THE PLANT COMMUNITY AS A WORKING MECHANISM

SPECIAL PUBLICATION NUMBER 1 OF THE
BRITISH ECOLOGICAL SOCIETY
PRODUCED AS A TRIBUTE TO

A. S. WATT

EDITED BY

E. I. NEWMAN

Department of Botany
University of Bristol
Bristol BS8 1UG, U.K.

BLACKWELL SCIENTIFIC PUBLICATIONS
OXFORD LONDON EDINBURGH
BOSTON MELBOURNE
1982

E. I. Newman (ed.) *The Plant Community as a Working Mechanism*

AFTER DESCRIPTION

JOHN L. HARPER
School of Plant Biology, University College of North Wales, Bangor,
Gwynedd, LL57 2UW, U.K.

SUMMARY

In this paper I discuss what appear to me to be dangers in recent thinking and writing by ecologists.

Plant ecology has been dominated until recently by description of vegetation and analysis of the biology of single species. Both types of study lead to predictive statements—predicting where we will find particular vegetation (or species) and what sorts of behaviour (or form) ~~we~~ will find among the organisms in a particular region. Almost inevitably such descriptions use the species as the basis for description—yet it is far from clear that the conservative and stable characters and the breeding isolation that may be used to define such taxa are appropriate to define ecological units—knowing as we do the wide range of ecologically different behaviours that are included within single species. The most immediately relevant ecological differences between organisms may often be those involving intraspecific variation between (ecotypic differentiation) or within populations (polymorphisms). We lack an appropriate taxonomy to handle such problems—but the absence of tools does not mean that there is no problem.

The explanation for the behaviour of a particular organism, both its distribution and its physiology, may be explained in proximal terms—how its present properties explain what it now does and where it lives, *or* in ultimate terms—how it has come to possess its present properties and distribution. These two levels of explanation often become confused—particularly in the use of the word 'adaptation'. The word implies a teleology—that the organism is goal-seeking and its evolution has had goals and ends. It also implies that in some way the organism has gained a fit to its environment and that for many ecologists the task before them is to demonstrate how this fit works. It is suggested that most evolutionary processes lead to a narrowing and specialization such that restrictions are placed on what the organism can do and where it can live. What we see proximally are the consequences of such limitations and we might, with profit, change the nature of our question to take the form—what are the limitations in the form and behaviour of organisms that account for their present highly restricted distributions and behaviour? The ultimate question then becomes, how have such limitations arisen? A variety of forces, of which natural selection is only one (*perhaps* the most important) have to be taken into account as possibly restricting the range of species, forms and activities that have evolved and survived. The optimism of simple adaptive explanations is suspect.

Ultimate 'explanation' of the present behaviour and distribution of organisms depends on evolutionary speculation based on proximal observation of evolutionary forces in action; we assume that what we are now seeing in a short time is essentially what has continued over long periods. If this is so, ultimate ecological explanation has to be focused on the nature of present evolutionary processes in action, which must imply the study of genetic individuals and their descendants. It is questionable whether study at the community or habitat level, or holist studies of area performance can approach these problems. The case is argued for a concentration of effort on the lives and deaths of individual plants—a reductionist approach—as the most likely to reveal those forces at present operating to determine the distribution and abundance of plants, and those most likely to hint at the evolutionary forces that have left most present forms in their narrowly limited ruts of specialization.

INTRODUCTION

In this paper I attempt to place the ecological studies of A. S. Watt against a background of what appear to me to be dangers in much ecological writing by other authors. Excessive preoccupation with the distribution of taxa (cartography for taxonomists), confusion about the compromises that have to be made between generality, precision and realism in ecological science, facile adaptationist and holist interpretation and the loose use of language appear to me to be especial dangers in the development of our science. The work of A. S. Watt offers model examples of ecological investigation and writing that is free from these dangers.

Much of the activity devoted to plant ecology, since the development of the subject as a science in its own right, has been essentially descriptive. It is natural that the first stages in the growth of any science (physical or biological) should consist of the description and ordering of the material for study. The next stage is to search for correlations between and causation of what has been described. In plant ecology the procedures for providing description have concentrated at two distinct levels—that of vegetation and that of the intimate study of the biology of individual species. The description of vegetation, whether in the hands of continental phytogeographers (Braun-Blanquet, Tüxen, etc.), the British tradition of Tansley, the American schools of Cain, Whittaker, Curtis, or the Russian schools of Sukatschev and his successors, has almost always been in terms of species composition. Vegetation is defined, whether objectively or subjectively, as assemblages of species which are treated as objects for classification or ordination and may be used in the construction of maps. In the ordering of vegetation types, other features of the environment (soil, climate, etc.) may either be used as sources of information with which the vegetation can be correlated (the one to predict the other) *or* combined with information about the species to give an ordering or classification, not only of the vegetation, but of habitat-environment complexes and ecosystems.

In contrast, in autecological description (e.g. in the Biological Flora of the British Isles) the aim has been to produce monographic treatments of individual species, their form, behaviour, distribution, and response to environmental factors such as frost, drought, soil nutrients, pathogens, predators, etc. Again the emphasis is on species; the taxonomic bias pervades almost all of descriptive ecology. These two broad categories of description give ecologists the equivalent of the telephone directory and 'Yellow Pages', the one describing who we can find where and the other describing who (plant or community) does what (and again where we can find him).

