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THE PHYSIOLOGY AND PHYSICS OF CROPS IN RELATION TO THEIR BREEDING

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ABSTRACT

Plant breeders have made substantial progress towards improving crop yields, mainly through genetic changes that have eliminated agronomic defects influencing yield. Elevation of genetic yield potential has been more difficult. This is partly because breeders have had few clear guidelines about plant traits associated with high yield potential which are observable and can be selected in breeding programmes. In the absence of adequate guidelines from physiologists, selection for high yield has mainly been empirical.

We suggest an alternative approach based upon knowledge of physiological and physical processes. First, the principal factors which control yield should be established, and those which can be genetically influenced identified. Then this information should be used to identify practicable selection criteria for breeding programmes.

We have selected a simple analytical model, based upon five main physiological determinants of yield, as a framework to examine the prospects for breeding for improved yield potential. The determinants are defined at the crop level of biological organisation rather than in terms of single physiological or physical processes. They therefore overcome many objections to extrapolation across levels of organisation. A further advantage of the model is that the determinants of yield can all be estimated from simple field measurements.

The importance for yield potential of each determinant is discussed, and an assessment is made about the prospects for using it successfully as a selection criterion in breeding programmes.

KEYWORDS

Yield potential, selection criteria, radiation interception, growth duration, radiation-use efficiency, dry matter partitioning and loss.

INTRODUCTION

Plant breeders have made substantial progress towards improving the yields of arable crops. The improvements are mainly attributable to changes which fall into two categories: first, genetic changes that eliminate agronomic defects which influence yield and second, elevation of genetic yield potential (Fischer, 1977; Evans, 1981). Historically, most advances have occurred in the first category. Examples are the development of resistance to various pests and diseases; selection for insensitivity to herbicides and pesticides; elimination of seed dormancy and susceptibility to lodging and shattering; and modification of the timing of crop life cycles so cultivars are better adapted to their environments.

Genetic yield potential improvements are more difficult to achieve (Fischer, 1977), although this aspect of yield improvement is equally important. It is likely to be the main avenue of progress in the future as the agronomic defects which constrain yields are progressively eliminated in modern genotypes. When assessing progress towards improved yield potential, it is important to distinguish between potential and actual yield. Evans (1981) defined the genetic yield potential of a cultivar as the yield achieved when it is grown in environments to which it is adapted, with nutrients and water non-limiting, and with pests, diseases, weeds, lodging and other stresses effectively controlled. How closely the actual yield approaches the genetic potential of a cultivar in a particular situation depends on how well its physiological characteristics are matched to the local environment, and on the level of agronomic inputs.

Evans (1981) made the above distinction when he showed that in several countries wheat breeders have achieved substantial increases in genetic yield potential. However, despite breeders' concepts of desirable plant types, improvements have only been detected at the yield-testing stage (Fisher, 1977). More efficient progress has been limited, partly because breeders have had few clear guidelines from physiologists about observable and selectable plant traits associated with high yield potential.

We suggest an approach based upon knowledge of physiological and physical processes. First, the principal factors which control yield should be established, and those which can be genetically influenced identified. Then this information should be used to identify practicable selection criteria for breeding programmes. This approach would allow more discriminating selection for yield-positive plant traits, especially in the early generations of breeding programmes.

In this paper we consider reasons for the failure of interaction between plant breeders and physiologists in the development of high yield potential cultivars. We then examine the possibilities for breeders to use a simple physiologically-based approach to analysing yield potential. This approach, which overcomes the main causes of previous failures, identifies five main determinants of crop yield. We discuss the importance for yield potential of each determinatn, and assess the prospects for using it successfully as a selection criterion in breeding programmes. The approach outlined here is primarily for annual crops; however it may be adapted to perennial crops with relative ease.

