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Ecology – the science of agriculture in the 21st century

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SUMMARY

Most current biological problems in agriculture occur at the higher levels of organization: populations, communities and ecosystems. These are the levels addressed by the science of ecology rather than other biological sciences. Therefore ecology will by necessity become the central science of agriculture. Agricultural production will be seen as a form of applied ecology or ecological engineering. This change in perspective has major implications for agricultural research. It brings the discussion of the assumptions of a research programme into the open and forces researchers to prioritize among potentially conflicting objectives. It sees agricultural strategies in terms of trade-offs, rather than improvements, and it suggests that agricultural research needs to be more bold and ambitious if it is to solve the most important problems facing us in the new century.

LEVELS OF ORGANIZATION IN BIOLOGY AND AGRICULTURE

The coming years will see major changes in how agriculture is taught and researched, as well as in agricultural practices themselves. The present paper explores the relationship between the emerging scientific discipline of ecology and agriculture research and education. The word ‘ecology’ here refers to a scientific discipline, which can be defined as the study of the interactions that determine the abundance and distribution of organisms (Krebs 2001). Ecology can also be defined by its domains: the biology of populations, communities and ecosystems. ‘Ecology’ is not used here in its other common meaning: a set of environmentally friendly values, or a set of farming practices that are also referred to as ‘organic’ or ‘bio’ farming (Weiner 1998). The arguments below are as relevant to conventional as they are to organic agriculture. Finally, while the arguments below apply to agriculture in general, the examples used are from arable crop production systems.

There are many sciences of agriculture: crop science, food science, chemistry, veterinary science, weed science, etc. How can one argue that ecology will be THE science of agriculture? Ecology will be the science of agriculture because ecology is the science at the appropriate level of organization to address most of the scientific problems and issues in agriculture. Agriculture is a hierarchical (O’Neill *et al.* 1986) or layered (Passioura 1979) system in which each layer is related to the one below and the one above (Fig. 1). We look to the layer below for explanation; this is the scientific method called reductionism. Similarly, understanding of each layer can contribute explanation to the layer above. If research occurs at only one level, then the research is descriptive rather than explanatory, according to the reductionist paradigm (Hull 1974).

Ecology addresses the higher levels of organization. So does agriculture. As discussed below, yield, a basic agricultural quantity, is an attribute of a population. The farmer is not interested in the yield of individual plants, but with the yield of a plant population in the field.

Most of our agricultural sciences occupy the lower levels of organization, and these lower levels of organization have shown much progress over the last century. We have obtained much knowledge of molecular biology, cellular metabolism and how viruses and microorganisms cause disease. But it is not possible to ‘scale-up’ chemical interactions within a cell to the level of the whole individual, let alone to higher levels (Weiner 1996). It is rarely possible to explain a phenomenon with mechanisms several levels of organization below the phenomenon (Hull 1974). One cannot sufficiently explain behaviour of the individual organism at the cellular level; one must understand the organization, form and physiology of the whole individual. The same is true at the higher levels. Most scientific problems in agriculture are concerned with populations, communities and ecosystems, and these

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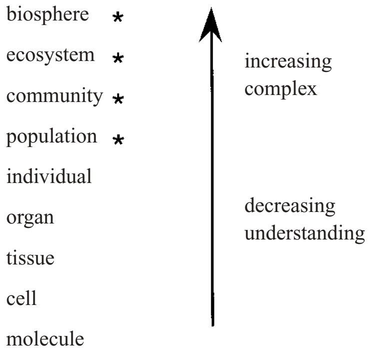

Fig. 1. Levels of organization in biology. Ecology occupies the top levels (asterisks). Most current scientific problems in agriculture also occur at these higher levels.

are the domains of ecology (Begon *et al.* 1996), not of other biological sciences. Ecology is a relatively young science that cannot yet deliver answers to many of the questions agricultural researchers are asking. But this does not mean that the answers can be found elsewhere. One cannot solve traffic problems through the engineering of automobiles alone. One needs to use traffic engineering, even if traffic engineering is not as highly developed as automobile engineering. Automobile engineering may play a role in solving traffic problems, but only in relation to the higher levels of organization. For example, the number of automobiles on the road is not primarily a function of the design of automobiles themselves.

