The individual basis of plant diversity

G.R. Squire, J. Bown[1], J.W. Crawford[1], B. Marshall, G.W. Wright, E. Pachepsky & D.L. Trudgill

The concepts discussed in the preceding article on microbial diversity apply equally to plants, but the advantage of plants as experimental subjects is they can often be defined as individuals, either in their natural locations or as accessions removed and characterised. The same problems with the species as the unit of diversity remain, however[1], and limit our understanding of diversity and function in variable populations. Our approach to this is to treat the individual as the basis of diversity.

Plants are examined in terms of trait 'space' comprising many axes that define an individual's phenotype. At any time, an individual occupies a point in the space, and during its life cycle moves along a unique trajectory through the space. Groups of plants or populations form a collection of trajectories through time, which meander or contort as the individuals interact and are buffeted by pests and environment. The population is therefore an intermeshing net of trajectories. The trajectories have potential to exchange information at reproduction. The biological diversity at any time is described as the distribution of individuals across trait space.

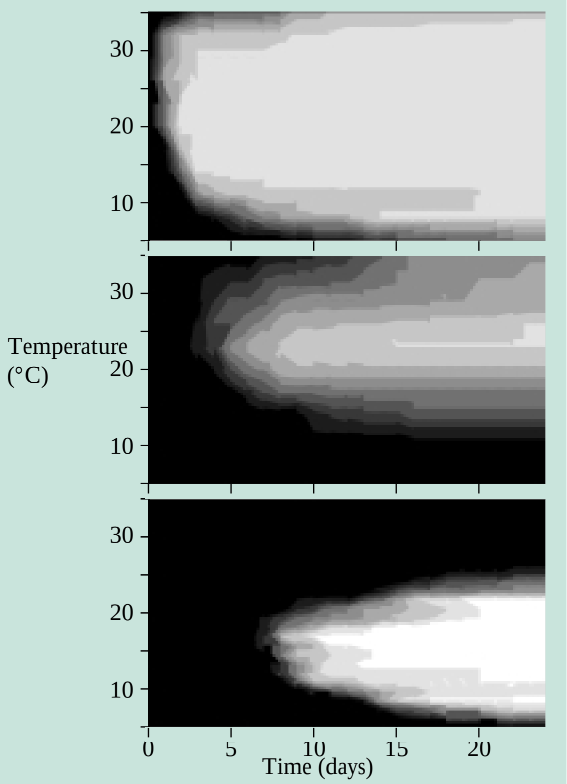

Figure 1 Time-temperature trait maps for germination of *Anisantha sterilis* (upper), *Brachypodium pinnatum* (middle) and *Saxifraga tridactilytes* (lower). From re-analysis of data supplied by the Unit of Comparative Plant Ecology, Sheffield.

The simple trait space of germination The concepts can be illustrated for the primary step of germination, which is commonly governed by conservative relations between time and temperature. Data collected and supplied by the Unit of Comparative Plant Ecology, Sheffield were used to construct a space of time, temperature and % germination for a range of species. In a preliminary survey[2], the weeds and other wild plants examined displayed rate-temperature curves similar to those found many times previously with crops. In principle therefore, a wide range of cultivated and wild species could be examined by a similar analysis. A deeper re-analysis of the data revealed time-temperature trait maps (Fig. 1) that are highly characteristic of a species or population. The contrasting *Saxifraga tridactylites* and *Brachypodium pinnatum* represent extremes in the flora, each differing in the time to first germination, the amount of non-germination indicated by the grey shelves in the maps, the temperature at which seeds do and do not germinate, and many other features, especially the spread of trait values within the population at any temperature or time. In contrast, the grass weed *Anisantha sterilis* (= *Bromus sterilis*) displays a very wide map, germinating near to 100% over much of the ranges of temperature and time.

The grey shelves are particularly important for population dynamics over long time scales, since they generally indicate regions of trait space where seeds do not germinate, but are generally alive in a condition of induced dormancy. This 'drop-out' from the actively developing population, as conditions move away from the optimum, is an indicative feature of populations. The drop-out phenomenon occurs in later developmental stages also, and has important implications for how we examine a net of trajectories.