INTERACTION BETWEEN BREEDING AND PHYSIOLOGY

The contribution of physiology to the advances in yield potential achieved by breeders has long been a subject of debate. Undoutedly, breeders have benefitted considerably from specific areas of physiological research, particularly the development of new methods. Examples are techniques which improve the rate and efficiency of breeding programmes, and screening procedures for assessing particular quality or disease resistance characteristics. Passioura (1981) suggested that the greatest scope for physiology to impact on breeding is to continue to provide tools for speeding the 'random search' part of breeding programmes.

However, physiologists have aided breeders little in the search for high yield potential. Moreover, physiology has not been particularly successful as a retrospective science; Fischer (1977) suggested that it has been hard pressed to explain the yield advances achieved by plant breeders, let alone to provide breeders with clear guidelines to further advance yield potential. It is therefore perhaps not surprising that many breeders have a sceptical attitude towards physiology, and consider that physiology has contributed little to breeding (Pugsley, 1983). Passioura (1981), a physiologist, also referred to the many 'barren marriages between physiology and breeding'.

What are the reasons for the gap between physiology and breeding, and what are the prospects for more profitable collaboration in the future? Passioura (1981), Evans (1981) and Fischer (1977) reviewed these questions with respect to wheat and offered several answers. The most pertinent was that breeding aims to improve performance at the community level, whereas physiologists study plants at several levels of biological organisation, from the crop community through the descending levels of whole plant, organ, tissue, cell, membrane, and molecule. The difficulties inherent in extrapolating results from lower to higher levels of this hierarchical organisation largely explain many failed attempts by physiologists to provide sound guidelines to breeders. Passioura (1981) used examples to show clearly that research at lower levels must have direct relevance at the community level to have any impact on a breeder's objectives, but in too many cases it does not. He suggested that physiologists often begin their studies at too low a level of organisation, and argued that coarse dissections of crops were more likely to produce information relevant to the breeder. This also implies a need for crop models which integrate process-oriented physiology research results into the whole picture.

The reviews cited above suggested coarse dissections of crop yield might be of direct practical use to breeders, and could also provide frameworks for physiological studies of yield improvement at lower levels of organisation. They would therefore help establish the missing link between the disciplines. In the remainder of this paper we examine the practical prospects of a dissection of yield not mentioned in those reviews, but which we believe offers realistic possibilities.

PHYSIOLOGICAL DETERMINANTS OF CROP YIELD

We have chosen to examine the prospects for breeding for improved yield potential by using a simple approach proposed by Charles-Edwards (1982) as a framework for analysis. He identified five determinants of crop yield, all based on established physiological principles:

- The amount of radiation intercepted by a crop each day during growth (*J*, with units of $MJ/m^2/day$).
- The duration of crop growth (*t*, in days).
- The efficiency with which intercepted radiation is used in the production of new dry matter (*e*, with units of g(DM)/MJ).
- The daily partitioning of new dry matter between different crop parts, especially into those of economic interest (denoted by a dimensionless coefficient, n).
- The amount of dry matter lost each day during growth (*v*, with units of $g/m^2/day$).

The net amount of above-ground dry matter produced over a growth duration of *t* days (W_T) can be written in terms of the five determinants as:

$$W_T = {}^{i=t} (n_T.e.J - v)_i \qquad (1)$$

where the subscript T denotes parameters relating to the above-ground parts of the crop.

Charles-Edwards (1982) emphasised that these determinants, which can all be estimated directly from field measurements, are defined at the crop level of biological organisation, not in terms of processes occurring at some lower level of organisation. Nevertheless, they can be further analysed in terms of more basic physiological and physical processes of plant growth (Charles-Edwards and Vanderlip, 1985).

We chose this level in the physiological research hierarchy for three main reasons. First, we believe there is ample room for co-operative progress by breeders and physiologists if both groups work at this relatively simple level of yield analysis. Second, the approach overcomes many of Passioura's (1981) objections to extrapolation across levels of biological organisation. Finally, it offers realistic possibilities for identifying the yield determinants most amenable to screening in breeding programmes.

