

## Crop physiology: some recollections and current perceptions

G.L. Wilson

Department of Agriculture, University of Queensland, St. Lucia QLD 4072

Crop physiology attained an obvious presence only during my working life. I became involved in it and then severed formal contact ten years ago while it still seemed not to have a well understood identity; nor indeed perhaps such agreed content as to permit a tangible identity. I have accepted the challenge presented by the theme of this Conference to reflect on the development of ideas, worthwhile contributions to crop production and prospects. As we proceed along this time sequence my lack of continuing contact will become increasingly apparent.

It is not the intention to review the state of knowledge for the benefit of crop physiologists, who should know far more than I do. They may have some interest in my perception of directions. It is rather the general agronomists who may be interested and by no means least, those whose undergraduate training occurred between 10 and 25 years ago (when I was teaching the subject), and who went to the workplace quite unconvinced that crop physiology served a useful purpose.

In the course of doing this I shall be referring to the work and writings of other people, but because this is not addressed to the crop physiologists, few references in the conventional sense are given. Those inspired to follow up some issues will find their way *via* those references which are given. Also, my examples from recent years have an obvious bias towards work done by people I know, they being most of my ongoing contact with the subject. The short time available for me to prepare this paper did not allow me to catch up on the literature accumulation of a decade!

We can start with the crop in the field, a community of genetically fairly uniform plants, representing the 'genotype'. During its cultivation, the particular combination of above-ground and soil conditions, management, pests, diseases and weeds, not to mention competition between crop plants, forms a unique environment which, interacting with the 'genotype', leads to the expression of the 'phenotype', and this includes the crop performance of economic interest. In order to change the phenotype - the crop result - we must do so *via* either the genetic base or the environment. The only pathway from the genotype to the phenotype is by way of the growth processes of the plant, that is, its physiology. If we wish to base our advances in crop production on understanding, we have to face up to that physiology. The formal treatment of plant physiology was however arranged in a way which told us something of how the crop grows, but little of how we might manipulate it to achieve particular results.

Plant physiology is now an old discipline, concerned with plant function. The general trend of research direction has been analysis of processes downwards towards their biochemical, biophysical and ultra-structural components. Integration is of course concurrently studied and presumably the long-term objective is to know all the parts and how they fit together, not only qualitatively but quantitatively. The impetus is however simply to know and to understand.

The much newer discipline of crop physiology is focussed on our wish to intervene in the processes determining yield. Although it becomes necessary to understand physiology in order to do so, we are not interested in that understanding *per se*. We look down only as far as is necessary to understand the upper level responses, and are in fact quite prepared to accept working approximations if they appear to serve reliably our purposes.

The first use of the term 'crop physiology' did not arise as a description of our application of plant physiological knowledge to crops but as a suggestion towards interpreting their behaviour. The agronomist, W.L. Balls, perplexed by the responses of cotton crops to irrigation treatments, concluded that little is to be gained by recording only the end results of experimental variables. Rather, it is necessary to observe the changes in plants which lead to the results. This, he noted, is what plant physiology does, and he wrote that the knowledge thus acquired 'might be called crop physiology' (1).

We can trace the development of the discipline, as it now stands, in a fairly continuous stream back to about that same time. It arose in work which departed from the plant physiological preoccupation with the unravelling of plant functions down to their ultimate components. It viewed the whole plant as a single structure engaged in a single process, growth, and sought quantification of that. The rate of growth (dry weight -  $W$  - increment) was seen as a measure of the efficiency of existing material in producing new material; the Efficiency Index,  $\Delta W/W \times 1/t$  ( $t$  = time). Subsequently this was renamed Relative Growth Rate (RGR).