Agriculture can best be understood scientifically as an ecological process (Carroll *et al.* 1990). In this view, the crop is a population, while pest and diseases are populations of organisms with which the crop population interacts. This ecological community includes not only the crop and its pests, but also the natural enemies of these pests, plus many other species with which the crop interacts directly or indirectly, such as N-fixing bacteria and mycorrhizal symbionts, and decomposers in the soil. The agricultural field can be thought of as an ecosystem, embedded within a landscape.

INDIVIDUAL VERSUS POPULATION OPTIMA

Does this perspective really change anything? Below is an example from the author's own field within ecology, plant population biology, of the difference between thinking of agricultural production at a lower (individual) versus a higher (population) level.

One might assume that if we have the genotype and the environment that result in the maximum individual yield for a crop species, we also have the genotype and the environment that will give the maximum population yield. But this is not always the case. Let us assume a field has many different genotypes of wheat growing together, and some of these individual genotypes are to be selected for production. As crop breeders have learned, the genotype that has the highest individual yield in the field when surrounded by other crop plants is probably NOT the genotype that would give the highest population yield in a monoculture of that genotype. Why not? There is always some degree of competition among the individual crop plants. If there were no competition within the crop population then all available resources would not be used by the crop population. If crop plants were sown at so low a density that they did not shade each other at all, this would imply a very low level of ground cover. Maximum yield per unit area occurs when there is some competition. But the optimum strategy for an individual plant experiencing competition would not result in the optimal performance at the population level. The optimal strategy for the individual crop plant is very close to the concept of Darwinian fitness (Futuyma 1986). When there is competition among plants, the optimal individual strategy is to allocate a significant amount of resources to structures that enhance competitive ability. For example, a plant with taller stems than others will shade its neighbours, instead of being shaded by them (Grime 1979). Plants that do not allocate sufficient resources to the competitive structures will be suppressed in competition by those that do. The plant pays a cost for this ability, i.e. if competition is not intense, the competitive genotype will not grow as fast or produce as many seeds and fruits (harvestable yield) as another plant that does not pay this cost. If there is no competition, a better strategy is to not waste resources on competitive mechanisms, but just produce leaves on a short stem, and later flowers, seeds and fruits.

If a whole population is of the very tall competitive genotype, i.e. those that had the highest individual yield in a competitive environment, then the whole population pays this cost. If most competition is intraspecific (e.g. if there is effective weed control), then the population's yield will be higher if all the crop individuals are *poor* competitors, rather than good competitors. If all individuals are poor competitors, the whole population will use fewer resources on competitive structures, and will therefore have more resources available for growth and reproduction, including yield. This is C. M. Donald's original concept of the crop 'ideotype' (Donald 1968). Similarly, it has recently been demonstrated that below-ground competition among soybean plants results in excess 'wasteful' root production at the population level (Gersani *et al.* 2001).

Much of the success of cereal breeding that has contributed to today's high yields has been due to the development of shorter varieties with less biomass allocation to stems with less competitive ability. In the language of life history theory, they are '*r*-strategists' (Begon *et al.* 1996). Donald (1981) has argued convincingly that virtually all the improvements in the yield of wheat due to the development of cultivars in the 20th century can be attributed to accidental improvements in the Harvest Index, the percentage of the biomass that is harvestable, not to physiological improvements of the crop. To an ecologist, Harvest Index usually corresponds to reproductive allocation. Wheat breeders were trying to select for physiological characteristics that plant physiologists, working at too low a level in the biological hierarchy, had suggested. The effects on allocation were mostly accidental, but it was these changes, not the physiological traits suggested by plant physiologists, that were primarily responsible for the huge increases in yields (Donald 1981).