Amount of radiation intercepted (*J*)

At a given location and time, the same amount of radiation is available to all genotypes of a crop. However, the total amount of radiation intercepted (*J*) varies between genotypes because they intercept different proportions of the available radiation during growth. There are two main reasons why, in most species, there is considerable genetic variation in ability to intercept incident radiation during a season. First, genotypes differ in their rates of canopy expansion to maximum interception early in growth. Second, genotypes have different durations of growth before complete canopy senescence occurs. The desirable combination for maximum *J* is rapid early leaf area expansion and long growth duration.

Incident radiation is readily measured directly, or can be estimated from sunshine hours. The proportion of the incident radiation intercepted by a crop can be estimated in two ways: either by involved calculations using basic parameters of the canopy architecture of the crop or by direct, simple measurement in the field. The second method is used most frequently. Charles-Edwards (1982) showed that the former approach produces results which agree with field observations, confirming that an analytical approach based on physical principles can be used to describe an important determinant of crop behaviour.

The dependence of crop growth on *J* is demonstrated in Figure 1. The results are from two experiments at Lincoln, New Zealand in 1984-85 and 1985-86. Four very different wheat cultivars were sown in early May at about the same plant population (250 per m^2), were adequately supplied with water and nutrients throughout growth, and were kept free from weeds, pests and diseases. Growth was related linearly to *J*, even though yields differed between seasons and among the four cultivars.

Most agronomic constraints on yield can also be interpreted in a similar fashion. Water or nutrient deficits, for example, affect *J* by restricting canopy expansion and/or, most commonly, by curtailing the duration of growth by accelerating senescence. The timing of such deficits determines the actual sequence of effects, and therefore the components of yield which are adversely affected.

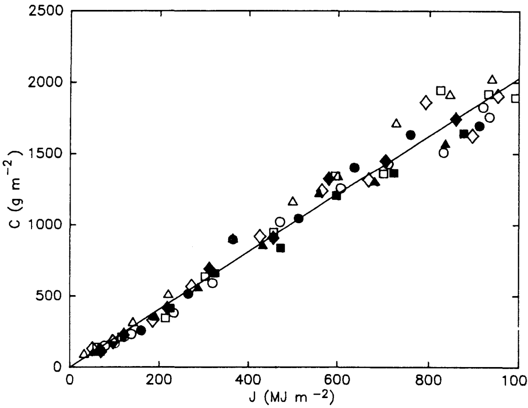

Figure 1. Relationship between cumulative total above-ground dry matter production (C) from successive harvests, and intercepted photosynthetically active radiation (J) for four wheat cultivars (Rongotea (o), Bounty (□), Avalon (◇), and Moulin (△)) in the 1984-85 (open symbols) and 1985-86 (black symbols) seasons. The slope of the regression line is 2.04 ± 0.02 g/MJ (r^2 = 0.98*). (unpublished results, D.R. Wilson and P.D. Jamieson).**

Duration of crop growth (*t*)

The duration for which a crop intercepts radiation is obviously a very important yield determinant. It is also an important aspect of crop adaptation because it determines whether the timings of phenological events are optimised for a particular environment (Evans, 1981; Fischer, 1977). In most crops there is considerable genetic variation in growth duration, so there are good prospects for breeding to improve yield potential and environmental adaptation. To establish appropriate selection criteria, it is first necessary to understand the factors which determine duration.

It is desirable to analyse crop duration in terms of two distinct measures of time: chronological and photothermal time. The chronological time, or duration (*t*), from emergence to maturity limits the opportunity to intercept radiation. In addition, the division of the total duration among the three principal growth phases of a crop (vegetative growth, growth of flowers and seed set, and seed growth) affects the formation and growth of the various components of yield. Photothermal time, defined as thermal time modified by a photoperiod factor, determines the phenological development of a crop which, in turn, determines *t* for each growth phase. Thus the capacity of a genotype to intercept radiation ultimately

Table 1. Chronological and photothermal durations of principal phases of development of Avalon and Rongotea wheat sown at Lincoln on three dates in 1984. CT = chronological time in days; PVTT = thermal time in degree days, base 1 °C, modified by photoperiod and vernalisation factors; PTT = thermal time in degree days, base 1 °C, modified by a photoperiod factor; TT = thermal time in degree days, base 9 °C.