We chose to examine drop-out in the common weed, feral oilseed rape, since it gives rise to overwintering

[1] University of Abertay Dundee (J. W. Crawford from February 2000)

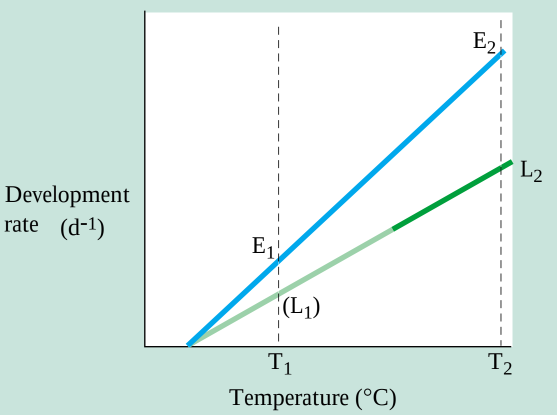

Figure 2 Representation of rate-temperature analysis of developmental stage, to illustrate the drop-out conundrum. Four phenotypes are indicated for early (E) and later (L) developers at two temperatures (1 and 2) - E1, E2, L2 and (L1); (L1) is in parenthesis because it would only have existed at that location if it had developed, but it had dropped out at low temperature. The question is - do non-developers, in this instance (L1) at low temperature, occupy a specific ranking in the population (e.g. L2) at optimal temperature?

and persistence in the soil if the seeds experience sub-optimal temperature or reduced water potential during imbibition. The trait maps in oilseed rape were analysed and quantified by converting time to a rate (1/t) and fitting curves of 1/t on T for a range of percentiles[3]. We then posed the question as to whether seeds that dropped out of the germination map at sub-optimal temperature arise from any part of the map at optimal temperature. For instance, did slow seeds at optimal temperature drop out at low temperature (Fig. 2). This seemingly mundane question has great implications for population biology and for tracing trajectories in particular. Usually, ecophysiologists compare a mean trait value at one developmental stage with a mean trait value at a later stage, and assume that the collection of individuals nearest the mean or mode is the same at both stages. Clearly, if they are not, because some have dropped out, then we are not relating like to like. In this instance, both circumstantial and molecular evidence confirmed that slow individuals at optimal temperature were indeed more likely to drop out at sub-optimal temperature. Variation between varieties and other seed lots was also shown in the physiological and molecular parameters.

Structure independent of composition in plant communities? Such germination and dormancy traits have great importance for the arable seedbank community - the populations of buried seed that provide both a reservoir of diversity and future weed problems - which is one of the Unit's main foci. As already admitted, the balance of species is several steps removed from the detailed behaviour of individuals. Nevertheless, a frame is sought that enables us to move between and compare communities that consist of different species. Recent opportunities for synthesis in this area arose following completion of two major experiments on ADAS farms. The experiments examined the effect on a range of economic and biological indicators of less intense rotations that included more fallow and less use of herbicide. SCRI's role was to examine the seedbank. The dominants, and in fact most of the species, were different at the sites, but measures quantifying the communities displayed a consistent response to reduced inputs at the three sites. As inputs decreased, the mean and standard deviation of the species-abundance distribution both increased (Fig. 3). With abundance on a log scale, this meant that for each new species that increased above the detectable level, the common species produced many more individuals[4]. It was impossible in these circumstances to increase the number of rarer species without causing a potential major weed problem. The study generated ideas about the way production and arable diversity are to be balanced, i.e. there is an optimum point in the system that management should aim for, and is a constructive example of how SCRI's work on population biology can contribute to more applied, farm-scale experiments in the UK. The primary need for policy and management now is to put a price on rarity and on habitat for wildlife that can be directly compared with yield and profit.

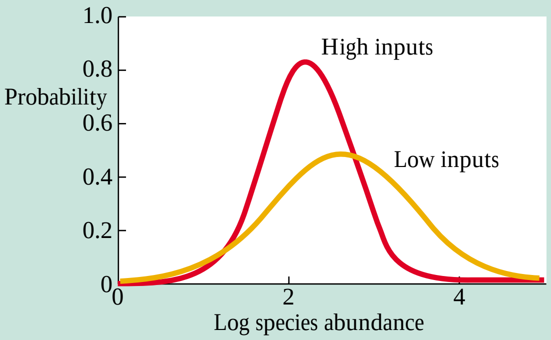

Figure 3 Shifts in species abundance curves in the arable seedbank in response to decreasing chemical inputs. Note abundance is on a log scale.