Another index of dry weight productivity was suggested, the rate of weight increase per unit of leaf area (LA). This was based on the idea that leaf photosynthesis is the source of plant material rather than is the whole plant, and that the amount (area) of leaf might be the determinant of the amount of such material. This Unit Leaf Rate, later re-named Net Assimilation Rate (NAR), is  $\Delta W/LA \times$

Net Assimilation Rate is related to RGR *via* the ratio of LA to  $W$  ( $LA/W$ , Leaf Area Ratio, LAR). Thus  $RGR = NAR \times LAR$ . This was known as Growth Analysis, the analysis of growth rate into 'leafiness' of the plant and the net photosynthetic activity of that leaf. (There is of course a large error in calculating the net photosynthetic activity from whole plant DW increase, since almost half of leaf photosynthesis is subsequently lost in respiration.)

Conceptually however this was a useful analysis, resolving growth rate into two seemingly independent components of differing kinds; one a 'process' with some already well known dependence on a number of environmental variables, the other a 'structure' which might vary in relation to some different influences.

The stream I seek to trace goes more into a whirlpool than ahead for perhaps a decade. There was much experimentation using Growth Analysis, putting numbers on what happened in particular situations but not advancing our understanding nor indicating useful new directions. It was left to D.J. Watson to perceive its usefulness in the study of crop yield.

He replaced RGR with Crop Growth Rate ( $C$ ), the absolute rate of dry matter increase per unit area of land, a measure of clear importance in the development of crop yield. He noted that 'variation in the partitioning of assimilates between different organs is rarely sufficiently great to offset variation in total dry weight'. Translated to the terminology of some twenty years later, that says that biological yield is more important than is harvest index in determining economic yield variation. Thus for his purposes, biological yield was a surrogate for crop yield. He retained NAR as previously defined but replaced LAR with Leaf Area Index ( $L$ ), the amount of leaf area per unit area of land. The new analysis was  $C = NAR \times L$ . Furthermore, he introduced a new concept, that of Leaf Area Duration (LAD) to accommodate the variation in  $L$  throughout the crop duration, an important factor in determining biological yield.

He examined, experimentally, variation in crop yield; between species or varieties within a species during a season, and within a species across seasons (18). This showed that, in general, variation in leaf area (as both  $L$  and LAD) was the main factor determining differences in yield, variation in NAR being of much less importance. In fact, the general observation that the rate of extension of leaf surface was more important than NAR in determining dry weight accumulation in plants had been made some years earlier, but Watson brought things together in a clear way for crop physiology.

Time has shown that Watson's analysis was not in detail so useful and those who follow these things will know why. But what he did for crop physiology was to provide us with a framework for the analysis of dry matter production in terms of radiation interception (the successor to  $L$  and LAD), the efficiency of its conversion to dry matter and to point to the partitioning of that dry matter to economic yield.

Although the stage had been set by 1950 for significant developments, the stream I am following seemed to go underground, to resurface as sporadic springs which did not coalesce until some fifteen years later, subsequently to split up into several courses.

I saw things in that period from the restricted perspective of a somewhat isolated teacher of formal Botany courses, including plant physiology. I was aware, as were no doubt countless others in my position, of the gap for agricultural science students between the course in plant physiology and their needs. I added, about 1960, a course, Plant Physiology for Agriculture, with the objective of strengthening those topics which seemed of particular relevance to agronomy and bringing in some of the historical developments to which I have referred; without however, as I recall, a useful link-up of the two things. If nothing else, it fortunately attracted a few good students to go on to post-graduate work.

Notwithstanding my suggestion that not much had happened in the world outside, a look back at what we covered shows that many of the questions which remain important must have been asked or at least suggested by someone, somewhere. We were, in fact, a very small part of the rapid expansion of research in crop physiology which took place in the 1960s and which established the general pattern of enquiry which has continued; although there was to be a more critical approach in later work and continuing addition of new themes. And the recognition that there really was a worthwhile disciplinary field of crop physiology emboldened me to offer a course under that name!