TAXONOMIC CHARACTERS AND ECOLOGICAL VARIATION

When we describe a species as having a particular distribution or particular ecological attributes we make a statement about a taxonomist's unit. Unfortunately for the ecologist, the criteria used by the taxonomist for the delineation of taxa are chosen deliberately from the conservative and stable features of morphology that are not subject to marked genetic variation, polymorphism or phenotypic change. These same criteria that are appropriate for the taxonomist may be quite inappropriate for describing the ecologically relevant differences between individuals, populations and communities. The problem is illustrated by considering the meaning to be attached to the statement that a particular species has a 'wide distribution'. This may mean either (a) that the individuals of the species, though genetically narrowly based, have wide tolerances or plasticity so that individuals sampled over the range of the species will behave equally well over that range, and are mutually exchangeable (Baker (1965) considers that many weeds have such all-purpose genotypes); or (b) that the individuals have very narrow tolerances but the nature of the species is such that the taxonomist includes a wide range of locally specialized genotypes within one taxon. In the first case information about the distribution of the taxon tells us something about the physiology of individuals and in the second case about genetic variation within and between populations.

The second class of species is illustrated by the work of Bradshaw and his colleagues (Antonovics, Bradshaw & Turner 1971) on *Agrostis tenuis* of which local populations on metal mines may be tolerant of zinc, copper, lead or other toxic minerals; the tolerances are specific. The species, *Agrostis tenuis*, has a wide distribution, but the populations are locally specialized and apparently incapable of persisting in each others' habitat. Individuals are not interchangeable over the range of the species. When we find that individuals of a species are not interchangeable between places in its distribution, the statement that the *species* has a particular distribution tells the taxonomist where he could find a plant to which he would give that name, but it does not tell the ecologist which plants will live where. The very extensive studies of Turesson, Gregor, Clausen, Keck, Hiesey, Bradshaw, and others have shown that plants of a single species sampled from a wide range of habitats and grown together in an experimental garden differ, often profoundly, in features of growth, form and life cycle. More recently Clegg (1978) and Turkington & Harper (1979) have made reciprocal transplant experiments which demonstrate that locally differentiated populations occur within small, superficially uniform areas of vegetation and, more significant, that such plants of the same species are often not mutually interchangeable. Not only are individuals within a local population different, but the differences are ecologically relevant, affecting fitness attributes. Such fine scale biotic differentiation as occurs between clones of *Trifolium repens* within one small pasture (1 ha) (Turkington & Harper 1979) and between populations of *Ranunculus repens* across woodland/grassland borders over distances of less than 50 m (Clegg 1978), emphasizes the impossibility of making predictive statements, about what genotypes will grow where, over even small distances. The same point is nicely made by Haukioja's (1980) study of the distribution of *Betula pubescens* in Finland. This species has a wide distribution from north to south but reciprocal plantings, made between northern and southern populations, showed striking differences in the damage done by insect predators (*Oporinia*) to the plants growing in their alien and natural environments. The same sorts of differences were found between populations on the slopes of a single fjell over an altitude gradient 80–330 m above sea level. The distribution map of *Betula pubescens* in Finland tells us where a taxonomist could expect to find a plant to which he could give that name—it does not in any sense tell the ecologist which plants bearing that name would suffer heavy insect defoliation in different parts of that distribution or which would live or die.

The failure of taxonomic categories to fit as ecological categories is not surprising when it is remembered that the taxonomist searches for stable, conservative characters for his groupings, yet it may be just the taxonomically useless characters that are mainly responsible for determining the precise ecologies of organisms. Properties such as the degree of plasticity, germination time, and form of the whole plant can clearly be critical in determining the life or death of individuals and so contribute to their fitness. Similarly, the position that a plant comes to occupy in a hierarchy of competing neighbours of its own and other species depends greatly on its branching form and stature, yet it is the shape of the conservative organs, the bits, such as leaves, petals, etc., not the form of the whole, on which the taxonomy is usually based. It may be that it is just those differences between plants that the taxonomist avoids, which the ecologist needs most strongly for effective description.

The ecological significance of intraspecific variation is often displayed where populations of a species are polymorphic and so individuals with different biologies are found intermingled within a single habitat. Even the sexual dimorphism of dioecious species is such that plants of the two sexes may play quite different roles within the community. The vegetative precocity of males compared to females in *Rumex acetosella* (Putwain & Harper 1972) and in *Spinacia oleracea* (Onyekwelu & Harper 1979) illustrate such ecological differentiation. Ecological differences between the sexes may extend to a geographic scale—males of *Petasites hybridus* are locally common throughout the British Isles, but females have a narrowly limited distribution (Clapham, Tutin & Warburg 1962).

A variety of ecological studies have been made of cyanogenesis polymorphism in *Lotus corniculatus* (Jones 1962) and *Trifolium repens* (Dirzo & Harper 1982a, b). The expression of cyanogenesis is under genetic control at just two loci; if cyanogenesis is expressed the plant is almost wholly protected against being eaten by slugs or snails. If slugs and snails are abundant in a pasture this simple genetic difference may determine whether individual plants will live or die and such intraspecific variation may be at least as important in the ecology of *Lotus* and *Trifolium* as the presence or absence of other plant species in the sward.

The extent of ecologically relevant polymorphism in plant populations within small areas is emphasized by Burdon (1980) in his study of *Trifolium repens*. In the 1-ha field of permanent grassland intensively studied at Aber, near Bangor, North Wales, and already referred to in this paper, *T. repens* is abundant. Fifty clones, sampled from a grid spaced across the field, differed from each other on average with respect to 3·3 non-flowering characters, apparently all genetically controlled. One pair of clones differed in thirteen statistically significant respects! The characters included major aspects of growth such as relative growth rate, leaf area, petiole length, resistance or susceptibility to two pathogens, cyanogenesis, leaf marks and other characters. Each of these characters had been shown to be of selective importance by one author or another in *T. repens* or some other species of *Trifolium*. A descriptive ecology that simply records *T. repens* as present, its abundance, its microdistribution, its relationship to other species and to physical factors hides all such information. Any attempt to progress from a descriptive ecology that describes where species are found to an interpretative ecology that accounts for the distributions should ask, in each case, how far the taxonomist's species represents an ecological unity or a compendium of significantly different ecologies. Problems of the distribution and abundance of species may need to be seen as essentially problems in genetics!

