Systems approaches for crop and pasture research

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One of the traits which marks a professional agronomist is a strong capability in systems concepts. It has been our tradition to be knowledgeable about crops not only in aspects ranging from adaptation to production technology but also about the farming systems in which they apply. In earlier times, a qualitative understanding of these things was adequate. In fact, given the state, 50 years ago, of scientific knowledge of plants and their environments, one could make very few quantitative integrations and predictions about agricultural systems.

As the simplest issues of crop and pasture management have been clarified, yield levels have advanced dramatically. We now face new questions about the limits to crop performance and the proper directions for research. The new questions are more apt to involve subtle genotype-environment interactions and we have seen increases in the sophistication of the methods and training required for agronomic research. At the same time, the size and the degree of sophistication of the supporting base of scientific information has expanded enormously. We have at hand many new facts and concepts, particularly at the cellular and molecular levels of organization, which might apply to field behaviour. As a result, agronomists now need more disciplinary training and awareness. Through necessity, we have become increasingly specialized and our "systems" have contracted to smaller parts of the real systems.

Parallel to those events, there have been changes in the manner of funding agricultural research. We have gone from an approach based on institutional funding of local research units (departments, research stations) to one which emphasises competitive grants from national authorities. The institutional approach favored the development of team structures and a focus on long term projects. That is a good way to accumulate systems knowledge and to develop careful and detailed solutions to difficult problems. More important, research priorities whether for "basic" or "applied" studies can be ordered from the agricultural significance of the issue. However, the criteria of significance depend heavily upon the quality of local leadership and facilities, and too frequently unproductive directions in research are pursued too long. The competitive grant seeks to avoid those problems and to give more opportunity to new ideas and new directions, and to give more weight to merit in the division of scientific resources. However, its effectiveness is very much dependent upon the quality of a remote scientific leadership and the political support which they can gather for public funding. Such funding tends to be individualistic at the local level and thus work against the development of a team structure competent in systems views. Scientific significance tends to be defined by the availability of funds. Problems also arise from long lags between problem identification and funding, and the short time frames for which funds are available. In the United States, the past 10 years have seen energy, nitrogen fixation, soybeans, stress physiology, rising CO_2, "biosalinity" and "biotechnology" emphasized sequentially in an ad hoc fashion by funding agencies.

Given these circumstances, we need to think about what approaches can be employed to establish a strong and modern capability for systems research. On the one hand we need to take advantage of the ad hoc specialized information as it becomes available and, if possible, to influence the directions of such research. On the other, we need to integrate that information in a quantitative way with existing knowledge. My purpose here is to describe some ways in which we can do that and the type of training which will be needed by future agronomists.

Dissection of a problem

The principal requirement in systems research is a clear analytical view of the problem. We can do this through dissection of the problem into controlling factors and processes. While our main purpose is to form a conceptual model of the main features of a system, there are many cases where the analysis can be surprisingly quantitative.

Water and nutrient-limited systems offer examples where simple holistic analyses can be accomplished with the first law of thermodynamics since material and energy balances must obey that conservation law. Knowing only the first principles of nitrogen cycling and supply, the compositional range of nitrogen in cereal tissues, and something of the agricultural system, one can construct approximate nutrient budgets for wheat fields in medieval England (1) and maize fields under modern agricultural management (2). The fundamental point is that a unit of available nitrogen can be equated to some units of grain yield and that for the system to continue the nitrogen must inevitably be replaced.

A similar approach can he taken where water supply is the main limitation to plant growth. de Wit (3), Fischer and Turner (4) and Tanner and Sinclair (5) have summarized the obligate relationship between photosynthesis and transpiration by which we now define water use efficiency (WUE) and have demonstrated its relative constancy for a given genotype in a given environment.

We can illustrate the dissective approach with an analysis of M. Calvin's (6, 7) claims regarding the potential for oil production from Euphorbia lathyris L.. Basically, Calvin claimed that he had produced 3380 kg of "oil" ("10 bbl per acre") in a year from that plant grown as a crop on a nutrient-poor soil under semiarid conditions without irrigation. Since the oil was reported to represent 8 to 1.0% of the aboveground biomass, aboveground production was between 33 and 43 t ha^{-1}. That yield level alone should have raised serious questions since 43 t ha^{-1} equals the greatest annual production ever observed for any C3 species (8). Even with a very small nitrogen content (1% of dry weight); the crop would have contained between 340 and 410 kg N ha^{-1}, a very unrealistic expectation for a nutrient-poor soil. If we apply a WUE value of 30 kg biomass ha^{-1}mm^{-1} (about the largest ever observed), we find that between 1100 and 1400 mm of water had to be transpired for just the aboveground production. If the environment was indeed semiarid (ca. 200 to 500 mm of annual precipitation), it is immediately clear that first law principles were violated for water as well as nitrogen. Such suspicions are enhanced by a check through the European floras where E. lathyris is found to be a cool season annual (during the winter in the Mediterranean region hut as far north as the Shetland islands in the summer).