It seems to me now that the slow exploitation of Watson's clues to appropriate research might be substantially attributed to the lack of an effective review of developments, indicating more specifically the studies needed and bringing together the relevant scattered activities of the intervening years. The belated need was met in 1975 with Evans' 'Crop Physiology, Some Case Histories', and in particular his chapter 'The Physiological Basis of Yield' (3). This critically evaluated the state of knowledge on the main topics which had emerged from research aimed at identifying what might be limiting factors in the development of yield.

That does not lead me to attempting a definition. Milthorpe and Moorby (13) referred to it as understanding the ways in which the various (growth) processes are integrated to produce the response shown by (crops) ...'. Implicit, is the identification of processes, understanding their interactions and, to the extent that they have independent influences, relative importance. The implementation of these objectives has resulted in two particular emphases of enquiry which Loomis, in addressing the Hobart meeting of this Society, referred to as dissective and integrative analyses (11). In giving an example of a dissective analysis, he provides a reminder that notwithstanding the generally integrative thrust of crop physiology, a component can be isolated and assessed to give unequivocally useful information to permit a decision about crop production. His integrative approach refers to modelling, of which something later.

Loomis' distinction is perhaps particularly appropriate to the application of crop physiology to crop problems, but for the person not engaged directly in the subject, it should be pointed out that the last few years have seen a great surge of research which is nothing other than plant physiology. It is however selective physiology, driven by the need for additional understanding in those areas perceived to be relevant, and strengthening the continuum between the two disciplines.

I should add that I recognize yet another 'force', an influence which has quietly permeated the thinking of agronomists and breeders, so that there has been a marked shift in their approaches towards the less empirical; resulting not only in their thinking increasingly in terms of processes but more importantly, in more research collaboration. One local example will suffice. A breeding programme to strengthen weathering resistance in mungbean seed was making no progress in spite of there being known variability for it. Recognizing that they were up against a problem of genotype x environment interaction, the scientists turned to a study of the physiological basis of weathering. Understanding the processes involved and their environmental responses, the correct test environments were selected and the breeding programme was successfully completed (8).

The three areas (or to maintain my metaphor, streams) of activity - limiting process research, modelling and physiological analysis - are all based on the three component systems referred to, namely interception, conversion and partitioning.

During the 50's and 60's, it seemed that the main thrust of endeavour was deliberately away from detail of plant physiology which had seemed so remote from the end results of interest to crop production, and the

knowledge of which was in any case so incomplete as to offer little hope of successfully carrying an idea through from a small part of the system to the whole-plant consequence. Certainly the beginnings of the subject, in Growth Analysis, set such a pattern of thinking.

I am referring to those topics which had somehow emerged from scattered work, as being likely to point up limitations to yield development. Perhaps a criterion for their adoption was that they might not have too broad a physiological (including structural) base, and thus some independence one from the other, this permitting manipulation of one without compensation or a limitation by the others. A correlated feature might be relatively simple genetic bases which would hold out hope for breeding for the characteristics. They were the topics reviewed by Evans in 1976 and to which I have referred earlier.

What I have just said however, emphasises only one aspect of the motivation, that of finding some short-cuts, *via* agronomy or breeding, to improvement. For other scientists it was a step down the reductionist pathway from integrated performance to the identification of the more important controls, using a guide which might point to areas of control which could more profitably be explored. If that had not been their initial intention it was at least soon forced on them. What were being hopefully examined as yield-limiting 'processes' were often quite complex aggregates and in a number of cases, not in the least independent of one another. Our aim being to control plants on the basis of our understanding, there was really little to lay our hands on. We had still been contemplating more what was happening than what caused it to happen.

