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Concluding Remarks

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Ladies and Gentlemen: for this kind of symposium you need someone to open the meeting, someone to make an after-dinner speech, and someone to close it. It is a little embarrassing to find you have reached the age to do one of these jobs. This job has the disadvantage that when you would like to relax, you must sit in your room and do some thinking. However, the advantage is that you do not have to listen to one of these three speeches.

Professor Hudson opened this symposium with the question: "is it necessary to update the potential production estimates made about 10 years ago?" The answer to this is, essentially, no. The estimate for wheat was then about 9000 kilograms per hectare. The only reason to alter this production estimate would be the advent of a cultivar which ripens much later, say in September, but otherwise we consider that we are still working to the same maximum productivity level.

This brings me to a point which has not been discussed here, and that is the control of what are loosely called ripening diseases, which has led to big increases in wheat yields in recent years. When the effect of such control is analysed, the main result is found to be an extension of the period during which potential growth rates of about $200 \text{ kg ha}^{-1} \text{ day}^{-1}$ are maintained. Whether the analysis is done by means of enclosures, simulation or by determining seed yield, the extension of the growing period gives a yield increase of the order of 1500 kg ha^{-1} .

A problem which is not yet solved with regard to the differences in yields of barley and wheat, is the question of translocation. From experiments with wheat in the Netherlands it may be concluded that there is not much translocation from the vegetative state to the generative state, but the Nottingham data on barley show otherwise. I have no idea of the reasons for this difference. However, in passing, I want to remark that the usefulness of sophisticated physiological and micro-meteorological experiments in situations of relatively low yields may be questioned. And with regard to terminology, I suggest that the apparent high maintenance respiration in the later stages of growth (shown

by Biscoe) should not be called maintenance respiration because this high rate is probably due to the high energy cost of the observed translocation during the ripening phase.

Professor Hudson also suggested that you need luck to achieve potential yields. Well, this may be so with apples but with wheat it is possible to achieve near-potential production under a wide range of conditions. A range of cultivars may all be induced to yield practically the same (about 9000 kg ha⁻¹) on various soils and in different regions provided they are kept disease-free.

Keeping the latter condition in mind, it is surprising that we discussed weather and crops and the inter-relation between weather and crops, but we did not talk about diseases and the inter-relations between weather, crops and diseases. Surprising, because many of us are becoming more and more convinced that one cannot leave diseases out of these discussions. For instance, Jackson remarked to me the other day that a large proportion of the variation of cotton yields with weather conditions in the Sudan, from the 1940s onwards, could be attributed to pests and diseases. When these were controlled in the 1960s, the fluctuations in yield became much lower and the relation between yield and weather much more stable. I have, in the last few years, considered this question of pests and diseases in somewhat more detail, and I am forced to the conclusion that many agronomists with a leaning to crop physiology know very little about diseases, and that many plant pathologists know little about plant physiology, and very little about crop physiology. The inter-relations between these aspects is an area which we must cover and it would be most interesting if, within the next few years, we could have a symposium on weather, diseases and crops where plant physiologists, weather specialists and plant pathologists could all come together.

This symposium, as so many others in recent years, has generated much discussion about modelling, and I have to stick out my neck here. Modelling is not only hypothesis formation. We have on the one hand the analytical approach in the laboratory and on the other hand we have problems in agriculture, ecology and management. Working at a plant physiological institute, I have always felt that we need a discipline to provide the link between plant physiology in the laboratory and problems in the field. Models should provide this link, and thus function as a bridge, a basis for generalization, and also lead to new ideas for experimentation.

Much modelling is, of course, open to Elston's criticism that modellers tend to ignore results which do not accord with theory. But we must be careful about delivering broadsides without really aiming. It is certainly possible to score many hits by firing broadsides at modelling, because modellers, excited about possibilities, sometimes start from good results and arrive at nothing useful, or start from what appears to be nothing and arrive at some prediction. However, this is not done always by every modeller.