There seems no need to similarly examine Johnson and Hinman's (9) claim that 8900 kg oil ha^{-1}year^{-1} might be produced by that plant under desert conditions without irrigation. Such analyses were not made, however, by the editors of numerous scientific journals, by granting agencies, or by scientists (including agronomists) who applied for the grants, and many millions of scarce research funds have subsequently been expended on E. lathyris research. In this case, scientific significance was established by the statement of a Nobel laureate and its uncritical acceptance by scientific panels. Careful investigation of the sources of Calvin's original data revealed that the crop was grown in a cool, coastal environment with adequate fertilization and frequent irrigation. Further, border rather than interior plants were harvested thus inflating the yield by a factor of 2 and the oil yield was taken as equal to the solids extractable with a hot, polar solvent which dissolves many minerals, amino and organic acids, and sugars as well as lipids. Petroleum solvents removed only 4% of the dry matter so the choice of solvent further inflated the yield 2 to 2.5 fold. Stripped to its original data base, E. lathyris is shown to be inferior to any of our existing oil crops ranging from sesame to soybean; in fact, it is even inferior to maize. This kind of simple, semiquantitative, conceptual analysis should be within the range of every agronomist.

Integrative analyses

Many situations quickly become too complex for relatively simple factor analyses such as that which we accomplished above. The system may have many parts, it may be influenced by a number of forcing variables, or internal feedback and thus require a time- dependent dynamic analysis. Until recently, the mathematical analysis of really complex systems was essentially impossible. Much of the basis for engineering design was found in empirical rules drawn from previous experience. The first breakthroughs came with analogue computers and engineering methods for electrical network analyses. The appearance of computers led quickly to the rapid development of simulation techniques for a wide range of complex systems. Certain aspects of soil and atmospheric physics were among the first agriculturally related topics to be studied through simulation. The comparative formulation of animal rations (a complex calculation rather than a simulation) was also advanced significantly by computers. The simulation of crop growth has advanced steadily since its early beginnings in the 1960s with C.T. de Wit in The Netherlands

and R.B. Curry in Ohio. The number and diversity of uses for such dynamic simulations are now quite large (10, 11). Penning de Vries and van Laar (12) provide an elegant introduction to the methods which may be employed.

A proper crop growth model needs considerable detail relating to the simulation of the crop microclimate (radiation and energy balances, soil and canopy temperatures, etc.) since these are the forcing variables for the plant processes. Production processes (e.g. photosynthesis, respiration, water uptake and loss) and partitioning of new assimilates (growth and morphogenesis) should be considered in the plant sections. Models with hierarchic structure (lower and higher levels of organization) become explanatory of plant behaviour and can thus achieve considerable realism. They also then have more flexibility for use with different genotypes and management systems. In contrast, same- level models, where performance of a variable such as leaf area is presented as a regression of past observations of leaf area, are only descriptive and are not adaptive to new environments.

However, with hierarchic structure, such description at one level can be explanatory of the next, higher or lower level.

With so many options, it is not surprising that there is great diversity among existing crop and pasture models. The field is still youthful and chaotic. There are too many models, very few of which have been carefully polished and validated, and too many of these were constructed without specific uses (objectives) in mind. Experience has shown that it is much easier to construct a preliminary crop simulator than it is to find and correct its weaknesses and to define the range of conditions over which it performs legitimately. The guiding principle of many modelers is that one's objectives should be defined rather precisely and that the simplest model with the fewest variables meeting those objectives is the one which should be used. Like Occam's razor, the aim is to cut to the heart of the problem in the simplest way possible. While there is merit in that approach, it leads to model proliferation -- an alfalfa model for irrigation studies, one for pest management, one for growth studies, etc. -- with all the attendant problems of validation and user confusion. With the rapidly improving capacities of computers, it is becoming clear that we should give our attention to the construction of only a few really good (and necessarily large and highly detailed) models for each crop. Such "grand" models in fact can be structured in very simple ways with separate small sections for each main process (12,13).