	Avalon			Rongotea		
Emergence:	26 May	14 May	27 August	23 May	12 July	25 August
Emergence to double ridge:						
CT	93	71	57	86	64	37
PVTT	274	268	298	—	—	—
PTT	—	—	—	246	240	170
Double ridge to anthesis:						
CT	86	67	54	88	65	60
PPT	423	417	429	387	343	387
Anthesis to end of grain fill:						
CT	41	38	35	42	43	39
TT	222	226	250	230	235	234
Emergence to end of grain fill:						
CT	220	176	146	216	172	136

depends on the sensitivity of its development to temperature and photoperiod. Therefore, the balance between the two measures of time for a cultivar is crucial for its yield potential. In general, selection for more rapid development is likely to reduce yield potential, but it may improve the adaptation of a cultivar to the seasonal cycle (Evans, 1981).

Variations of response of phenotypic development to temperature and photoperiod are generally under simple genetic control and amenable to manipulation (Pugsley, 1983). Consistent and readily measured parameters quantify the development of a genotype in terms of photothermal time accumulated during each growth phase. This approach is well established for wheat, and was described by Weir *et al.* (1984). They defined four types of photothermal time to characterise a cultivar. From sowing to emergence thermal time is calculated using a base temperature of 1 °C, but there is no photoperiod adjustment during this phase. From emergence to double ridge thermal time (base temperature 1 °C) is modified by photoperiod and vernalisation factors, and from double ridge to anthesis by the photoperiod factor only. From anthesis to maturity, a base temperature of 9 °C is used to calculate thermal time, and there is no photoperiod adjustment. Observations of phenological development of a cultivar exposed to different temperatures and photoperiods can be analysed to determine its photothermal requirement during each growth phase. As an example, Table 1 gives the results from an experiment in which we sowed two contrasting wheat cultivars on three dates at Lincoln, New Zealand in the 1984-85 season. The cultivars were Rongotea, which develops rapidly and has no vernalisation requirement, and Avalon, a slower developing cultivar with a large vernalisation requirement and which usually substantially outyields Rongotea in favourable growing conditions.

For each phase of development both cultivars had consistent photothermal requirements even though *t* varied considerably when the time of sowing was changed. The anomaly between emergence and double ridge for the third sowing of Rongotea suggests the photoperiod factor used in the calculations may have been incorrect, and could also be partly explained by the difficulty of identifying precisely when double ridge occurs in late-sown wheat plants. There were differences between the cultivars. Avalon had the longer chronological growth duration, especially with later sowing, because it developed slower from emergence to double ridge. It also had a larger photothermal requirement from double ridge to anthesis, but its *t* during this phase was similar to Rongotea because it occurred later when temperatures were higher. Nevertheless, Avalon had more opportunity for growth when yield potential in the form of dry matter and grains per unit area was being determined. During grain fill the two cultivars had similar thermal requirements, although *t* was less in Avalon because it occurred later, during a period of higher temperatures. However, *t* was still sufficient to realise the higher yield potential (about 1 t/ha) established earlier. This leads to the inference that yield potential in a cultivar with Rongotea's characteristics could be limited by insufficient growth duration before anthesis.

It is clear that this type of information has important practical implications for breeding programmes. It could be practicable to use the approach to routinely characterise genotypes because the information can be derived from simple field observations. The example for wheat showed how assessment of a cultivar's capability to establish high yield potential, and its ability to realise that potential, was assisted by examining the partitioning of the total chronological and photothermal durations among the principal growth phases. Also, such examinations allow useful inferences to be made about the likely performance of a cultivar in different environments. Finally, the observations can be analysed to obtain quantitative information about a cultivar's sensitivity to temperature and photoperiod and, in the cases of those with an obligatory cold requirement, to quantify the vernalisation requirement.