A more fundamental example of this point is that net primary production (biomass production) is determined primarily by ecological, not crop physiological, factors. The increases in biomass production in agriculture over the past century have been due to changes in the crop's environment, such as fertilizers, pesticides and irrigation. With the same inputs, weed communities would produce the same amount of biomass (Snaydon 1980). Plant breeding has not resulted in increased primary production in the field. Rather, modern varieties of cereals have been selected to utilize the unnaturally high resource levels that modern agriculture has created and convert them into harvestable yield. They do this primarily by allocating less of their biomass to structural organs, so they don't 'waste' resources competing (or fall over when exposed to nitrogen levels that plants have never previously experienced in their evolutionary history).

Clearly, problems must be addressed at the appropriate levels of organization. Advances in molecular biology have led many to believe that almost all problems can be addressed at the molecular level, but this is simply not the case. Much agricultural research is at much too low a level for the questions we want to address (Passioura 1979), and thus represents a type of naïve or 'crude' reductionism. The future of agricultural research will depend on understanding higher levels of organization, and these are the levels addressed by the science of ecology.

Some researchers have questioned the reductionist paradigm. 'Holism' or 'systems theory' has been put forward by some researchers as alternatives to reductionism (e.g. Wilson & Morren 1990; Jørgensen 2002), and these approaches imply a shift in focus towards higher levels of organization in agricultural research. A discussion of holism versus reductionism in biology is beyond the scope of the present paper (see Looijen 1999; Keller & Golley 2000), but the point here is that 'systems' approaches focus on the analytic framework and a set of methodologies, not explicitly on the level of organization being investigated. Ecology cannot be defined by the methods used; ecologists use many methods and approaches, including holist, reductionist and even historical (McIntosh 1987; Weiner 1995). The argument for an ecological perspective on agriculture and the argument for a 'systems' approach to agriculture are not to be confused.

There is much agricultural research at the higher levels of organization and there are several international journals that emphasize such research. However, most of this research is not understood as ecology, and this has constrained the focus of the research. For example, much research in nutrient cycling in agroecosystems is conceived and formulated in the context of plant nutrition. This tends to keep the conceptual framework close to the level of plant physiology rather than the community and ecosystem level. Similarly, the modelling of crop growth in the field is physiological in concept (Donatelli *et al.* 2002), and this has influenced the way that competition, herbivory and soil–water relations are included in the models.

AGRICULTURE AS APPLIED ECOLOGY/ECOLOGICAL ENGINEERING

In the future, agriculture will be understood scientifically as applied ecology, or, if one prefers, a form of ecological engineering: the manipulation of populations, communities and ecosystem for human purposes. This change will reflect a change in the scientific context in which agriculture is conceptualized, from agriculture as production to that of agriculture as ecosystem manipulation. Such a change in thinking does not, in principle, have anything to do with the difference between organic and conventional farming. The perspective of scientific ecology does not *ipso facto* favour organic agriculture over conventional agriculture, and ecological science will be central to conventional as well as organic agriculture.

Some of the differences between the traditional view of agricultural production, which can be called 'the farm as a factory' (not to be confused with 'factory farming') and the newer view of 'the farm as a managed, harvested ecosystem' are outlined in Table 1. One of the central differences is that the factory model is self-delimiting, and therefore many of the factors that influence production are considered to be externalities with which the agricultural system does not interact. In the ecosystem view there are many fewer externalities, because more of the factors affecting production, including many aspects of the environment, are now considered to be within the agroecosystem. Both the 'factory' and the 'ecosystem' models have advantages and disadvantages.

Table 1. *Comparison of two metaphors for agricultural production*

	Farm as a factory	Farm as a managed ecosystem
Values and objectives	Built in Often hidden Rarely discussed	Not built in Open to discussion
Quantities measuring value: 'currencies'	One or few clearly defined	Many different possible currencies
Delimitation of system	Self-delimiting	Not self-delimiting
Externalities	Many	Few
Scale	Small spatial and temporal scales emphasized	Equally applicable to all scales
Concept of yield	'Production' from inputs + internal farm processes	'Harvest' of numerous processes both inside and outside the farm

The factory model may have been appropriate for the needs of agriculture through much of its recent history, but it is not very good at addressing the problems facing us in the 21st century.