Before leaving this aspect however, it would be unfair to imply that no practical good came from *it*. In the first place, the discussion within it was an important contribution to the diffusion, throughout crop science, of crop physiological thinking, to which I previously referred. And there are instances of successful direct application to production problems; for example: K.S. Fischer and colleagues at CIMMYT contemplated the relatively poor yields of tropical lowland maize. It had been shown that assimilate for the maize ear is supplied mainly by adjacent lower leaves. These leaves were, compared with those in temperate maize, relatively heavily shaded by a much-branched tassel and upper leaves whose size and arrangement were theoretically unfavourable for light penetration. After six cycles of selection against the morphological characteristics hypothesized to be unfavourable, grain yields were increased by about 12 percent (5). There was an accompanying harvest index increase of some 17 percent, showing a reduction of non-grain parts; in fact a reduction of upper stem, leaf and tassel material. Thus some, but not all, of the advance was by way of the understood competition between vegetative and reproductive growth during the early stages of the latter. In another programme with this material, sixteen cycles of selection against stem height increased yield by about 60 percent, associated with the same increase in grain number, and an increase in harvest index from 0.30 which is low for a cereal, to an acceptable 0.45 (10). In this trial, the hypothesis that concurrent, and competitive, stem and early reproductive growth is at the expense of numbers of grains produced, appears to have been supported, as is also that number of grains is in some way a determinant of yield.

It is necessary to make a brief excursion through the interception, conversion, partitioning components of yield to see what sort of things are discussed as potential limitations, or to look at it more positively, might be the bases of enhancement.

Interception deals with the canopy and two aspects are relevant. The first is the amount of leaf ( $L$ ), depending on rates of initiation, rates and duration of expansion, size potential according to level of insertion, numbers produced (some of these things affected in predictable ways by temperature, photoperiod, and water and nitrogen supply), plant populations, branching (or tillering) and losses by senescence and damage. The physiology of this is fairly well known and is not of interest in the present context. In high input agriculture the usual requirement is to maximize interception, that is, to reach high  $L$ , as quickly as possible. Under other circumstances that may not be so; thus at low soil water supply, light interception with consequential high transpiration may have to be avoided. In general, agronomy is now able to look after  $L$  development and maintenance and we need not consider it further.

The other aspect of interception, its manner, in the sense of how the radiation is distributed over foliage surface, is a little more controversial. The fact that full interception of incident radiation requires  $L$  of

perhaps about 3.0 means that on average, surfaces are illuminated at about one third of horizontally measured levels. We know that the efficiency of photosynthetic conversion increases with decreasing irradiance (in the C3 plants; much less so in C4). Presumably the most efficient use of available radiation is to distribute it over a high L at low irradiance per unit of L. One of the early seemingly important quantitative contributions to crop physiology was the description of canopy structure which would achieve this. The plant type aimed for in the successful breeding of high-yielding tropical rice was based on, amongst other things, an appropriate canopy structure. But the 'theory' of radiation distribution is dependent on the direction of incident radiation which varies with latitude, diurnal solar elevation and whether it is direct or diffuse. The great importance originally attached to small, upright, uniformly dispersed, vertically well separated leaves has to be qualified as the result of more thorough consideration (as with many earlier 'hopes'). Note also that at early stages of the crop, a quite different structure is necessary, to maximize interception by the low L, amount of interception being more important than the efficiency of its conversion. Detailed models of canopy photosynthesis do incorporate the radiation penetration characteristics (expressed as the light extinction coefficient,  $k$ ), but this does not attest to its importance; it is merely a requirement for the procedure of calculation. And finally, simpler although very reliable simulation models of productivity are able to ignore distribution, working only on amount of interception.

Crop physiology has focussed very strongly on a few crop species which have been taken, via agronomy and breeding, to high yield potential. This has led to a perception that limits are being approached (although disputed by some), in which little is to be gained by seeking advances in interception or harvest index (equivalent to partitioning). Therefore net photosynthetic activity is being scrutinized closely.