When using this approach breeders must aim for the most desirable total growth duration and partitioning of the total among the principal growth phases. This aim usually requires a compromise between yield potential and environmental adaptation. For environments with adequate water and nutrients, cultivars should have slow development rates (low photothermal sensitivity and a large vernalisation requirement) and therefore long duration and high yield potential. However, although such cultivars can produce high yields in favourable conditions, they will generally perform poorly when conditions are adverse. So there is also a need for cultivars adapted to less favourable environments, perhaps the most common limitation being drought. Then, cultivars are required which develop rapidly (high photothermal sensitivity and no vernalisation requirement), thus increasing their chance of successfully growing to maturity during periods of adequate soil water availability (Passioura, 1977, 1981). However, it must be emphasised that yield potential is compromised, and the ability to produce high yields in favourable conditions will be restricted by the cultivars' relatively short growth duration. In particular cases, for example where there is a high risk of damage to reproductive development by late frosts, long duration of the vegetative phase may be a desirable adaptive attribute.

The duration of the seed fill phase is especially important, because it determines whether or not the previously established yield potential can be realised. In most crops there is considerable genetic variation in the duration of seed growth. Whatever the yield potential of a cultivar, the thermal duration of seed fill should be selected to ensure that the chronological duration in the cultivar's target environment closely matches its ability to establish yield potential in the first two phases. With incorrect matching, seeds are either filled incompletely ('source limited') or there is surplus assimilate ('sink limited').

Radiation-use efficiency (*e*)

The efficiency with which a crop uses intercepted radiation to produce new dry matter can be estimated in two ways: either by calculation from fundamental physiological parameters or by analysis of field growth data of crops. Charles-Edwards (1982) demonstrated that both approaches produce similar results. The first approach accounts for several physiological and environmental factors, including leaf photosynthesis rates, canopy architecture, radiation intensity, temperature, and the conversion efficiency of assimilate to new dry matter.

The simpler approach is to estimate *e* as the slope of the regression of dry matter produced by a crop upon the cumulated amount of radiation intercepted. Ideally, the regression should be based on measurements of gross dry matter production. However, these are seldom obtained because of the difficulties of measuring root growth and losses of dry matter as plant organs die. Therefore, most estimates of *e* are based only on measurements of total above-ground dry matter, and are most likely underestimates.

There are many examples of this approach, and results show that *e* differs among crop species and is affected by agronomic treatments (Charles-Edwards, 1982; Charles-Edwards and Vanderlip, 1985). However, we know of no evidence that it varies among genotypes of a species, provided that they are subjected to the same management. The results in Figure 1 show that *e* did not vary among the four wheat cultivars tested. In other experiments, *e* was consistent among cultivars of potatoes, field peas and wheat (Allen and Scott, 1980; Wilson and Jamieson, 1985; Wilson *et al.*, 1985).

We suggest that selection by breeders for improved radiation-use efficiency by crops is unlikely to be profitable in the short term. This is at variance with the approach often suggested of selecting plant genotypes with increased rates of leaf photosynthesis, for example. However, increased photosynthesis rate is often associated with adverse canopy architecture changes, with the result that *e* remains consistent (Charles-Edwards, 1982).

Dry matter partitioning (*n*) and losses (*v*)

The fate of plant dry matter, whether it is new material being partitioned into different crop parts or dead material being lost from the crop, is a very important determinant of yield. It is also probably the least well understood. Therefore, most descriptions of dry matter distribution in crops are empirical.