The description of the autecology of plants is beset with many of the same problems—not least (following the above arguments) that the ecologically relevant biology of an organism is not defined by attaching a binomial. Even supposedly fundamental physiological attributes such as the relative growth rate may be genetically variable within a small local population (Burdon & Harper 1980).

Autecological studies may be expected to provide an accumulation of data for a matrix from which we might extract significant ecological generalizations. It is an expectation that the variety of species and forms present in a particular type of habitat will have features in common. We expect that the plants that are found in, say, a waterlogged habitat will all possess properties that enable them to live in a waterlogged habitat and we can then use these similarities as a demonstration of the powerful forces of evolution and ecology that constrain the range of forms found in a particular environment. However, it is also a reasonable expectation that species that live together in a habitat will differ. It is part of the conventional wisdom of theoretical ecology (Gause's hypothesis) that two or more species that persist together in a habitat without one succeeding at the expense of another must differ in the ways that they exploit that habitat—differing in such a manner that each suffers more from its own increasing density than from that of its neighbours. (This problem is discussed for plants by Harper *et al.* (1961) and Newman (this volume).) We thus have two contrasting expectations. If all the plants in a waterlogged habitat contain aerenchyma this can be seen (and taught!) as a splendid example of convergent evolution; if some have aerenchyma, some have superficial roots, others have mechanisms that prevent the formation of toxic anaerobic byproducts and yet others are able to metabolize such products, we have a splendid example of evolutionary divergence, a variety of 'solutions' to a single environmental 'problem'. Thus, if the biologist finds similarities between organisms in a habitat, he can feel satisfied that he has an ecological convergence and he can find equal satisfaction in demonstrating differences that illustrate necessary ecological divergence. There are no losers in this type of investigation—theory is so broad that every observation can be fitted. Both similarities and differences can be accounted for as 'adaptations' to the environment ('Eureka' ecology!).

ADAPTATION, STRATEGY AND STRESS

The concept of 'adaptation' is fundamental to most ecologists who seek to extend descriptive syn- or autecology to invoke causal (as opposed to purely correlative) explanations of ecological phenomena. Organisms are thought of as fitted in a precise lock/key relationship with both the physical and biotic factors of the environment. If an organism is found more or less reliably in a particular type of environment it is easy to take this as a demonstration that it has, in some way, been programmed to that end. It then remains for the ecologist to discover and describe those properties that confer this precise fit. Darwin (1859) carefully denied that the process of natural selection was the sole cause of the evolutionary process—yet post-Darwinian Victorian optimism continues in much ecological thinking—that the organism should and can be interpreted as a perfected product of an all embracing, idealizing and optimizing process of natural selection. Gould & Lewontin (1979) have cogently and wittily criticized this Panglossian paradigm in evolutionary theory. The organisms that we study behave and live where they do because of properties passed to them by their ancestors. Some ancestors have left more descendants than others so the nature of populations, species and communities has changed; they have evolved. A variety of forces influence which organisms (or genes) leave descendants and so determine their behaviour. There is much more to these processes than the naive view of all powerful natural selection constantly moulding and idealizing each population towards optimal behaviour in a preferred niche. Factors that seem likely to have determined which individuals have contributed the descendants that now make up our flora (and fauna) include the following seven.

(1) *Founder effects.* When new populations establish after catastrophes or invasions of new areas the gene pool represented in the founders may be very limited and hence chance elements may play a role in the direction of subsequent evolutionary change.

(2) *Archetype effects.* No evolutionary process starts with a fresh sheet: always the

process acts on ancestors that are more or less complex organized systems, and there are therefore limits on what new changes are possible. It is for this reason that Jacob (1977) has described the evolutionary process as 'tinkering'—existing systems are altered, patched, twisted and refitted, but always carry some of the imprint and limits imposed by the nature of the original. (It is relatively easy to tinker a saucepan, but not a bicycle, from an old kettle.) Stebbins (1971) considers the effect that the same selective force acting to favour increased fecundity might have, when applied to a population of lilies and of a grass. The archetypic constraints within the Gramineae make it exceedingly unlikely that the grass will respond by increasing the number of ovules per ovary and more likely that the response will be to increase the number of ovaries per plant. In contrast, the lily with already multi-ovuled ovaries, may be more likely to respond to selection by increasing the number of ovules per ovary. In each case the direction that an evolutionary pathway takes under selection will be under archetypic constraints. The response to selection follows the easy line of least resistance, not necessarily the optimal route (Stebbins (1970) has called this process 'selection along the line of least resistance').

(3) *Available genetic resources.* Different populations and species contain different and limited resources of variation. The direction of an evolutionary pathway under a particular selection pressure will be determined in part by which mutations and gene recombinants are exposed in the population. Resistance to triazine herbicides has developed in *Poa annua*, *Senecio vulgaris* and *Chenopodium album* (see, for example, Holliday & Putwain 1977). These triazine-tolerant forms, but few other species, now colonize some agricultural habitats in which these herbicides are regularly used. Presumably, this reflects the difference in the nature of the genetic variability available within populations of the different weed species at the time at which the selection process acted. It is not a necessary consequence of the application of a selective process that a population will respond by genetic change in the direction that minimizes the effect of the selection. The direction of evolutionary change in a population (if any) is constrained within the limits of its genetics. Consequently, we cannot argue in reverse that those features that we observe in an organism in nature are, in any sense, optimal solutions to past selective forces.