We can estimate broad limits to biomass productivity. A leaf, after losing some radiation by reflection, converts what is absorbed at an upper limit of photosynthetic efficiency, these two things allowing a maximum of about 20 percent efficiency. In the crop situation, much of the upper, more active foliage is illuminated for most of the day on the light-saturated (i.e. carbon dioxide limited) part of the light response curve, which reduces the average efficiency of the canopy. Subsequently, of the total photosynthesis, the whole plant loses something like 40 percent of it in growth and maintenance respiration. The end result of all this is that only about 6 percent of intercepted photosynthetically active radiation exists as equivalent plant dry weight (i.e., a radiation use efficiency, RUE, of about 3.5 g DW/MJ). Experimentally determined RUE values going into some simulation models just exceed 3.0 g DW/MJ, higher values being perhaps more associated with C4 plants in which the light saturation factor introduced into the estimate of potential (above) is not important.

This is no place to consider environmentally induced variation in RUE. But there is much interest in ontogenetic drifts, especially the typical decline during grain-filling because this could mean an important loss of potential grain weight. What does attract interest is that, apart from effects of water supply, nitrogen, perhaps other nutrients, diseases, extreme temperatures etc., there does seem to be genetically based variation. Pursuit of this was encouraged in the 1960s by the availability of infra-red gas analyzers but it bore no fruit in high photosynthesis plants. As much as anything this might be attributed to ignorance (at the time) of the fact that the photosynthetic rate of a leaf is so influenced by its previous history, its age and the demand for the product that it is very difficult to make valid comparisons between leaves. Another confusing issue was that some agronomically advanced crops have lower leaf photosynthetic rates than their ancestors, suggesting, at the best, no advantage of the characteristic. Study showed a negative relationship between leaf size and rate. Apparently then, in selecting (unwittingly) for larger leaves which increased interception, we selected against photosynthetic capacity. The phenomenon is under study. Thus this possible source of useful variation should not be discarded yet.

Some other approaches are under study and no doubt more will be added as detailed physiological study goes ahead. Thus, in the C3 plants, a significant proportion of the carbon entering the leaf at the initial step of chemical incorporation is lost almost immediately through the action of an enzyme which has been suggested to be largely an evolutionary anachronism; left over from the time when ambient carbon dioxide was abundant and oxygen scarce - the reverse of the present position. This is photorespiration.

The suggestion has been made - and is being explored - that present-day ingenuity might be able to modify this enzyme in a way which retains its useful role but deletes its wasteful activity.

An aspect of particular interest is that while we tend to think of assimilate supply (the outcome of photosynthesis) as a driving force in growth processes, growth itself, as a consumer of assimilate, can have a feed-back effect on photosynthesis. We must therefore think of changes, both agronomic and genetic, which could increase demand. This brings us back to an old question of crop physiology, does source or sink limit grain yield in cereals (and let us think only in relation to the grain-filling period)? High yield is strongly associated with grain number, which suggests a sink limitation. Or does the large sink size (higher number) determine, *via* a greater demand, increased source activity, suggesting a limitation there?

One last thing about DM production. Respiration is a very large loss of carbon. It is not of course to be seen as a loss which can be avoided. All growth processes must be fuelled and much of the initial production becomes that fuel. There is however some belief that respiratory activity is not always fuel efficient and that there may be points at which a reduction is possible. There is work on this but it is not for me to assess progress.

And so we come to dry matter partitioning, but only with respect to the accumulation of economic yield. The end result is seen in the harvest index (HI) which is of course only a final description and thus tells us nothing of how we got there. In the grain crops which have attracted most attention, something like all post-anthesis DM production goes to the grains and therefore HI approximates to the relative magnitudes of pre- and post-anthesis production. The reduction of the pre-anthesis duration in many crops has sometimes been compensated by improved rates of leaf area growth and perhaps also of photosynthesis (by way of nitrogen and water supply, crop protection etc.), but sometimes the reduced duration predominates. Nevertheless the framework of economic yield has been adequately developed, and the post-anthesis DM production (economic yield) has at least been maintained, and perhaps increased if higher RUE continues. Thus HI may rise with reduced crop duration to maintain yields at least, or with increased biological yield but unchanged HI yield may increase. If we look at the history of yield increase in these improved and generally high input crops, agronomy has been mainly responsible for increased rates of DM production while breeding has had more of an influence by raising HI. As implied above, some of this change has been achieved by changing the relative durations of the two periods of growth.