The dry matter of most interest in a crop is the harvestable portion, which is usually in the form of seeds. Most crop physiologists and breeders simply analyse partitioning into seed yield as the product of the total standing above-ground dry matter of a crop at maturity and the harvest index (HI), defined as the fraction of the total found in the seed. The significance of the HI concept is a matter of debate. There is little doubt that for several crops, particularly cereals, most of the yield potential improvement achieved by breeders can be attributed to increases in HI, with much smaller concurrent changes in total dry matter production (Fischer, 1977; Austin *et al.*, 1980; Evans, 1981). However, most of the improvement in HI has occurred fortuitously because it has accompanied changes in other characters sought by breeders, including simple selection for yield (Donald and Hamblin, 1976; Passioura, 1981). Although this approach is indirect, it seems likely that further scope still remains to improve HI by the same means (Evans, 1981). However, it is more doubtful whether selection for improved HI as an explicit breeding objective will lead to higher yields.

There are several objections to the use of HI for this purpose. First, its correlation with seed yield can be artificial and spurious because statistical variation in total dry matter yield is much less than in the seed yield it is being related to (Charles-Edwards, 1982). Second, and more importantly, responses of HI to environmental influences are variable and unpredictable. Therefore, although it is useful for interpreting environmental effects on yield, it is less suitable as an explicit selection criterion. Third, HI has no physiological meaning so it adds little to our understanding of crop performance. It is merely a coarse integrator of the many phenological, environmental and physiological events which have affected the growth, partitioning and loss of dry matter during the life of a crop. It is not surprising, therefore, that physiologists have made little progress towards identifying the causes of its historical increases.

A final major objection to the use of HI as a selection criterion warrants more detailed comment. The common assumption that HI is stable among plants within a crop community is often invalid. Ambrose and Hedley (1984) and Hedley and Ambrose (1981) showed that the stability of HI among plants in field pea crops differed substantially between cultivars, even though they all produced about the same total amounts of dry matter. Overall crop HI, which describes the average plant response, was therefore a poor descriptor of the performance of the plant communities because of the variable genotypic plant-to-plant variation within the populations. In all cultivars they examined, some plants had HIs as high as 70% while others produced no seed (i.e. their HIs were zero). The distribution of individual plant HIs between the extremes of 0% and 70%, and the proportion of barren plants, determined the overall crop HI of a cultivar. The examples in Figure 2 illustrate the different distributions of individual plant HIs for two contrasting field pea cultivars.

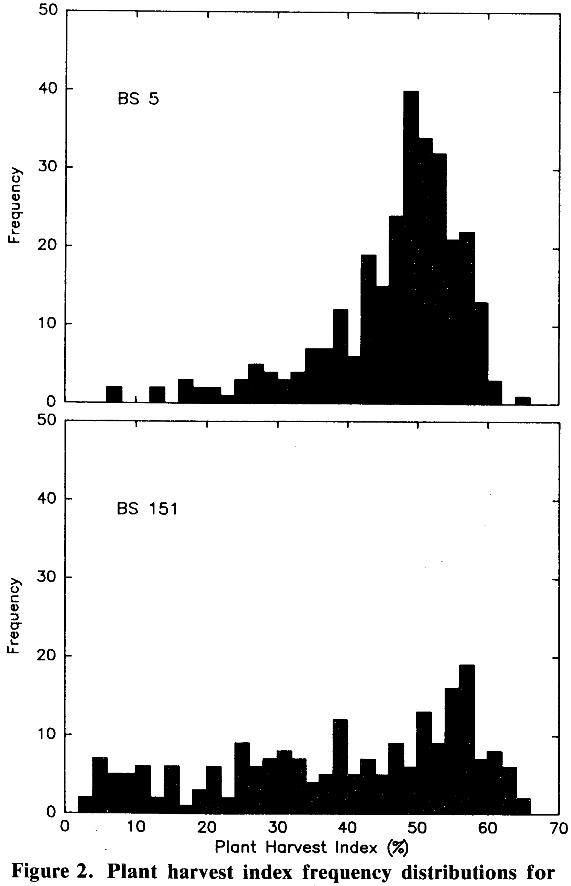

Figure 2. Plant harvest index frequency distributions for two contrasting field pea cultivars grown at 123 plants per m². Barren plants (2.1% for BS5 and 30.2% for BS151) were excluded. Crop harvest indices were 48% for BS5 and 38% for BS151. (from Ambrose and Hedley, 1984).