The factory model is easier to apply in production and as a research tool, because it is relatively easy to define variables that are to be maximized, such as yield, economic profit or profit per unit capital invested. The disadvantage of the factory model is that these easily defined variables may not be the most important ones for agriculture today. For example, society's demand for a reduction of nitrogen in runoff is difficult to integrate into the factory model. It can be treated only as a fixed externality – there is a specific limit, specified in government regulations, for how much nitrogen is permitted in runoff. The factory view of production in terms of inputs and outputs is dynamic, but its view of nitrogen or glyphosate in runoff is static, so the model is not very good at addressing these factors.

The ecosystem view acknowledges from the start that there are several, sometimes conflicting, 'currencies'. This is problematic, but it offers the promise of addressing problems that the factory model cannot easily address. The disadvantage of the ecological perspective is that it becomes more difficult to define simple single variables to maximize or optimize, because many currencies are not interexchangeable. For example, how much money would compensate for groundwater polluted by glyphosate or nitrate? How much is a rare species worth? But this disadvantage can also be seen as an advantage, in that the model forces us to address these issues from the beginning, before a research project starts. The values and objectives of the research are open to discussion, rather than hidden as implicit assumptions. The assumptions must be discussed explicitly and agreed before applying any model in research or in practice. Such discussions can help agricultural research to maintain its integrity.

Table 2. *Three possible objectives for yield management, in biological and economic terms*

Biological	Economic
1. Maximum yield	Maximum short term profit
2. Maximum sustainable yield	Maximum long term profit
3. Maximum yield stability	Maximum economic survival

CLARIFYING THE OBJECTIVES

An ecological perspective suggests three possible objectives for crop yield management with respect to yield or economy (Table 2). The ecological view forces us to ask about our objective; the objective is not already built in.

The objective of modern industrial agriculture and agricultural research has usually been to maximize short-term yield (1), which requires high input and environmental costs, and high nutrient and capital fluxes. The interests of the farmer and society might be better served by the very different goal (2) of maximum low-flux, sustainable yield (Jackson 2002). The objective of maximum yield stability (3) may be the most appropriate goal in agricultural systems in some developing countries where many farmers live close to subsistence. The factory model addresses objective (1). It can also address (2), although it rarely does. Objective (3) is addressed even more rarely by the factory model. This is because the factory model, like capitalist industrial production itself, tends to have a short-term perspective. Most businesses plan their strategy so as to obtain maximum profits in the short or somewhat longer term. Few businesses try to minimize the long-term likelihood of bankruptcy or of being bought by another

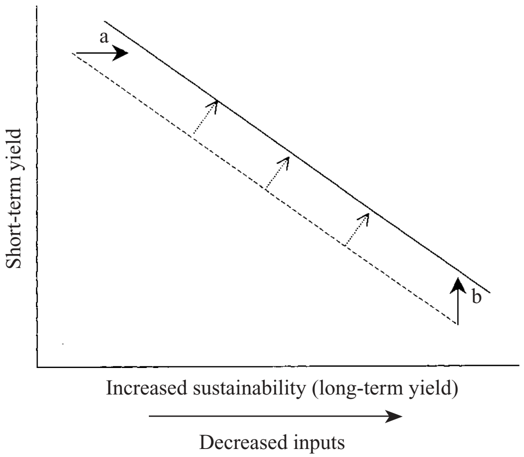

Fig. 2. The relationship between short-term yield and long-term sustainability is negative (dashed line) – a straight line is shown for convenience. Agricultural research can shift the relationship in a favourable direction (dotted arrows), giving greater yield at a given level of sustainability (dark line), but the relationship will still be negative. The horizontal arrow (a) and the vertical arrow (b) represent different research strategies for increasing sustainability.

firm. Such a strategy may not be a good one for most businesses, but it may be very appropriate for managing most agricultural systems. The ecosystem model can easily be applied at larger time scales, as well as higher organization scales. Indeed, larger scales in time and in space are closely related (O'Neill *et al.* 1986).

