degree, with a uniform spacing of all culms. Depending on the appropriate seed rate, (say 250 kg seed/ha) the drilling of uni-culm plants in 18 cm rows would give ordinates for each plant of about 18 cm $\times$ 1 cm (a rectilinearity of 18:1), while the ordinates for square planting would be about 4.2 cm $\times$ 4.2 cm. Square planting at this density, or its approximation by sowing in say 5 cm rows, would present mechanical problems, though probably not of insuperable kind.

It should be noted that the advantages discussed earlier for single culm plants are independent of planting arrangement and would be expressed in 18 cm rows. Regular spacing is potentially a further source of increased yield.

4. *Competition with weeds.* A disability of cereal varieties with erect leaves is their weaker capacity to suppress weeds by shading. TANNER et al. (1966) have recorded that a wheat variety with erect leaves, unable to suppress weeds effectively, gave the lowest yield in a variety trial in a weedy situation; on the other hand it gave the highest yield on a site which was weed free; and conversely for varieties with floppy leaves. Thus the use of varieties with erect foliage will involve greater attention to weed control by methods other than by competition from the crop.

5. *Water supply.* The basic ideotype, being unable to tiller, will attain its full potential as a photosynthesizing community only if the water supply and seed rate are constant in all seasons – a situation approached only under irrigation or in favoured wheat growing regions. Here a constant seed rate will give the optimal population density of culms and ears in all seasons.

But in regions of fluctuating rainfall, the optimal density of ears will vary between seasons. In present-day tillering cultivars of wheat, the principal adaptation to ample or deficient water supply within the season is a variation in the number of tillers and ears per plant. Thus a constant rate of sowing in all seasons is acceptable, even though imperfect. This will not be so with a uniculm cultivar. KASPER (1929) has well illustrated this relationship among older cultivars of grain sorghum; the free-tillering cultivar, Milo, gave maximum yields at the same spacing (60 cm rows) in both dry (ca. 230 mm rainfall) and wet (ca. 740 mm rainfall) seasons. On the other hand the sparse tillering variety, Kafir, gave its highest yield in 90 cm rows in dry years and in 7.6 cm rows in wet years.

A uniculm wheat thus seems to have prospective limitations in an environment of erratic seasonal rainfall. It would presumably offer satisfactory yields (relative to other cultivars) if the rainfall were predictably and reliably low, and a low seed rate were chosen accordingly, but it cannot show phenotypic adaptation to more favourable seasons by tillering. In areas of erratic rainfall a limited capacity to produce tillers in favourable seasons thus seems desirable. Probably a range of one to three culms per plant according to conditions would suffice for the full array of seasons likely to be experienced in such regions.

In the longer term, tillering may become redundant and undesirable even in areas of erratic rainfall. If the ear were of adequate capacity and plasticity relative to the culm and its environment, then it could carry the present role of the tiller number in adapting to a range of seasonal conditions. Such is the case for the modern, non-tillering or weak-tillering U.S.A. cultivars of sorghum. The same cultivars are grown under irrigation and under low rainfall, except where length of season is a restricting factor; the sorghum head varies in size according to the favourability of the environment (D. E. WEIBEL, private communication). The same adaptability to season holds for uniculm maize and its ear. Such a relationship may also be attainable in wheat once ear size is divorced from its reciprocal relationship with ear number and if the ear has an adequate range of capacity for photosynthates. Meanwhile it is proposed that the uniculm habit may first prove of value under irrigation or high rainfall conditions.

6. *Alternative uses.* The wheat ideotype here proposed is intended specifically for high grain production. In situations where yield of straw or recovery from grazing or any other attribute is important, considerable modification of the basic ideotype would doubtless be needed.

THE PRODUCTION OF AN IDEOTYPE

It will be clear that the wheat ideotype here depicted is unlikely ever to be developed in breeding programmes based on selection for yield under prevailing agronomic practices. It has a low yield per plant; it is susceptible to competition by other genotypes or by weeds; it is unsuited by current seed rates; and it may need novel sowing machinery. All newly wrought ideotypes may similarly involve changed practices, and it seems that advantageous combinations of radical ideotypes and radical practices will be attained only by hypothesis and test.

The ideotype here formulated may prove an imperfect image. Yet the design, breeding, testing and exploitation of plant ideotypes is a logical step towards new levels of yield and should be pursued with imagination. Eventually most plant breeding may be based on ideotypes.

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