A more serious problem, which arises particularly in ecology, is the handling of unique situations as may exist in nature conservancies. In my opinion, unique situations are not open to modelling because it is impossible to verify the model: you cannot experiment with unique situations. Even a perfect model of a unique situation, given to us by some deity, would not be very useful. Such perfect models must be initiated and when you do this you run the risk of disturbing your unique situation. It seems to me that many biologists are still comparable with the old-fashioned physicist, who says "we know all the laws, so tell me how many molecules there are in the room, their position and velocity at a given moment, and I will calculate for you, from here to eternity, where the molecules will be in the room". Unfortunately, the question with respect to position and velocity of each molecule at a given moment is unanswerable. Similar problems apply in ecology, and I believe that the applicability of models of unique situations—and this certainly holds for so called world models—is very close to zero. Applicable models may be developed for situations which recur and can be re-created again and again. For this reason, the first attempts at modelling in the biological field have been in agriculture and, for some time to come I would restrict such attempts to agriculture.

In the field of mass transfer, that is micrometeorology, soil physics, plant-water relationships, CO₂-assimilation, synthesis cost etc., we have a considerable body of knowledge obtained by analysing recurring problems in agriculture. Our main problem is not to advance this body of knowledge, but to apply it by means of models, simulation techniques or any other method which suits the purpose. A good example is soil physics, where from 1955 onwards development was mainly sterile and academic, but in recent years things have been moving again in the applied direction. In all the fields mentioned we may go on studying details forever without developing our knowledge any further. It is very difficult to terminate this work with which we are familiar, but we should try it; we should reduce our analytical efforts and synthesize and unify, using not only our own data but also the information available in the literature. However, there is now so much literature that it is often easier to invent something, or even to do an experiment, than to find the information you need.

The problem of morphogenesis, of the development of form and function, has been touched upon in this symposium, but if we really wish to advance with an understanding of agriculture, we should spend much more time on this problem. From whatever angle it is approached, it is a difficult problem. The view of the analyst is still largely descriptive, agriculturally the problem is still very ill-defined, and models, if any, are rudimentary. We must, therefore, in the coming years, force a break-through from this unhappy stage; a break-through may come from the reductionist, the agriculturalist or the modeller, but I hope it will come and that we will use each other's information and ideas and accept each other's criticism.

The modellers have to answer an important criticism from the reductionists—that there are no hormones in the models. That is true enough because modellers do not know how to handle hormones. The counter-criticism is that students of hormones are so occupied with studying the messenger (hormones) that hardly any time is left to study the message that is transferred. To bridge some of the gap from my side, I will end these closing remarks by airing some very preliminary ideas about how modellers might try to identify the messages and couple them to messengers of some kind.

At present, most dynamic modelling is done according to the state-variable approach. State-variables of plant systems are such tangible quantities as the area and weight of the leaves, the amount of roots, the reserves and water content of the tissues and so on. We assume that mathematical expressions may be formulated to calculate the rate of change of these state-variables at any moment in time from the state of the system and the value of the forcing variables. These rates of change are then used to update the model over a short time interval by some numerical integration technique. Then this procedure is repeated again and again to advance in time.

Sometimes I compare myself with a small shopkeeper who tries to evaluate his business by means of a balance sheet and inventory at Christmas, but neglects to record his turn-over of goods and his cash-flow and therefore continually makes the wrong decisions. Just as a shopkeeper needs running averages of the flow of money and material to understand his business operation, the plant needs records of the current magnitude of rates of change to achieve a coherent growth and development.

Now, I know little about hormones, but I visualize that some of these tangible materials reflect the current state of affairs as far as the activity of the plant is concerned. Still I shy away from modelling hormonal levels because too little is known about their rate of production, consumption and decay. The most I can suggest at present to modellers is to recognize running averages of the main rates of change over periods ranging from a few hours to a few days, as state-variables, and try to relate the development of form and function to their current values. For instance, the running average of the rate of photosynthesis per shoot or growing point may govern the rate of tillering or the rate of abortion of young fruits. The running average of the rate of root growth and the rate of root decay undoubtedly affects shoot growth, since even Brouwer is very much aware of the fact that his functional balance of shoot and root amounts will explain only a part of the phenomena.

In my view, hormonal specialists and modellers would at present benefit mutually from a much closer cooperation. The modellers would be forced to introduce and analyse a new set of intangible state-variables—running averages of rates—and consider their influence on growth of form and function. The hormone specialists would be forced to think less in static terms and to consider

more the quantitative aspects of production, consumption and decay of their tangible substances.

If we start now, some future Long Ashton Symposium could bring many of us together again to discuss the progress and any lack of advance in this important area of applied research. I hope that Professor Monteith will then make the closing remarks to prove that he had indeed changed horses, and that Professor Hudson will still feel competent enough to present an after-dinner speech, full of wisdom and humour.