To address the problems confronting agriculture, the focus of agricultural research will have to shift from the physiological/molecular levels up to the higher, ecological levels of organization: populations, communities and ecosystems. Even gene technology will be seen in terms of its ecological role, especially at the population and community levels. Many of the naïve expectations concerning gene technology are based on the type of 'crude reductionism' criticized here. Similarly, ecology will become central to agricultural education, as we are beginning to see at many agricultural universities.

THE IMPORTANCE OF TRADE-OFFS

An ecological engineering perspective on agricultural production sees alternative production strategies in terms of trade-offs rather than 'improvements'. For example, principles of engineering suggest that the relationship between maximum short-term yield and sustainability will inevitably be negative. Research cannot change this general trend, but it can change the position of the relationship (Fig. 2) or its shape. It is naïve to believe that increased sustainability can be achieved without any cost in short-term yields. Research can reduce these costs, but it cannot remove them completely.

The inevitability of trade-offs forces researchers to prioritize their objectives. Shall we try to maintain yields close to the current levels and investigate how we can increase sustainability (arrow (a) in Fig. 2)? This is what most agricultural research concerned with sustainability tries to do. An alternative would be to set the degree of sustainability we want, and try to see how we can increase yield with that constraint (arrow (b) in Fig. 2). This alternative strategy is often applied in organic agricultural research.

THE NEED FOR MORE AMBITIOUS AGRICULTURAL RESEARCH

The ecological perspective also suggests that agricultural research needs to be much more aggressive and ambitious if it is to address agricultural problems in the 21st century. Agricultural research has often been too restricted by the pressing but narrow problems posed and the constraints on possible solutions (Lewontin & Berlan 1990). Agricultural yield or profit will vary as a function of many factors. One may borrow the metaphor of the 'adaptive landscape' first described by the evolutionary biologist Sewall Wright (Provine 1989). The essence of this metaphor is that there are numerous 'peaks' and 'valleys' in the parameter space (Fig. 3). In evolutionary theory the adaptive landscape itself is extremely dynamic, but a static representation is useful here. Current agricultural production is at or close to a local optimum. Most agricultural research is directed towards approaching ('climbing') this peak. There may be other, even higher peaks, but agricultural research as normally practiced will never discover them, because it does not explore areas far away from the current region. If agricultural research is to discover these other possible peaks, it must jump over the 'valleys' in between. Of course, it is impossible to explore anything approaching the full parameter space. The only way to find other potential optima is to search very broadly. This means investigating radical ideas by varying factors and their combinations much more than is usual in agricultural research. More aggressive, 'high-risk/high reward' research in agriculture is needed, but this is opposed by the tradition of conservatism in agricultural research, which is often directed toward immediate problems. Applied researchers are often asked to solve a particular problem (e.g. pest attack or nitrogen runoff), but to do so without changing the system of production very much (Lewontin & Berlan 1990). The best solution may involve changing many things, but such possibilities are rarely explored. Strategic agricultural research needs to be more bold if any information about the broader parameter space, of which modern agriculture occupies