The grain-filling period is relatively poorly understood. *Is* the shorter period in some low-yielding circumstances a contributor to low yield or a correlative consequence of reduced rates of grain-filling? *Is* the lowered RUE, typical of the period, attributable to the age of the foliage? *Is* the rate of production sufficient to meet needs and would a higher rate increase grain growth rate? *Is* the RUE decline caused by nitrogen loss to the grain and could that be at least to some extent circumvented, or is it caused by declining demand from the grain? *Is* there some endogenous control which determines leaf senescence as grain maturity approaches?

It is events during this partitioning which were the main inspiration for the research focus of the post-Watson years: relative importance of sink, source and transport; the relative importance of particular photosynthetic sites as suppliers to the economic parts; and the role of assimilate storage in later supply to grain. We have already noted that it directed attention to the need for more detailed study of processes, and also inspired some improvements in crops.

Partitioning research has centred greatly on the cereals, but similar considerations appear in crops of different yield characteristics. In a study of cassava (a long season, root storage crop) intercropped with soybeans, competition from the latter suppressed early growth of cassava. One consequence was reduced branching. By the time soybean was removed, cassava had commenced tuber development but did not resume branching. Assimilate is partitioned between continuing shoot growth and tubers, preferentially to the former. Reduced branching is not at the expense of sufficient L and tuber growth was favoured. Harvest index was increased and in spite of biomass loss caused by the early competition from the intercrop, yield was maintained (17).

In looking at yield development in terms of the three components (interception etc.), we exclude, as a topic, the physiology of water relations. Certainly, the influence of water status or supply on the processes is considered, as is conversely, the influence of the processes such as leaf area expansion on water use and thus on plant water status. But since water supply imposes, on a world scale, such an enormous limitation to crop production, why does it not occupy a more conspicuous position in crop physiology? It is not that we are short of information on the water relations of plants, whether as internal physiological processes, soil water balance, evapo-transpiration or anything else that has a bearing. Perhaps it is simply that the strong linkage between transpiration and photosynthesis (via the shared carbon dioxide and water vapour pathways) gives limited scope for physiological modification. Of course agronomically, there is great opportunity by manipulation of space and time, such as the adjustment of plant populations, planting dates and crop durations (and thus water use) to water available to the crop. Although such management strategies long preceded plant physiology, our current knowledge of the latter greatly facilitates our inventiveness.

Clearly, selection for adaptation to water deficits has occurred over the years and in modern times, breeding has sought to exploit, usually on empirical grounds, the genetic variability, sometimes with success. Again an example from the CIMMYT maize work: After only three cycles of selection, a 22 percent yield increase at severe soil water deficit was obtained (6). Concurrently, a number of plant characteristics likely to be associated, on physiological grounds, with advantage under dry conditions were monitored and seen to change in the expected direction. Thus again we see the diffusion of crop physiological concepts into crop improvement work.

A systematic approach to the utilization of physiological knowledge has been undertaken by Ludlow and Muchow (12). They summarized the physiological attributes which might confer yield advantage under water-limited conditions and applied the criteria that it is necessary to know how the trait contributes and whether there is genetic variation for it. They concluded that in addition to the low hydraulic conductance of seminal roots in cereals (the now well-known work of Passioura and Richards), the most promising trait is osmotic adjustment. This is already a feature of Morgan's work with wheat and now a programme is under way to attempt to introduce, by the new technologies, the genes for osmotic adjustment into rice (M.M. Ludlow, pers. comm.).

