

Plant phenotypic plasticity and non-cognitive behaviour

Received wisdom is sometimes just closeted ignorance. In March, an international workshop organized by Ariel Novoplansky met at the desert campus of the Ben-Gurion University of the Negev, Israel, to discuss the unlikely topic of behaviour in plants. While arguments raised the temperature in the meeting room, the desert outside was drenched in freezing rain. Environments can be unpredictable and this is precisely why plants as much as animals need a repertoire of responses to environmental stimuli. Broadly, these responses are defined as phenotypic plasticity (Box 1), which is conventionally regarded as a component of the variation that occurs *between* individuals growing in different environments (Carl Schlichting, University of Connecticut, Storrs, USA). However, individual plants alter their phenotypes as they grow from one micro-environment to another and as the local environment changes.

It is logical and consistent with zoological terminology to describe such phenotypic plasticity expressed within an individual during its lifetime as 'behaviour', although ignorance of the wide repertoire of responses found in plants sometimes elicits derision of the term 'plant behaviour' from the incognoscenti. As long ago as 1950 Agnes Arber¹ observed that behavioural responses in plants are a natural consequence of their modular growth and construction because this permits them to respond to environmental change through adjustments in the type and placement of new organs. Recent research, particularly on clonal plants, amply illustrates this point.

Michael Hutchings (University of Sussex, Brighton, UK) described how branching in the clonal herb *Glechoma hederacea* is locally determined and increases abruptly when a stolon grows from poor into rich soil conditions. Plant ecologists have long regarded this as foraging behaviour (Box 1). He also showed that a variety of plastic responses occurring at a local scale enabled clones in patchy environments to produce more biomass than those in uniform environments with the same total nutrient supply. The extent to which growth increased under heterogeneous conditions depended both upon the scale of resource patchiness and on the contrast between poor and rich patches. In *G. hederacea*, the length of a horizontal spacer (the piece of stolon between two nodes) also alters with environmental conditions, but this is unusual for clonal plants.

Heidrun Huber (University of Utrecht, The Netherlands) showed that a repeating pattern, when erect and clonal herbs in the same genus are compared, is for vertical spacers, such as the leaf petioles of clonal species or the stem internodes of erect species to elongate in shade. Horizontal spacers such as the petioles of erect herbs or the stolon internodes of clonal herbs, are relatively unresponsive.

Phenotypic plasticity of a behavioural kind is by no means confined to morphological responses, but also includes physiological responses, such as acclimation (Box 1) to light (Carlos Ballaré, University of Buenos Aires, Argentina). These responses can be extremely rapid, but an initial stimulus may also lead to longer-term potentiation (Box 1), causing, for example, greater drought resistance in crops that have first experienced a brief episode of water shortage or an amelioration in the dose/response relationship between UVB irradiation and DNA damage with length of UVB exposure. Opinion in the meeting was divided as to whether it was useful to describe physiological acclimation as a form of behaviour, but discussion made it clear that any restriction of the term 'behaviour' to morphological responses alone would be arbitrary. Philip Grime (NERC Unit of Comparative Plant Ecology, Sheffield, UK) commented that physiological acclimation in slow-growing species replaces morphological changes in fast-growing ones because the short pulses of nutrients that occur in the impoverished habitats typical of slow-growing species require a rapid response by roots and cannot be acquired by the growth of new organs.

Having established what plant behaviour is, we must also be clear what it is not. Quite drastic changes in morphology often accompany plant development, such as the transition from seed to seedling, from gametophyte to sporophyte in ferns, from juvenile to mature stages in trees and from shrub to scandent forms in some climbers, but these ontogenetic changes (Box 1) represent the unfolding of a developmental programme where there may be phenotypic plasticity in the timing of the change but not in its nature (Tsvi Sachs, The Hebrew University, Jerusalem, Israel). Thus, the timing of seed germination is invariably sensitive to environmental stimuli (Yitzchak Gutterman, Ben-Gurion University, Sede Boker, Israel), but germination itself is a manifestation of development, not behaviour.

Maxine Watson (Indiana University, Bloomington, USA) described the clonal growth of mayapple (*Podophyllum peltatum*) in which the 'decision' whether a particular node will develop a vegetative or a sexual shoot is made between one and two years before the shoot appears above ground. In this and many other such cases of organ preformation, the developmental programme of the plant severely constrains its scope for behavioural response. In mayapple, the vegetative/sexual switch is mainly controlled by the internal resource state of the plant, but this of course has an environmental component. Decision-making in animals also involves an interaction between internal states and external cues.

It is one thing to demonstrate that a plant behaves in a certain manner, but quite another to establish that the behaviour enhances fitness and is adaptive. Johanna Schmitt (Brown University, Providence, RI, USA) described her work (in collaboration with Susan Dudley and Kathleen Donohue) with inbred lines of the annual plant *Impatiens capensis*, which elegantly demonstrates that the elongation response of this plant to shade from vegetation increases fitness at high density but is costly when plant density is low. A recent reciprocal transplant experiment has demonstrated that such density-dependent selection is stronger in an open site than in a woodland environment, supporting the hypothesis that genetic differences observed between lines from the two populations are adaptive. This experiment also permitted a direct test for costs of maintaining the ability to elongate in the woodland environment.

Peter van Tienderen (Netherlands Institute of Ecology, Heteren) described selection experiments with the rosette herb *Plantago lanceolata* sampled from a pasture population with short leaves. Plants selected for long leaves under simulated shade also had many of the other characteristics of plants found in hayfields where the vegetation is taller than in pastures,

Box 1. Definitions

Acclimation: Reversible physiological changes that help maintain the functioning of an organism under changed environmental conditions.