Donald and Hamblin (1976, 1984) advanced a similar argument for wheat, although Hedley and Ambrose (1985) provided evidence that the variance of HI between plants is less in cereals than for peas. They suggested that the difference between these crops may be a reflection of their ancestral derivation. Cereals have been developed from natural community plants, while the cultivated pea is similar to its wild ancestors which are solitary scrambling plants not adapted to growing in a monoculture.

Nevertheless, these observations have important implications for plant breeding and selection procedures. Traditionally, 'desirable' plant types are selected for their superior performance as single plants, and usually those chosen are competitive, dominant types. However, Ambrose and Hedley (1984) hypothesised that when these are grown in communities they have the most variation of HI from plant-to-plant, the lowest overall crop HI, and therefore poor seed yields. Most of the seed is produced by a few dominant plants, while most other plants produce very little. To produce large seed yields, the individual plants making up a crop should be weak competitors, with poor performance as single plants. Therefore, the selection of vigorous and productive plants in early generations may actually work against selection in later generations on the basis of plot yield. Evans (1981) argued that this hypothesis is supported by physiological analyses of historical improvements in yield potential. Increased allocation of dry matter to seeds has been at the expense of other plant organs, so each plant of cultivars with improved yield potential is smaller and more weakly competitive. He suggested that their selection and use in agriculture has only been made possible by increasing agronomic inputs. Continued successful selection for improved HI will further weaken individual plant competitiveness and require even more agronomic support. To quote Evans (1981): 'The meek shall inherit the croplands of the earth'.

Despite all these objections, HI remains an attractive selection criterion and indicator of progress for breeders because it is relatively simple to measure, and because there are no practicable alternative measures of dry matter partitioning. Conventionally, HI is based on total above-ground dry matter at maturity. This is merely a measure of net production because it fails to account for partitioning to roots or for dry matter losses which may differ substantially among genotypes. HI would be a more acceptable criterion if seed yield was assessed as a proportion of gross production. However, this is difficult to measure, especially the root growth and dry matter loss components. Therefore, a compromise would be to base HI on maximum total above-ground dry matter production. This is a more stable and reliable measure of production because it occurs well before maturity and before substantial senescence losses begin.

A more satisfying and rational approach in the longer term would be to identify the physiological mechanisms and environmental factors which control dry matter partitioning and losses, and which are genetically controlled. Ideally, partitioning loss events should be analysed at they occur during the life of a crop and their consequences for yield potential determined. However, much more research is required by physiologists before useful selection guidelines are likely to be available to breeders.

Two important processes should receive priority. First, in cereals, most yield potential advances from plant breeding have derived mainly from increases in seed number per unit area (Fischer, 1977), and this component of yield is very dependent on the ear population at harvest. Therefore tillering is a crucial process in yield determination, and there is considerable genetic variation in ability to produce and sustain viable tillers. Understanding the factors which govern the allocation of assimilate for tiller production and which determine tiller survival or loss is therefore very important. Second, although rarely considered in breeding programmes, partitioning of dry matter to roots can have a marked influence on yield (Passioura, 1972, 1977; Taylor, 1980). Shoot to root dry matter ratios may vary considerably between genotypes (Welbank *et al.*, 1974). The amount of assimilate invested by crops into their root systems can be appreciably more than previously thought since roots may release substantial quantities of organic compounds into the rhizosphere (Milchunas *et al.*, 1985). There can also be a marked turnover of roots during plant growth (Taylor, 1983; Gibbs, 1986). One means of lessening the amount of assimilate invested in a crop root system could be to breed plants which grow fewer roots with a greater hydraulic conductivity. There appears to be sufficient variability in root hydraulic conductivity within species for this (Newman, 1966; Reid and Hutchison, 1985). Such an approach could increase the dry matter in shoots without adversely affecting their water relations.