Modelling trait space in physical space The trait map of germination provides the starting grid for the net of trajectories that describe later development and

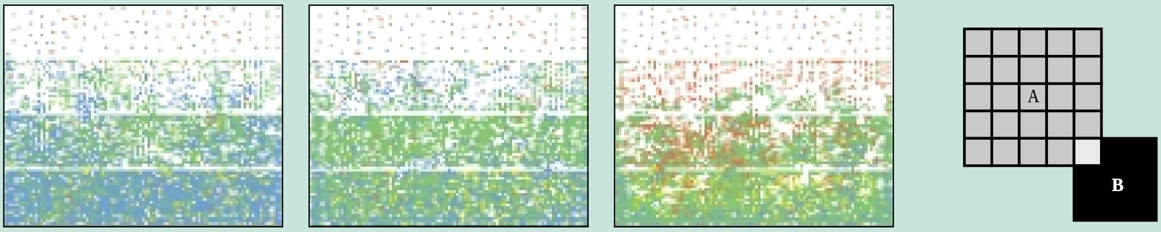

Figure 4 Spatial output of modelled plant types, showing patterns that give a clue to the arrangement of individuals and species in the field[5]. The resource is arranged in four bands, increasing in amount from top to bottom of each map. The three maps show the temporal change in proportion of four interacting plant types. Blue (rapid growth, early reproduction) gives way to Green then Red (slower growth, greater resource storage). Inset shows two individuals interacting through their resource capture area. The spatial patterns can be analysed to reveal 'species-abundance'and 'species-area' curves typical of much larger ecosystems.

that must ultimately, over several generations, give rise to the community-scale features of the seedbank and other vegetation. It is relatively easy to measure early development in a population and again the number and abundance of species. It is also relatively easy to measure the trajectories of individuals taken from systems and grown *ex situ*. The difficulty is that the trajectories of only a finite and quite small set of individuals can be measured so as to trace the links between the physiological trait and the community of species *in situ*. Some of the experimental designs in which these links are traced in annual populations have been described in previous reports. However, it is very difficult, if not impossible, to trace the links in perennial systems. Yet questions are repeatedly asked of these links: for instance, how does the introduction of a new trait, in say a new crop cultivar or weed, propagate through the populations to alter the productivity and diversity of the vegetation as a whole; and how does a restriction applied 'top-down' to the community, perhaps a change in micro-environment, agronomy or grazing intensity for instance, determine the types and numbers of individuals that can co-exist in that community? The challenge, then, is to show how a general collection of individuals defined by a set of traits form a community described by a set of species.

To probe this complexity, we have developed unique mathematical models of communities in which individual plant types are defined by physiological traits that govern the way they interact with their environment (Fig. 4). The traits have been carefully chosen, based on a wealth of wider research in plant ecophysiology and growth analysis in many environments. They describe the basic processes of uptake of resource, allocation of resource to plant parts, reproduction and dispersal. The environment is defined by a resource-base that itself can be assigned various characteristics such as holding capacity and replenishment rate. The 'plants' grow and interact with each other through the resource base. The basic model[5] was designed so that its traits could be parameterised by data from experiments on plant development and growth. This further, major step forward was achieved using data from physiological work carried out at MLURI on nitrogen cycling and carbon accumulation in the grassland species *Rumex acetosa*. This co-operation is an example of the melding of physiology and modelling through the Co-ordinated Programme in Vegetation Dynamics (a SERAD-funded initiative). Comparable work has defined the seedbank traits of common arable weeds such as *Poa annua*, *Stellaria media*, and *Chenopodium album*, and aims to reconstruct the seedbank community.

Running the model with plants types selected from the *Rumex acetosa* trait space, revealed that most types were quickly exterminated, after which a set of types then coexisted for long periods. Analysis of the abundance of these types revealed systematic patterns highly reminiscent of those in large ecosystems. It was as if the individual variation in one species was arranging itself over two-dimensional space in much the same way as the different species in a grassland, an arable field or an archipelago. This finding gives the stimulus to much further work on real populations. It means that quantitative hypotheses can be set on, for instance, the trait distributions – the diversity among individuals - that should be measurable at a small scale in the real environment.

Searching trait space with a genetic algorithm This modelling approach can also be the basis of a 'search' for the most appropriate plant community in a given situation. A genetic algorithm search technique was therefore examined for its usefulness in this respect[5]. A plant type is identified by a letter (A, etc., a number of traits (1, 2, etc., where 1 might be maximum resource uptake, 2 might be distanced proportioned uptake, and so on) and a trait value (a, b, c, etc.). The total trait space that plants can inhabit in the search is defined, as in physiological studies, by all the traits and their values. A group of plant types, in effect a community, is represented by a string of trait values, which in search terminology is known as a 'chromosome' (Fig. 5). The community can be pre-defined to represent known functional types or selected randomly from trait space.