I am profoundly ignorant on the subject of simulation modelling which has come to occupy a dominant position in crop physiology, as my comments may show. It was not that I had not been told in good time of its eventual necessity. Milthorpe and Moorhy (13) had written in what was perhaps the first text book of crop physiology in 1973, that in addition to knowing, by way of physiology, what contributes to yield, it remained necessary to put the relationships together 'in such a way that the magnitude in any set of circumstances can be predicted and of then assessing the interplay between the different component processes so that the behaviour of the whole plant can be predicted'. And they went on to state the case for quantitative simulation models.

In fact by the 60's, sub-systems were being modelled and in the 70's whole systems had been attempted (4). These earlier simulations were strongly mechanistic, incorporating as much of the known plant physiology as could be useful. The rationale was that the more a model was based on physiology, the more reliably it would simulate the performance of the plant (or crop), and at the same time point up deficiencies in our knowledge, thus stimulating research to fill the gaps. Moreover, such a model would allow the testing of hypotheses about the consequences of altered physiology, which is of obvious importance to those concerned with the modification of crop performance.

Such modelling continues and the philosophy appears valid. The problem is, that the needs of those charged with improvement in crop productivity need the tools now; and just as they once found plant physiology unable to help them and turned to crop physiology, so they are now asking for models which are immediately useful. And these are being developed at a rapidly increasing rate.

I am not referring here to purely empirical models designed for specific agronomic purposes and which are proving very useful. It is those still based on the crop physiological framework of interception, conversion and partitioning which we have been following, but in which experimentally determined

relationships may be incorporated in place of fully mechanistic simulation, provided they are shown to serve reliably the purposes for which the model was designed.

A common form generates radiation interception from leaf area development, which is a physiologically based simulation, that is from a knowledge of leaf numbers, sizes etc. which has been referred to earlier. Additional to  $L$ , the light extinction coefficient characteristic of the crop is used to estimate the proportion of radiation, and thus amount, intercepted. The two following components are however much simplified. The conversion to dry matter avoids all detail of photosynthesis throughout the canopy followed by discounting for respiration (as undertaken in more elaborate models). It works simply on an experimentally determined coefficient, radiation use efficiency (DW produced per unit of radiation intercepted) which may be modified (via the model) according to ontogeny, and for temperature, water supply and nitrogen status when these reach critical levels. Likewise, the partitioning to economic yield is handled quite simply by using a partitioning coefficient characteristic for the crop, in conjunction with the model-generated availability of dry matter. The duration of economic yield accumulation which, interacting with rate determines yield, is controlled by environmentally modified phenology.

Notwithstanding the relative empiricism of the second and third components, the whole thing is constructed on general crop physiological principles and the functions used in these two components are often far more robust than the proponents of more physiologically detailed models might have anticipated. An example again: Muchow *et al.* (15) developed such a model for one cultivar of maize in tropical Australia. They applied it to the prediction of yield over a range of cultivars and locations, the latter having extremes of 14° and 40° latitude and some 10°C difference in mean temperature, and the corresponding observed yields were 10 and 20 t/ha. (No adjustments were made to the model parameters for the different locations or cultivars.) Yields were very closely predicted. Thus the model responded well to environmental variation, the purpose for which it was designed.

Models of a similar level of complexity have been developed for crops of differing yield characteristics, for example, kenaf, in which the stem is the economic harvest (14) and sunflower (16), or in relation to particular agronomic uses. An example of the latter is one designed for the purpose of assessing climatic risk in sorghum cultivation, particularly as affected by drought (7). Again, it predicted yield well, using meteorological data for some years and over a wide latitudinal range, for which yield records were available. It was then used, in conjunction with long-term meteorological records, for sorghum producing areas in Australia to calculate yields over years at locations in order to estimate risk in cropping.

It is difficult to see how important questions such as those implicit in these examples could have been answered in any other way. And incidentally, the expectation that modelling might indicate gaps in physiological knowledge is met in the course of designing and using these simpler models. For example, the prediction of phenology is particularly important but it has been revealed that the controls are not as well understood as plant physiology suggests.