Many of those sections can be almost identical from crop to crop. At that level of detail, such models consist of only simple concepts and relations of the type which we might identify through dissection analysis as outlined earlier. When the controlling response functions are input as tables, rather than being embodied in mathematical equations, it becomes a simple matter to find and change those functions needed to properly represent a different genotype or farming practice. It also is not difficult, providing one looks to the internal working of the model, to find and change conceptual errors which lead to poor simulations. The only limitations rest with one's understanding of the crop and the relevant environmental physics and plant physiology. Those limitations are the reason why crop models are not more advanced, and why modeling has proved to be such a powerful guide to experimental research.

A case study in dissection and integration

Rooting pattern and osmotic adjustment are topics for which there is considerable interest at present in relation to drought resistance of plants. Through changes in rooting patterns, we might change the amount and timing of water availability to a crop, and with a greater degree of osmotic adjustment by plant cells, we might lower the soil water potential which marks the limit to the availability of water. Such tactics could increase the amount of water transpired (which times CUE would increase the biomass yield) or improve the harvest index (HI, which times biomass defines the economic yield). The traditional view is that a large, vigorous root system, through avoidance of plant water deficits, is a major feature of drought resistance.

Passioura (14 and earlier papers) has dissected the rooting questions carefully in relation to the extraction of residual water which might otherwise be left at maturity. The components which he identifies include a) the capture of near-surface moisture before it might be lost by evaporation, b) the dependence

of the lower limit of available water (measured as the water potential or water content of the bulk soil) on root length density (RLD) and the root resistance to the axial flow, c) variations in WUE, and d) variations in HI. Passioura concluded that too little is known about the activities of roots in surface strata to form a judgement about the consequence of various rooting tactics. In lower strata, the residual water at maturity was seen to be mainly a function of RLD, with RLD > 0.5 cm cm^3 needed for rapid and near complete extraction whereas at the margins of rooting-depth extension, RLD is generally smaller than that. The question was also raised whether such residual moisture might be restored annually in contrast to representing an accumulation of several small amounts over years and thus of little moment to mean yield over years. The costs of root growth and maintenance represent clear diversions of assimilate which might have been used in shoot growth. Additional investment in roots, then, must return through the extra water gained an amount of assimilate at least equal to that investment. Further, it is clear that this is not always the case and Passioura concluded that selection for smaller roots might actually increase the aboveground yield. WUE calculated on aboveground yield clearly suffers as the fraction of total production partitioned to the underground system increases. Passioura focused his analysis of HI around the partitioning of use of a limited supply of water between the pre- and post-anthesis periods with small values of HI resulting from too- rapid use of water prior to flowering. Where the crop is growing on stored moisture, restriction in the rate of root extension or root conductivity (e.g. small xylem cross-section area) might conserve moisture to the more important post- flowering period.

Passioura conceptual dissection by itself provides a useful framework for further research in root physiology and it provides a number of guidelines for efforts in plant breeding. We could also strengthen the quantitative features of the analysis sufficiently so that we could make some prediction about the circumstances under which larger or smaller, or more or less conducive roots might be an advantage. However, since those calculations would involve variations in soil characteristics and depth, plant cover and photosynthetic abilities, current weather, and a myriad of other factors, it is clear that we can expect an infinite array of solutions. The apparent complexity and the dynamic-integrative nature of that problem immediately suggest an approach utilizing an explanatory simulation model. Jordan at al. (15) have done that for related questions with a model of sorghum having a modest amount of physiological detail.

Jordan et al. utilized the SORGF model developed by Arkin et al. (16) at their institute, employing 30 years of weather data from three Great Plains locations (Texas to Kansas) having distinctly different patterns or totals of rainfall. Performance under rainfed conditions was assessed for three characteristics which might contribute to drought resistance: early maturity; deeper rooting; and osmotic adjustment.

Early maturity was achieved by reducing the number of leaves produced by sorghum prior to anthesis thus shortening the vegetative phenophase. While that reduced leaf area and thus also the potential for photosynthesis, considerable water was saved and the risk of small yields in dry years was lessened. The early cultivar provided a yield advantage in only a few of the years at Lubbock, TX (small, evenly distributed annual rainfall), 33% at Temple, TX, and 17% at Manhattan, KS. However, while the later-maturing cultivar clearly carried greater risk (greater range in yield over years) its mean yield over years was also greater, justifying present practice.