Behaviour: Phenotypic plasticity expressed within the lifetime of an individual.

Foraging: Behaviour that enhances resource acquisition.

Ontogenetic change: Progress from one developmental stage to the next where the stages are fixed and do not have alternative phenotypes.

Phenotypic plasticity: The response by an organism to an environmental stimulus.

Potentiation: The effect of an initial stimulus in evoking a stronger response the next time it is received.

including larger seeds and reduced germination in the shade. Furthermore, plants from this line showed an increase in survival and reproduction when transplanted to a hayfield environment.

The elongation response in *I. capensis*, *P. lanceolata* and other plants is cued by the ratio of red to far-red light (660 nm to 730 nm) which is reduced at high density because leaves selectively absorb red light. The cue is sensed by photochromic molecules (phytochromes). Five distinct phytochromes are known, with some division of labour amongst them in the particular light responses that they control (Harry Smith, University of Leicester, UK). The phytochrome gene family has evolved through a process of gene duplication that appears to have increased the sophistication of plant responses to light from plants with few *PHY* genes to those with more. The molecular, genetic and functional study of this system in *Arabidopsis thaliana* is very advanced and offers the best model system for the understanding of plant behaviour at a molecular level. A phylogeny of the genes in *Arabidopsis* and related species may also soon produce the first phylogenetic description of how some important aspects of plants' behavioural responses to light and the presence of neighbours have evolved (Massimo Pigliucci, University of Tennessee, Knoxville, USA).

Graham Bell (McGill University, Montreal, Canada) discussed the environmental conditions under which natural selection favours a few phenotypically plastic

generalists over many genetically differentiated specialists. This question is not only relevant to the evolution of phenotypic plasticity, but also to the fundamental issues of the maintenance of genetic variation and the coexistence of species. Bell described selection experiments with cultures of the unicellular alga *Chlamydomonas*, which is a facultative heterotroph able to live in the dark if supplied with substrate and which exhibits phenotypic plasticity between individuals. In an environment that varied spatially between dark and light conditions, *Chlamydomonas* cultures evolved a diversity of dark- and light-adapted specialists, but in temporally varying environments that alternated between light and dark phases, the cultures evolved phenotypically plastic generalists. Such results are sensitive to the periodicity and duration of temporal variation and to the grain of spatial variation in the environment.

There are limits to the benefits that phenotypic plasticity can confer and Thomas Givnish (University of Wisconsin, Madison, USA) described a good example of how such limits could result in a switch in competitive advantage and a zonation of species with different growth forms along gradients of water depth in lakes. In the shallow water around lake fringes, emergent species overtop and outcompete floating and submerged species, but as water depth increases the cost of the longer and longer support structures required by emergents increases to the point where floating species, such as water lilies, whose

leaves are supported by buoyancy have a competitive advantage. As water depth increases yet further, the petioles that tether a lily's leaves to its roots must also get longer and this occurs at the expense of allocation to leaves. At their limit, these species are finally replaced by submerged species with short, less costly petioles.

The participants at this meeting represented at least three different approaches to phenotypic plasticity in plants: the physiological, the ecological and the genetic. The meeting was notable for bringing such a diversity of approaches together under one banner, but it was apparent that there is not yet a community of identity among workers in the field. I took away the impression that in the future we need to solve at least two problems of integration. How do plants physiologically integrate the locally determined behaviour of their parts creating a behavioural strategy for the organism? And how do we create an integrated discipline for the study of this subject? Perhaps the answer to the second question holds the solution to the first, and this meeting represented a first step towards the creation of a new discipline.

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Space invaders: modelling the distribution, impacts and control of alien organisms

Invasive alien plants and other organisms have become a worldwide problem, threatening ecosystem functioning, biodiversity, the integrity of species, water availability and the attractiveness of natural areas. The management of aliens is an expensive business in developed countries. Economically important plants, such as *Pinus* spp., have become invasive in some ecosystems. In developing countries, aid agencies recommend the planting of the very species that conservation agencies spend time and energy trying to control. Gardeners and plant nurseries import and export seeds of invasive plants without concern about the consequences. Causes of conflicting behaviour include inadequate policies, inability to predict

which plants will be invasive and differences in perceptions.

The first SCOPE (Scientific Committee on Problems of the Environment) programme (1984–1986) sought to provide answers to some fundamental questions: (1) what factors determine whether a species is an invader or not, (2) what site properties determine whether an ecosystem will be relatively prone to invasion, and (3) how should management systems be developed using the knowledge gained from answering these questions? This programme stimulated a large amount of new research on the ecology of invasions, resulting in several important books and numerous papers. Even so, however helpful the insights gained from this programme

may have been, they have not really fed into meaningful control programmes. At a global scale, the problem with invasive alien plants and animals has increased phenomenally over the past two decades. There is still a serious lack of essential technical tools to deal with the problem.

With these facts in mind, the Global Invasives Strategy Project, under the auspices of a new SCOPE programme, aims to (1) draw together the best management approaches for pest prevention and control and make these readily accessible to all nations, and (2) lay the groundwork for new tools in science, information management, education and policy that must be developed through collaborative international action. Project leaders in 11 topic areas will work with international teams to complete these tasks over the two-year (1998–2000) project timetable. The results of this work will be disseminated via published reports, international meetings, and, especially, through a network of information exchange and training to be