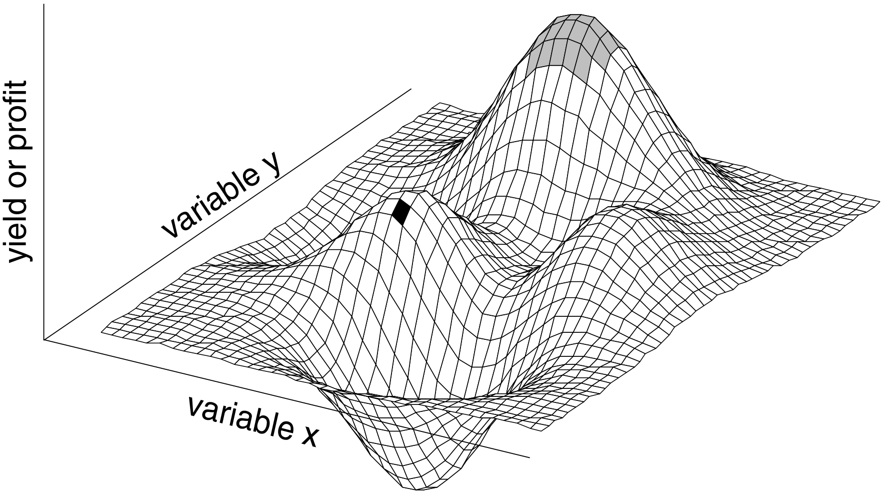

Fig. 3. Agricultural yield or profit as a 'fitness landscape' of peaks and valleys with respect to only two out of many possible variables. Many agricultural practices are close to a local optimum (black quadrilateral) and most research helps us climb the local peak, but it cannot discover other, possibly higher peaks (grey region).

a very small area, is to be obtained, and thereby have a chance of discovering other optima, which might be even higher than those close to current practices.

It is important to note that the metaphor of an adaptive landscape does not imply that an experiment must explore an area of parameter space that is on or very close to another peak if that peak is to be discovered. It only requires that the experimental treatments reach an area beyond the 'valleys' surrounding the current peak. If the base of another peak can be reached, less aggressive, incremental research can be used to 'climb' the other peak, and find out how high it is. If a research project has resources to look at 10 points in the total parameter space, it could be worthwhile to have some of these points far away from current practice, instead of doing extensive exploration near the local optimum. An example of searching for an alternative fitness peak in agriculture would be the investigation of very low input/low yielding/high sustainability systems, such as those proposed by Jackson (2002). If costs can be reduced more than yield, then there is a possibility for profitable, but very different, forms of agricultural production. An example in a very different direction would be the investigation of intensive hydroponic greenhouse production systems.

To use materials science as an analogy, the suggestion here is that we not only continue trying to improve the currently best class of materials for a particular purpose (e.g. steel for automobile engines and bodies), but also investigate other classes of materials (e.g. ceramics, plastics, fibreglass) as possibilities. Many times such an innovative approach will fail, but when something new is discovered, it will open new possibilities. Most material scientists agree that future materials for industry will probably not be limited to further improvements in steel and other metals, but new materials such as ceramics and plastics. If research in materials science were as scientifically conservative as agricultural research, these new materials would never have been discovered. Very different forms of agricultural production that have not yet been investigated might hold great promise for the future.

THE SCIENCE OF ECOLOGY FOR AGRICULTURE

An ecologist arguing for the importance of ecology for agricultural research is obliged to point out that the ecology that will be the science of agriculture in the 21st century is not exactly the science of ecology we have today. Ecology has developed in relation to the study of nature, and there is still an emphasis on the study on systems that are not highly influenced by humans. Historically, plant ecology has emphasized the description of vegetation, whereas other areas of ecology have become highly abstract and mathematical, inspired more by mathematics and physics than by biology. Ecology is just beginning to mature as a scientific discipline, in which knowledge is built up on an empirical base, with the beginnings of an understanding of mechanisms. The ecology for agriculture in the future will be more empirical and applied, based on observed patterns in the field, and less abstract (Weiner 1995). It is easy to understand why agricultural researchers and students of ecology at agricultural universities might come to the conclusion that many of the abstract mathematical models which fill up our ecology textbooks and journals are not relevant to the agricultural problems they want to address. Ecology itself needs to change to meet the challenges of the future, and many ecological researchers are aware of this (Simberloff 1981; Peters 1991).

One of the other disciplines that look at higher levels of organization in agriculture is economics, the social science of agriculture. Economics and ecology are similar in that they both put agriculture in the context of higher levels of organization. But these higher levels are different. A discussion of the similarities and differences between economic and ecological perspectives on agriculture is beyond the scope of this paper, but the prediction here is that ecology will, in the future, occupy a position in agricultural thinking similar to that economics has today: ubiquitous. Just as it is not possible to give a lecture on a new technique or idea in agricultural research at an agricultural university or research institute today without being questioned about its cost, so in 10 years it will be equally impossible to avoid questions about the ecological effects of the new idea, both inside and outside the farm ecosystem. Ecology is the science of agriculture, and that will be taken for granted in the future.

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