An increase in sorghum rooting depth from 1 to 2.8 m gave a significant benefit to yield in 20 to 40% of the years depending upon location. The benefit was least at Lubbock and greatest at Temple (moderate rainfall but mostly outside the growing season). In agreement with Passioura, the deep moisture was used later in the season at a time of soil cover and drier surface strata and, as a consequence, that use was with a larger WUE. Unfortunately, however, the assimilate cost of deeper rooting was not incorporated into the model so that the yield advantage was certainly overestimated. Passioura's point about possible negative benefits thus was not evaluated.

Osmotic adjustment was evaluated in a very simple way by lowering the soil water content at which turgor-dependent processes such as growth and photosynthesis would be affected. In agreement with experimental observations, there was little or no benefit to grain yield. Again, the assimilate cost of adjustment was not considered.

The work by Jordan and his colleagues shows something of the progress which has been made by modelers -- and something of how far they have yet to go. A proper model for the assessment of alternative rooting patterns and osmotic adjustment obviously must calculate the assimilate balances involved. There are many models which are structured to do that (e.g., 13) but really good solutions will be difficult. For example, information about mucigel formation around roots and maintenance respiration activities is very sparse. With osmotic adjustment, the costs will vary greatly according to the way in which that is accomplished. The adjustment of cell volume through cell-wall elasticity would cost little or nothing and the accumulation of mineral ions (e, Cl^-) and organic acids is only a small cost (0.5 to 2 mol ATP per mol osmoticum). Sugars by definition are costly but are mobile and may be used later in growth so the life-cycle cost will also consist mainly of transport costs.

The same cannot be said of amino acids, and suggestions about biotechnological enhancement of the abilities of higher plants to accumulate proline and betaine appear misguided. A modest wheat crop with 9000 kg of aboveground dry matter ha^s at anthesis will contain about 50,000 kg of H_20 when fully turgid. If we consider that a portion of that water is in non-osmotic space (the cell walls) and that another portion may be lost as the relative water content declines with the onset of stress, then perhaps 40,000 kg (40,000 liters) remain in the osmotic space. A lowering of that water potential by 6 bars would require 10,000 mol of osmotica (0.25 mol $liter^{-1}$). For adjustment with proline we would *need* 1150 kg of proline containing 140 kg nitrogen (M.W. of proline = 115 g mol^{-1} at 12.2%N). The biosynthesis of proline would consume 12,500 mol of glucose (2,250 kg) and 10,000 mol of nitrate. The ratio of nontoxic osmotica consumed to that produced is 2.25:1. Such adjustment would make available only about 10 mm of water per m of rooting depth in a clay soil or far less than would be required with a high WUE to generate the necessary glucose (10 mm x 30 kg $ha^{-1}mm^{-1}$ = only 300 kg).

We could reduce the cost of proline or betaine accumulation if we consider that it might have some special protective role relative to proteins. In that case, it would need to be present in only the cytoplasmic portion of the osmotic space involving a significantly small volume of water. However, one has to maintain a certain skepticism regarding the potential of proline and betaine as osmoprotectants (17). It seems more likely that they serve mainly in nitrogen storage.

The future

It is clear that agronomists must develop sharply improved skills for dissective and integrative analyses of agricultural systems. The fact that a small genetic change in the capability for growth of leaves or roots can dramatically alter the integrated behavior of the whole plant dictates that need. In the example developed for water, Passioura's dissection tells us what to look for and what effects might result from their alteration. However, testing those hypotheses would entail an enormous amount of breeding and experimental work since we must start with a rather large group of subtle hypotheses and with very few quantitative guidelines about the circumstances where any one of them might have a significant advantage. Jordan's approach has the potential to narrow the search by providing specific, quantitative predictions for each circumstance. To do that successfully, however, his model must encompass a much greater amount of physiological information, i.e., it must include the dissected concepts.

Successful systems analysis thus must at the same time be dissective, integrative, and quantitative. Looking to the training of our students, we need increased emphasis on subjects and approaches which will enhance such skills. Computer science is obviously necessary and, in my own experience, students with strong preparation in physical chemistry are the ones who adjust most easily to quantitative thinking about biological systems. Curricula are always under pressure, however, and there are limits to the breadth which can be incorporated. We could help ourselves by considering the development of new approaches in applied mathematics which would embody elements of analytical mathematics, statistics, and simulation techniques as a substitute for our present heavy emphasis on statistics. The main effort, however, must involve an increased content of analysis and modeling in our standard agricultural courses.

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