(4) *Pleiotropism and linkage disequilibrium.* Both of these phenomena may result in diverse properties of an organism being inherited together, with the result that one set of properties may be carried in the evolutionary process on the heels of another.

(5) *Allometry.* Gould & Lewontin (1979) emphasize particularly the role in the evolutionary process of allometries in which groups of apparently independent characters reflect a particular aspect of growth expressed in a variety of different organs. The phenomenon of gigantism is, for example, rarely confined to one organ on a plant but will normally be expressed in a large number of manifestations of growth.

(6) *Selection.* This implies a non-random (i.e. directional, stabilizing or disruptive) change in the genetic composition of a population and, of all the forces of evolution, is the one conventionally thought of (and probably rightly) as the prime cause. It may take the form of a process that leads towards some asymptotic condition in which members of a population become, over generations, tolerant of the major repeated hazards, particularly physical hazards, in the environment (e.g. drought, frost). However, selection may also be exercised by biotic forces, such as inter- and intraspecific competition from neighbours or predation and parasitism. In such cases the reaction to selection may not be asymptotic because each change in predator or prey or in one of a pair of competitors produces changes in the selective forces acting on the other which then exerts reciprocal selection. Such reciprocating selection has no obvious end point and the process of coevolution that results may continue until only the availability of further genetic variation places limits on

evolutionary change. The coevolutionary process is most beautifully illustrated in the breeding of crop varieties by man where it has become necessary continually to develop new strains of crop to combat the apparently endless coevolution of new strains of pathogens. The accumulation of batteries of alkaloids within individual species of *Senecio* (Barger & Blackie 1937) or of *Lupinus* (Dolinger *et al.* 1973) may represent a comparable phenomenon in nature involving an endlessly reciprocating selection between coevolving host plants and their predators. Where selection is biotic, so that coevolutionary processes may occur, the consequence is likely to be the accumulation of complexity; the interacting populations in the coevolutionary process each drive the other further into an ever-deepening rut of specialization (Huffaker 1964). This is a very different situation from a precise fit between organism and environment.

(7) *Compensation.* Any evolved change in part of an organism's form or behaviour seems likely to be developed at the expense of compensating changes in some other aspects of the life of the same organism. An increased expenditure of resources on reproduction is likely to reduce the resources available for vegetative growth; an increase in seed size is likely to be compensated by a reduction in seed number. Increased expenditure of carbon or minerals on root growth is likely to limit the resources available for shoot growth. There is every reason to suppose that most aspects of the form and behaviour of an organism represent the result of some set of compromises. Thus it is dangerous to search for interpretations of any isolated part of the form or behaviour of an organism and to give it an explanation in its own right as an optimal system. It is particularly tempting to do this when teaching students in the field and to assign *ex cathedra* 'explanation' to every feature of every organism present in a habitat. Facile adaptationist guesswork used to explain everything that we observe in nature scarcely serves to make ecology an effective medium for teaching the principles of science.

The list of evolutionary forces above is certainly not exhaustive. They have in common that they are all likely to constrain and narrow the range of activities of organisms (though they may increase the variation between them). They are also likely to limit the range of habitats in which organisms may complete their life cycles and leave descendants. This means that rather than concentrating on a search for the ways in which organisms are perfectly suited to their environments, we might more healthily concentrate on the nature of the limitations that constrain where they live. We might usefully ask not what is it about an organism that enables it to live where it does, but what are the limits and constraints that prevent it living elsewhere? It is perhaps because we usually seek to explain the perfection of plants (as does the zoologist for his animals—see Cain (1964)), that so little plant ecology has been concerned to discover what goes wrong with plants when they are grown in *communities* outside their normal range. This would appear to be the ideal way to demonstrate the real extent and proximal cause of the narrow specialization of most plant forms. The fact that forms of so many species can be grown successfully in cultivation, in alien soils and climates far outside their natural distribution, suggests that much of the narrow ecological range of species in nature is determined proximally and perhaps also ultimately by the biotic rather than the physical and chemical forces in the environment. It is for this reason that we need many more experiments in which plants are introduced to alien communities where they may reveal just what are the real causes of their failure to maintain themselves.

The word 'adaptation' appears so often in the writings of ecologists (including some of my own) that its meaning bears some examination. Stern (1970) has reviewed some of the usages. There seem to be three common meanings.

(1) It may mean the change that occurs in a phenotype as a result of some

environmental experience where the change is *assumed* to improve the ability of the organism to continue growth (or better, its chance of leaving descendants) compared with an organism that did not undergo the change. Frost hardening is an example. It is important, however, to recognize that no assumptions can be made that any phenotypic change in a plant in response to the environment is in some way an improvement. Indeed, some phenotypic responses, such as the formation of a restricted superficial root system by plants which become waterlogged in spring, probably reduce the chance that the plant will complete its life cycle later. It is certainly an act of gross optimism to *assume* that all environmentally induced phenotypic change increases fitness—that all reactions to environmental change are in such a direction as to minimize its damaging consequences and maximize the advantages. When the word is invoked to describe phenotypic change, it needs very precise usage if it is not to be trite.

(2) An adaptation is any aspect of form or behaviour that *at a reasonable guess* is the result of natural selection (see Williams 1966). This is probably the commonest usage and assumes that of the incomplete list of the evolutionary forces listed above, natural selection is so overwhelmingly the most important that we can assume it accounts for most of what we observe. It is doubtful whether we can ever make that assumption.

(3) An adaptation is any feature of form or behaviour that can, in retrospect, be called on to account for the ability of an organism to live where, or do what, it does. It is any feature of an organism that can be explained away as a 'good thing' in a perfect world: any feature that an intelligent creator might have provided had it been his intention that the plant was destined to live where it is now found.