The spatial model is then parameterised for the community and whatever resource base is required. The aim of the search is to maximise some aspect of 'fitness' of the community, which could be some measure (for instance) of resource in the plants, and abundance distribution or period of coexistence. The model is run separately for a number of 'chromosomes' (communities), each of which has a fitness parameter assigned to it on the basis of its performance. When the communities have run their course, they can be subject to genetic operators that bring about change through 'recombination' (where the strings of trait values cross over) or 'mutation' where the value of one trait might change independently of the rest, or even the introduction of new trait values. Recombination, followed by re-running the model, can be made between communities that have been successful in previous generations as a means of searching for a community of maximum fitness (Fig. 5).

Experience with the search so far suggests that optima in trait space – combinations of individuals that give high values of fitness of the community - are rare, but extended searches might allow the identification of areas of trait space that generally contain optimal solutions. Approaches such as this enable us to get a feel for the potential importance of different plant traits,

In the genetic algorithm search technique, populations or communities are represented by 'chromosomes' or strings of trait values (see text). The following simplified example uses 13 original plant responses collapsed into six traits (1 to 6) to reduce the dimensionality of the search space. For the purpose of demonstrating the technique, each of the traits is given 16 possible values (a to p), again limited for simplicity. Therefore the symbols in the trait space are:

Plant types: A to J (10). Traits: 1 to 6 (6). Trait values: a to p (16)

The chromosomes are of the form

$C_{A1}\ C_{A2}\ C_{A3}\ C_{A4}\ C_{A5}\ C_{A6} \qquad C_{B1}\ C_{B2}\ C_{B3}\ C_{B4}\ C_{B5}\ C_{B6}\ \ldots\ldots\ldots$

Where C_{A1} represents the first trait (resource uptake), for plant A, C_{A2} the second trait (distance proportioned uptake) for plant A, through the four other traits for plant A, and all traits for plant B, and so on up to plant J. An example chromosome for a set of ten plant types is

pijfpc hnfjbk ngkhnp jilhog ijhepd ehechm miedhk acmhjj gkpdic adfgck

The plants are separated by spaces, so the first plant is defined by the sixteenth (p) value of trait 1, the 9th (i) of trait 2, the 10th (j) of trait 3, etc. Each 'chromosome' represents a community of 10 plant types. The fittest community in this example is defined as the one that maintains all plant functional types for the longest period in coexistence. The upper limit of time was defined as a 1000 cycles, so that fitness was an integer between 1 and 1000. The model is run for a number of chromosomes (communities), 20 in this instance, and the ones that perform best according to the criteria then 'recombined' by cross over of the strings of characters at assigned points. The runs shown below identified one very fit community that evolved rapidly. The mean fitness of all 20 communities lagged behind because of the diversity of solutions. The error bars indicate the standard deviation in fitness values at each iteration.

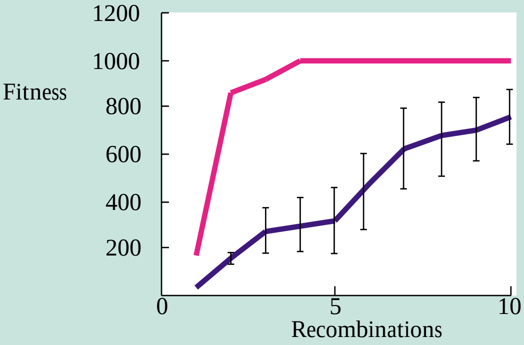

Figure 5 Searching trait space with a genetic algorithm (adapted from Bown[5])

and might enable us to assess the consequences of introducing new traits in plant varieties or invading species.

The model is now being parameterised for seedbank annuals, where a second 'layer' is needed for the dynamics of the buried seed. More detailed and more targeted experimentation is being planned to test the specific hypothesis that the approach is indicating. The concepts and associated analysis are now well developed for plants, but could in principle be applied to invertebrates. The ultimate aim is to treat the system as a collection of individuals of whatever taxonomic group.

References

[1] Squire, G.R. & Crawford, J. (1997). *Annual Report of the Scottish Crop Research Institute for 1996/97*. Scotttish Crop Research Institute, Dundee, 121-124.

2 Trudgill, D.L., Squire, G.R., & Thompson, K. (2000). *New Phytologist* 145, 107-114.

[3] Marshall, B., Dunlop, G., Ramsay, G. & Squire, G.R. (2000). *Journal of Experimental Botany* 51 (in press)

[4] Squire, G.R., Rodger, S.R. & Wright, G. (2000). *Annals of Applied Biology* 136, 47-57.

[5] Bown, J.L. (2000). *Ph.D. Thesis*, University of Abertay, Dundee.