CONCLUSIONS

Plant breeders have successfully improved crop yields by eliminating obvious agronomic defects. However, smaller increases in genetic yield potential have been mainly achieved empirically because breeders have had few clear guidelines from physiologists about yield-positive plant traits which can be selected in breeding programmes. This hit or miss process is inefficient and future progress will be slow unless breeders and physiologists co-operate more closely to identify practicable selection criteria. Although Passioura (1981) considered it very unlikely that physiologists will discover important new factors that will influence yield potential, we believe there is considerable scope to apply current knowledge of the physiological and physical determinants of crop yield to identify relevant selection guidelines for breeders. However, it is imperative to define the factors at a level of biological organisation which is directly relevant to the performance of crops in the field. Failure to meet this requirement has been a major reason for failed attempts at interaction between breeders and physiologists in the past.

Research at lower levels in the physiological hierarchy has for many years tended to concentrate on the assimilatory processes. However, we support the conclusion of Evans (1981) that to date in crop evolution by breeding the directly productive assimilatory processes, such as photosynthesis and respiration, have changed little. Radiation-use efficiency, a measure of assimilation efficiency at the crop level of organisation, varies little among genotypes within a species so cannot be recommended to breeders as a selection criterion.

Yield improvements have occurred mainly through changes to regulatory processes which control the duration of assimilation, and the partitioning of the assimilates. These are therefore the yield determinants we have emphasised in our discussion. The regulatory processes seem to offer the best prospects for further improvements in the future, primarily because they exhibit considerable genetic variation in most crops. The factors which determine growth duration by controlling phenological development are relatively well understood and can be quantified from simple field observations. However, knowledge of how dry matter partitioning and losses are regulated is deficient, and physiological research should aim to define the factors which govern them.

It is not sufficient for breeders merely to acknowledge the importance of these factors. If knowledge about them is to have any real impact on the search for genotypes with high genetic yield potential, breeders and physiologists must co-operate to identify the degree of genetic variability available in a species, and then to define specific selection criteria.

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SYMPOSIUM DISCUSSION

Dr T. Wolski, Poznan Plant Breeders

You spoke about the duration of crop growth and said it is unfavourable in some growing conditions. Would green leaf duration be a good compromise for those conditions where long growth duration is not favourable?

In our programme harvest index was dropped 50 years ago.

Wilson

I think your green leaf area is analagous to our direct measurements of radiation interception. I have tried to emphasise in my conclusions that the partitioning of dry matter is equally important. These two parameters of the five are the most important in our view.

Dr E.J.M. Kirby, Plant Breeding Institute

In the estimation of the various physiological growth phases, you were explaining the calculation in terms of thermal time or photothermal time were you using the same characteristics for both Avalon and Rongotea?

Wilson

We had one anomaly with Rongotea which is mentioned in the written paper. We used different parameters for the two varieties. The Avalon parameters were obtained from the British Wheat Modelling Group; the Rongotea ones we derived from an experiment in the previous year in which we had done similar observations. We did not have ideal agreement between the two years for Rongotea. I have tried to explain that anomaly in the paper. A major problem is trying to define precisely when double ridge occurs in late sown wheat. We thought that might have been part of the explanation but also we have not defined the parameters for Rongotea well enough. They were different from Avalon.

Dr R.D. Burdon, Forest Research Institute

One of the problems which has limited physiologists making more effective input into breeding has been a lack of input from quantitative and evolutionary geneticists. To illustrate from the evolutionary standpoint, one might ask whether any fundamental differences might reasonably be expected in the efficiency of the photosynthetic process, except as a trade-off of adaptions to stress factors. There has been a lot of work done on differences in photo-synthetic efficiency that seems to have led nowhere. I think the evolutionary geneticists would question that right from the start if asked. The same applies to indicators like harvest index. If physiologists were fully aware of formulae for the relative efficiency of indirect selection, they could probably identify quite early on where the prospects were poor.

Wilson

In reply to the first comment, I think crop physiologists who work with crops in the field would reach the same conclusions fairly quickly about photosynthesis.