I suspect that the word 'adaptation' has lost its value in biological science and now serves mainly to give superficial respectability to what is really intolerable teleology. The prefix *ad*, with its implication of *to* or *for* the future, enshrines the teleology; only deliberate substitution by phrases that say exactly what is meant in a given context, or new words, can rid ecological writing, and especially teaching, of the glib teleology that mocks the science. Perhaps *ab*aptation is a better word with the prefix *ab* now implying all those features of the organism's form and behaviour that characterize it by virtue of events *by*, *with* or *from* the past.

Ecological interpretation would gain in precision if every time an author used the word adaptation he forced himself to state precisely what he meant. In particular, this means differentiating between proximal and ultimate explanations for biological properties, i.e. differentiating between the behaviour of the organism as explained in terms of its present properties (proximal explanation) and the explanation of how it comes to possess such properties, i.e. the evolutionary forces that acted on the populations from which the organism's ancestors were drawn (ultimate explanation). This distinction becomes especially confused in the now common use of the word 'strategy' to describe the programmed biology, especially the life cycle, of an organism. The term 'strategy' sounds like a teleology—as if the organism has a planned campaign of behaviour aimed at the future. Ghiselin (1974) justifies the use of the word and puts it into terms appropriate for ultimate explanation: a strategy 'somewhat resembles the proverbial military school which produces officers admirably equipped to fight the battles of previous wars', i.e. a strategy is a property that is *by, with* or *from* the past. In most writing by ecologists, however, 'strategy' seems to imply a plan for future survival—a programme designed to achieve a goal.

Anthropomorphisms creep easily into science—perhaps because they are so often a means by which a teacher can create involvement and interest in a class of students.

Adaptation, Strategy and Stress are three emotive words that are now common in ecological writing. 'Stress' carries over easily from social and medical sciences to imply in biology 'what I don't think I would like if I was a (buttercup, kangaroo, flea, beetle, etc.)' Often the word is wholly redundant as in 'the effect of temperature stress' (= the effect of temperature), 'the effect of density stress' (= the effect of density) or 'the effect of water stress' (= the effect of drought or sometimes = the effect of waterlogging!). Sometimes the word is used to describe a force or a stimulus (drought, pollution, cold) and sometimes a reaction or response. Pickering (1961), a professor of medicine, wrote about the use of this word: '... stress, again an old word, but now part of the popular modes of expression in jargonese. I am never sure what it means. The classical language of biology uses two expressions—namely, *stimulus*, to describe a change in environment, and *response*, to describe the resulting change in the organism. The modern use of the word stress we owe to Selye, who uses it to express the first stage in the common reaction of the mammal to a variety of harmful environmental changes. It was thus the first stage in the *response* to certain kinds of stimuli.... Others quite clearly use the word to describe environmental changes, that is *stimuli*. For example a man is exposed to stress, or, in certain examples, to heat stress. This word is now in common use, and by the most distinguished scientists and laymen. Whenever I meet it, I set it aside, because frankly I do not know what it means and I fear it is, like shock, another of these words of deception. I find it difficult adequately to express my surprise and horror that contemporary science should tolerate this confusion of stimulus and response.'

PROBLEMS OF HOLISM AND REDUCTIONISM

If ecology is the study of the relationship between organisms and their environment, then agriculture and forest science are part of ecology—an applied sub-set of the science. However, in so far as ecology is an experimental science, the contribution from agriculture and forestry is much the largest part of the whole. For many ecologists the rightful field of study is in the description of the undisturbed wilderness of communities untouched by man—the natural communities of nature with their richness of biotic diversity within and between habitats. The special concern for the conservation of natural communities—as places in which the real world of nature can be admired and explored—sets some ecologists apart from those who study man-managed environments. There is an antithesis in the practice, and often antagonism between the practitioners, of ecology in the wilderness and ecology on the farm. This antithesis seems to have two elements. Firstly, land is a limited resource for which special interests compete—agriculture, forestry, conservation, recreation, roads, building, etc. There are expected tensions between these interests. It is healthy when ecology is less often identified with just one of these interests (e.g. conservation) and more often seen as a science underlying the study of all organisms in all environments (including man in factories and cities). Secondly, there has been a mainstream of holist philosophy among many ecologists—an almost religious view that natural communities of organisms have properties that are more than the sum of individual effects plus their interactions. To the holist, any man-made alteration of the whole is a sacrilege.

The holist attitude restricts the science that can usefully be practised to essentially descriptive and correlative activites. For those who make it an act of faith that the whole is more than the sum of its parts plus their interactions, the behaviour of deliberately simplified systems is irrelevant to understanding. Nowhere is this holism more apparent than in the way ecology is taught in many schools and universities with its emphasis on complex systems and the ways in which they can be described. There is probably no other science in which students are taught by being dropped into the deep end of complexity. Ecology is usually introduced to school children by showing them oakwoods, chalk grassland, an intertidal zone or a pond or lake margin and perhaps asking them to describe it. This is equivalent to introducing a child to chemistry by showing him the structure of haemoglobin or a DNA helix. The results of such holist teaching are to be seen in an emotive pseudo-science of ecology with its own language exemplified by a statement in the VIIth Report of the Royal Commission on Environmental Pollution: 'Until recently, agriculture has developed in harmony with the environment'. (What is harmony? How do we measure it?) If we accept (again as an act of faith) that the activities of communities of organisms are no more than the sum of the activities of their parts *plus* their interactions it becomes appropriate to break down the whole into the parts and study them separately. Subsequently, it should, again as an act of faith, be possible to reassemble the whole, stage by stage, and approach an understanding of its workings. This approach demands that we begin by looking at simple systems. It must mean looking at individual organisms and their behaviour alone and when brought together in the very simplest communities of single species in very simple physical conditions. From this stage, increasing complexity can be introduced step by step. To an ecologist who is not obsessed by holism it comes as a delightful surprise to realise that agricultural science (and to some extent forestry) has laid down just these basic elements of ecological science. Agriculture usually represents the growth of one or very few chosen species in simplified conditions (deliberately made uniform). It is indeed from agricultural science that the plant ecologist derives most of his basic information about:

(1) the effects of physical variables in the environment (temperature, nutrition, radiation, water supply) on plant growth;

(2) the effects of density on plant and crop performance (intraspecific competition);

(3) the effects of two species interactions at a single trophic level (weed-crop interactions, legume-grass interactions, the behaviour of crop mixtures);

(4) the effects of host-parasite interactions (crop diseases);

(5) the effects of predator-prey interactions (the grazing animal interacting with the grazing sward and the effects of pests on monocultures);

(6) the interactions of three species systems, plant-animal-animal (biological control of insect pests of crops) and plant-plant-animal (grazing effects on grass-legume pastures and the biological control of weeds by introduced insects);

(7) symbiosis (legume-*Rhizobium* associations);

(8) community assimilation, radiation capture and productivity;

(9) genetic variation within and between populations.

In agricultural science the workings of simple systems begin to be understood at a level that makes predictive ecology possible. A splendid examples lies in the management of ryegrass-white clover pastures where there is a highly sophisticated technology available for maintaining particular balances between grass and clover. Studies that developed particularly from the work of pioneer agronomists (e.g. Jones 1933) led to the remarkable situation in the 1950s in which various farming organizations were giving medals or silver cups and prizes to farmers who had achieved 'ideal' pasture composition. Careful balancing of nitrogen and phosphorus fertilizers and controlled grazing can produce a desired balance of species. There is probably no example among world vegetation types of a community so deeply understood and with its interactions so deeply researched (Wilson 1978). There is far to go before such a predictive ecology might be realized for the management of more complex vegetation. A single example illustrates the problem. The fritillary (*Fritillaria meleagris*) is a bulbous plant found very locally in Britain (and usually then in high abundance) in low lying hay meadows on neutral soil. The plant is beautiful in flower, spectacular en masse and the populations are cherished as objects for conservation. One fritillary dominated meadow (Magdalen Meadow) lies within the ground of Magdalen College, Oxford. It adjoins a once elm-wooded grove on which a herd of fallow deer has been maintained for many years. The deer carry a heavy parasite burden and should have a change of ground. The fritillary meadow is managed by cutting for hay after the fritillaries have flowered and set seed and is then grazed by bullocks. The 'simple' management question that has been posed to the ecologist is 'What would happen to the fritillaries if the deer were moved to the meadow?'. Such a problem has one simple holist answer—that the fritillary forms part of a system in which any change poses risks to the whole. Yet, deep understanding of the interaction of fritillaries with other plant species in the meadow, knowledge of the species' life cycle and population biology, its genetic variation and degree of local specialization, coupled with a knowledge of the differences between the grazing activities of bullocks and deer (dunging, urinating, trampling and defoliating), might allow a more subtle, useful and fundamental answer to the question. The holist answer is safe and ignorant. Presumably, this sort of question could be answered empirically on an agricultural analogy, by a simple randomized block experiment in the meadow involving deer *v.* bullocks, hay *v.* continuous grazing and coupled with a detailed analysis of changes in the flora of the plots. Such an experiment might, in time, give guidance for a changed programme of management of the meadow and of the deer. The results might, however, be locally specific and relevant only locally, unique to that meadow.

I presume that there is more to ecological science in the post-descriptive phase than acquiring the ability to handle unique, anecdotal management problems. I presume that it is a search for wider ecological generalizations that will dominate the post-descriptive phase in plant ecology. However, the search for generalities in ecology has been disappointing—more so in plant than in animal ecology. The few generalities that have emerged come from studies of stands of single species. The 3/2 thinning law defines the upper limits to the combination of sizes and numbers of plants that can persist in a monoculture (White & Harper 1970; Gorham 1979). This law has generality extending over more than eighty species ranging from *Sphagnum* to *Pinus* and from annual weeds to herbage grasses. Similarly, the law of constant final yield states that over a wide range of densities, yield per unit area becomes independent of the number of plants sown. This holds true for a great number of crop species and is probably a rather general law (White 1980).

PRECISION, REALISM AND GENERALITY

The search for generalities characterizes all sciences, and they usually take the form of established, reliable correlations or chains of causation. The ecologist sits on a trilemma in deciding at what level to search for correlation and causation. He may look for high precision, high realism or high generality or have to be prepared to compromise between these aims (Levins 1966). The search for precision may lead him to work with unique genotypes in controlled environments designed to minimize the background of environmental noise. The risks are then that his experimental results have no realism because natural populations are usually genotypically polymorphic and environments are normally noisy. He may emphasize realism by studying the behaviour of individual plants in the field; then only very large and extended studies may allow significant effects to be detected because of the magnitude of environmental noise and variance over space and time against which they must be compared. The search for generality may sacrifice both realism and precision and lead the ecologist to large-scale survey which runs the risk of yielding results that are only trite and superficial.

The research problem of deciding whether to place emphasis on precision, realism or generality is less in agriculture than in the ecology of natural systems. This is largely because it is in the nature of agricultural practice that the physical and biotic environments are simplified and variation from place to place is reduced by activities such as drainage or irrigation, fertilizer application, cultivation, pest and disease control and by the use of a limited number of crop varieties. Thus, local 'land' varieties of crops are replaced by more and more widely used specific cultivars or strains. In agricultural ecology precision, realism and generalization become more compatible in scientific enquiry. It may well be for this reason that much of the development of ecology as a science in the post-descriptive phase will come from the study of man-managed ecosystems.