At the last meeting of this Society, a workshop was devoted to ideotypes, to review the concept some twenty years after Donald (2) had proposed it. He had made out a forceful case for the design (by way of breeding) of crop plants on physiological and morphological criteria, and then went on to hypothesize the ideal wheat plant. Time has shown that his specifications for the latter were inadequate and this has been widely taken to mean that his concept of the ideotype is faulty. Increasingly we expect things about us to be designed on the basis of knowledge of materials, functional behaviour, end use and whatever else underlies a satisfactory product. That we can not do this with crops simply shows our lack of knowledge. Donald was pointing to that. His great contribution was to give prominence to a debate which at that time was centred on whether it could or should be attempted, but has now moved to how it will be done. Much breeding is now carried out with at least some crop physiological characteristics being exploited. I doubt that Donald envisaged anything like a complete specification for a crop but was rather proposing that known desirable characteristics be incorporated. That the information available to him at the time was sparse and indeed faulty is no argument against pursuing the goals.

It might be noted that prior to Donald's publication, an ideotype had been proposed (but not under the name) and which became the background to IRRI's high yielding rice (9). It included one of the earlier

crop physiological ideas, that a particular canopy structure is advantageous. This was referred to earlier. It was however more of a 'back-up' to the knowledge that the characteristic was correlated with yield in rice. Some of the other specifications were based on agronomic ideas but were revealed much later to have particular physiological significance. I have recently seen an IRRI publication which describes the requirements for new rice varieties suited to particular ecological situations, complete with detailed drawing of the desired types!

Of many other topics which might equally well deserve space here, I mention only two. Intercropping is of major importance on a world scale and of negligible interest in countries where strong agricultural research is centred, but there is only fragmentary research where the need lies. It is terribly hard to 'get hold of' intercropping in the research sense. The unlimited possibilities in combinations of crop species, relative proportions, planting arrangements, times of sowing and harvest and many other things, makes empirical experimentation, which is feasible in sole-cropping, almost impossible. Some sort of hypothesizing of desirable changes which can be tested experimentally has to be done. It does not seem where, beyond crop physiology, many ideas can come from. We have at present, in preparation for Field Crops Research, a special issue on intercropping which approaches the subject on a predominantly crop physiological basis. We hope this will not only be of some help to those working where intercropping occurs, but also that it might encourage more interest among scientists elsewhere.

The other topic also concerns 'developed' versus 'undeveloped' agriculture. It seems to me that the massive research activity in crop physiology in its broadest sense is not only centred in a few countries, but is also centred on a mere handful of crop species. These species have already been brought up, via agronomy and breeding, to high levels of performance. If what we learn of these crops is widely applicable, then they may provide a suitable research base; although I am not too confident that they encompass sufficient variety of yield characteristics. At the same time, what knowledge we have should be applied where it can be. I have no reason to believe that anything like a sufficient effort is going in to the improvement of these other crops which is possible on the basis of what we know. There should be some very easy pickings in applied research 'out there'.

It has often been said of crop physiology that it can explain what has happened. Many a respectable discipline had its origins in questioning what had been observed, and such enquiry is the way to understanding. We cannot predict until we understand. The systems which we contemplate are of great complexity and a sufficient understanding for prediction is not achieved rapidly. We have perhaps disappointed both ourselves and those whom we serve, with the overoptimism of youth in the earlier days, when we were tossing around some over-simplified yield-limiting 'processes'. Things have rather settled down now, some getting on with the slow, detailed study of what happens in the crop, others looking for opportunities to put our know-how to work in the service of crop production. My most pleasing current perception of what we have achieved is that crop physiologists, agronomists and breeders are talking comfortably together of things within which, so few years ago, we were taking our first - and sometimes false - steps.

## References

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