There is, however, one important difference between the ways that we approach the ecology of agricultural and forestry systems and those of natural environments. The measure of the efficiency in agriculture and forestry is the profitability of areas of land or of populations of the crop. Here, there are no semantic objections to using all the teleological concepts of efficiency, goal and adaptation. A variety of a cereal crop *is* 'adapted' in the strict sense of being planned for the future. The ecology of an agricultural system is managed with a goal (profit), using organisms bred to specific ends. The efficiency of such a system can be measured and compared with others in respect of profit made, dry matter fixed, nutrients cycled and food produced but there are dangers when this type of thinking is transferred to the ecology of natural communities. In nature, few individual organisms respond to the area of the community in which they live. Moreover, the driving force in both succession and selection within a community is the determination of which individuals will leave descendants rather than some property of the group or community. Indeed, those features of individual ancestors that have led them to leave more descendants than their neighbours in nature may be quite irrelevant to performance per unit area.

It is instructive to consider just which sorts of heritable properties of individuals will be favoured in the struggle for existence. In higher plants these may include a growth habit that overlaps neighbours, depriving them of light; the quick capture of nutrient resources, even in excess of individual requirements, if capture deprives a neighbour of the same resources; rapid exhaustion of water supplies if this leaves a neighbour disproportionately deprived; retention of, rather than recycling of nutrients (if this deprives a neighbour). Indeed, unless there are strong processes of kin-selection operating amongst plant populations, we might expect to see emerging in nature, predominately those evolved properties that confer 'selfish' individualistic traits. There is no reason to expect that the evolution of organisms has been conditioned in nature towards any goal of productivity, stability or community yield, yet it is by just these criteria that we judge the efficiency of man-managed crops and forests. For these we breed varieties of plant for their population or group yield—considerations of individual fitness cease to have the relevance that they have in nature. If it is true that natural vegetation is what it is because of the evolution of individualistic selfish traits, it is unlikely that we will find ultimate explanations of ecological phenomena in nature at the area or population level. Both area and ecosystem are highly appropriate ecological units for the agronomist and forester but may be inappropriate levels of study at which to seek 'ultimate' explanations of ecological behaviour. If this is the case, only superficial generalities about ecosystems may be expected to emerge from systems studies of natural communities.

It is not the aim of this paper to be iconoclastic or defeatist, rather it is to set a background against which to comment on the significance of the contribution by A. S. Watt to the science of plant ecology. It is doubtful whether any other individual in the history of the science has contributed so much to the detailed description of the proximal events that influence the behaviour of individual plants in nature. The attention of his research, whether on beech woodland (e.g. Watt 1934), stands of bracken (e.g. Watt 1940, 1945) or in the patterned communities of the Breckland (e.g. Watt 1957) has, in every case, focused on the intimate, proximal events that affect individual plants and that, taken together, account for the nature of the communities he has studied. The reductionist focus on which seeds of the oak produce seedlings, which fronds of bracken become frost-damaged or which plants occupy a point in space in succeeding years in the Breckland, give us a description of ecological events that combine the high realism of a field observation with high precision: it is particularly characteristic of his studies that they extend over long periods of time so that the year to year variations in climate and other factors do not obscure general trends. The sacrifice in these studies is, of course, in generality. The precise behaviour of the populations of plants on Watt's Breckland plots may not be repeated anywhere else on the face of the earth. Genotypes of bracken may behave quite differently in other places and *Fagus sylvatica* may behave quite differently away from the Chilterns. Watt's contribution to ecological generality comes at a quite different level. It is in his ways of looking at natural systems and his concepts of plant community behaviour (regeneration cycles, pattern and process) that he introduces generalized attitudes that profoundly affect the work of others. His work is perhaps the model of a reductionism out of which conceptual generalizations emerge. His writing is remarkably free of any confusion between proximal and ultimate causes. What he discovers happening in his communities becomes the type of phenomenon that other people then search for in theirs. I suggest that it is from the repeated studies by *individuals* like Watt of *individual* plants in particular local conditions that most ecological generalizations are likely to emerge. Many of these are likely to be concepts, not laws. Further, I suggest that it is from the work of many individuals, working scattered over a variety of parts of the world, but concentrating their attention over long periods on the behaviour of individual plants, that the development of ecology as a generalizing and predictive science may become possible. I have little faith that either holists or the big science of the large team will be as effective.

It is greatly to be hoped that others will build upon the long extended field observations of A. S. Watt, particularly in the Breckland. If, in such communities, about which we now know so much, there can be some concentration of effort in exploring the genetics and breeding behaviour of the plants present, and some controlled perturbations of the vegetation that may reveal the nature of its controlling factors, we have a reasonable hope, not only of obtaining proximal interpretation of the ecology of the organisms but of making better guesses about that nature of ultimate causes. The detailed analysis of proximal ecological events is the only means by which we can reasonably hope to inform our guesses about the ultimate causes of the ways in which organisms behave.

ACKNOWLEDGMENT

I am grateful to Dr J. W. Tinsley for telling me of the reference to Sir George Pickering's paper.

REFERENCES

Antonovics, J., Bradshaw, A. D. & Turner, R. G. (1971). Heavy metal tolerance in plants. *Advances in Ecological Research*, **7**, 1–85.

Baker, H. G. (1965). Characteristics and modes of origin of weeds. *The Genetics of Colonizing Species* (Ed. by H. G. Baker & G. L. Stebbins), pp. 147–172. Academic Press, New York.

Barger, G. & Blackie, J. J. (1937). Alkaloids of *Senecio*. III. Jacobine, Jacodine and Jaconine. *Journal of the Chemical Society*, 1937, 584–586.

Burdon, J. J. (1980). Intra-specific diversity in a natural population of *Trifolium repens*. *Journal of Ecology*, **68**, 717–736.

Burdon, J. J. & Harper, J. L. (1980). Relative growth rates of individual members of a plant population. *Journal of Ecology*, **68**, 953–957.

Cain, A. J. (1964). The perfection of animals. *Viewpoints in Biology*, **3**, 36–63.

Clapham, A. R., Tutin, T. G. & Warburg, E. F. (1962). *Flora of the British Isles*, 2nd edn. Cambridge University Press.

Clegg, L. (1978). *The morphology of clonal growth and its relevance to the population dynamics of perennial plants*. Ph.D. thesis, University of Wales.

Darwin, C. (1859). *The Origin of Species*. Harvard Facsimile, 1st edn., 1964.

Dirzo, R. & Harper, J.L. (1982a). Experimental studies on slug-plant interactions. III. Intraspecific variation in the acceptability of plants of *Trifolium repens*. *Journal of Ecology*, **70**, 101–118.

Dirzo, R. & Harper, J. L. (1982b). Experimental studies on slug-plant interactions. IV. The performance of cyanogenic and acyanogenic morphs of *Trifolium repens* in the field. *Journal of Ecology*, **70**, 119–138.

Dolinger, P. M., Ehrlich, P. R., Fitch, W. L. & Breedlove, D. E. (1973). Alkaloid and predation patterns in Colorado lupine populations. *Oecologia* (Berlin), **13**, 191–204.

Ghiselin, M. T. (1974). *The Economy of Nature and Evolution of Sex*. University of California Press, Berkeley.

Gorham, E. (1979). Shoot height, weight and standing crop in relation to density of monospecific plant stands. *Nature (London)*, **279**, 148–50.

Gould, S. J. & Lewontin, R. C. (1979). Spandrels of San-Marco and the Panglossian paradigm—a critique of the adaptationist program. *Proceedings of the Royal Society, B*, **205**, (1161), 581–598.

Harper, J. L., Clatworthy, J. N., McNaughton, I. H. & Sagar, G. R. (1961). The evolution and ecology of closely related species living in the same area. *Evolution*, **15**, 209–227.

Haukioja, E. (1980). On the role of plant defences in the fluctuation of herbivore populations. *Oikos*, **35**, 202–213.

Holliday, R. J. & Putwain, P. D. (1977). Evolution of resistance to simazine in *Senecio vulgaris* L. *Weed Research*, **17**, 291–296.

Huffaker, C. B. (1964). Fundamentals of biological weed control. *Biological Control of Insect Pests and Weeds* (Ed. by P. De Bach), pp. 631–649, Chapman and Hall, London.

Jacob, F. (1977). Evolution and tinkering. *Science*, **196**, 1161–1166.

Jones, D. (1962). Selective eating of the acyanogenic form of the plant *Lotus corniculatus* L. by various animals. *Nature (London)*, **193**, 1109–1110.

Jones, M. G. (1933). Grassland management and its influence on the sward. *Journal of the Royal Agriculture Society*, **94**, 21–41.

Levins, R. (1966). Strategy of model building in population biology. *American Scientist*, **54**, 421–431.

Onyekwelu, S. S. & Harper, J. L. (1979). Sex ratio and niche differentiation in spinach (*Spinacia oleracea* L.). *Nature (London)*, **282**, 609–611.

Pickering, G. (1961). Language: the lost tool of learning in medicine and science. *The Lancet*, 15 July 1961, 115–119.

Putwain, P. D. & Harper, J. L. (1972). Studies in the dynamics of plant populations. V. Mechanisms governing the sex ratio in *Rumex acetosella* L. and *R. acetosa* L. *Journal of Ecology*, **60**, 113–129.

Stebbins, G. L. (1970). Adaptive radiation of reproductive characteristics in angiosperms. I. Pollination mechanisms. *Annual Review of Ecology and Systematics*, **1**, 307–326.

Stebbins, G. L. (1971). Adaptive radiation of reproductive characteristics in angiosperms. II. Seeds and seedlings. *Annual Review of Ecology and Systematics*, **2**, 237–60.

Stern Jr, J. T. (1970). The meaning of 'adaptation' and its relation to the phenomenon of natural selection. *Evolutionary Biology*, **4**, 38–66.

Turkington, R. & Harper, J. L. (1979). The growth, distribution and neighbour relationships of *Trifolium repens* in a permanent pasture. IV. Fine-scale biotic differentiation. *Journal of Ecology*, **67,** 245–254.

Watt, A. S. (1934). The vegetation of the Chiltern Hills with special reference to the beechwoods and their seral relationships. *Journal of Ecology*, **22,** 230–270, 445–507.

Watt, A. S. (1940). Contributions to the ecology of bracken (*Pteridium aquilinum*). I. The rhizome. *New Phytologist*, **39,** 401–422.

Watt, A. S. (1945). Contributions to the ecology of bracken (*Pteridium aquilinum*). III. Frond types and the make up of the population. *New Phytologist*, **44,** 156–178.

Watt, A. S. (1957). The effects of excluding rabbits from grassland B (Mesobrometum) in Breckland. *Journal of Ecology*, **45,** 861–878.

White, J. (1980). Demographic factors in populations of plants. *Demography and Evolution in Plant Populations* (Ed. by O. T. Solbrig), pp. 21–48. Blackwell Scientific Publications, Oxford.

White, J. & Harper, J. L. (1970). Correlated changes in plant size and number in plant populations. *Journal of Ecology*, **58,** 467–485.

Williams, G. C. (1966). *Adaptation and Natural Selection.* Princeton University Press, Princeton, N.J.

Wilson, J. R. (1978). *Plant Relations in Pastures.* C.S.I.R.O., Melbourne, Australia.