The role and importance of canopy heterogeneity

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Most crops grown in western agriculture are monocultures; genetically identical individuals grown over extensive areas. This is an effective strategy for maximising yield in a high input, high profit, low risk agricultural system. However, where profits are minimal and impact on the environment of the inputs is 'costed in' then the strategy may be inappropriate. Genetic uniformity leads to vulnerability if the cost of inputs is too high to maintain profitability as such monocultures have less resilience to stresses whether from climate, weather and soil conditions (abiotic factors) or pests and pathogens (biotic factors), whereas heterogeneity leads to increased resilience to stress, so lowering risk.

Most natural ecosystems comprise a great diversity of genotypes at all taxonomic levels, each occupying a niche with both spatial and temporal attributes in dynamic balance. By inference single genotypes do not exploit the environmental resources available to them as effectively. While there is great potential for breeding single genotypes to much more effectively utilise resources available in the absence of competition, the potential is constrained by the total genome complement available in a single individual, excluding exploitation of temporal and spatial heterogeneity between individuals. Furthermore, selection to exploit particular resources frequently results in loss of ability to exploit others. In a heterogeneous community, by definition there is more variation present and therefore more potential for optimum response to changes in resource availability. Modern varieties selected for maximum resource exploitation in intensive agriculture may not be successful in heterogeneous communities if appropriate competitive traits have been lost. The nature of the interaction between plant genotypes therefore needs to be understood in order to ensure enhanced resilience to stress and beneficial productivity in both single genotypes and heterogeneous combinations.

Plants do not simply compete with other plants. Plant leaves and stems create an environment or canopy in which many other organisms live. This environment can be very heterogeneous, providing niches for a diversity of organisms from other plants and plant saprophytes, to parasitic, saprophytic and symbiotic arthropods and microorganisms. The environmental niches will vary in traits such as wetness, humidity, light quantity and quality, nutrients, temperature and morphology. Changes in canopy structure can result in considerable differences in the community of organisms they support.

Rhynchosporium secalis is the fungal species which causes 'scald' or 'leaf blotch' on barley and is common in many regions. It is splash-dispersed, first from the soil where spore inoculum survives on crop debris, then from leaf to leaf as it forms necrotic lesion and sporulates. An open canopy will enable rapid transmission by rain splash up the plant. Epidemic progress can be reduced by molecular and morphological mechanisms. Genetic resistance results when specific genotypes (races) of the pathogen are recognised by plant defence genes causing induction of resistance expression mechanisms. However, if the host plant has only a single recognition gene then the pathogen will mutate to produce new races not recognised by the pathogen. Multiple host plant genotypes with many different recognition genes prevent this becoming a problem, particularly as complex races capable of avoiding all recognition genes are normally less 'fit' and will therefore not survive as well. Morphology can be manipulated by affecting plant height and leaf angle, and by providing a complex canopy structure disrupting vertical splash dispersal pathways for pathogen dispersal. Multiple contrasting morphological types are particularly effective in this.

In a natural community plant genotypes are very unevenly distributed in terms of numbers and spatial distribution. Understanding these patterns is critical to understanding the stability or resilience of the system. To mimic this in order to obtain the benefits in agriculture we are limited by available genotypes and technology such as seed drill design. However, we can at least vary the component number and the proportions of the components. It may also be possible to distribute the components in an even or patchy structure at a range of scales. Patchiness may be important in creating 'refuges' for pests not adapted to multiple components of the mixture, and the size and distribution pattern of such refuges, particularly their connectivity, may be critical for stability of the system. The optimum structure will depend upon the 'objective' and, for example, for disease control it will differ

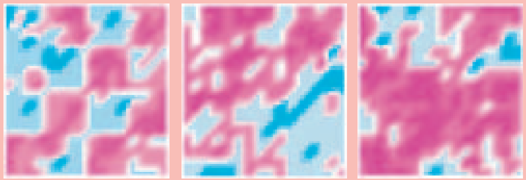

Figure 1 Disease progression (*Rhynchosporium secalis*) over successive times showing lessening effect of underlying 4 x 4 plot host (barley) planting pattern.

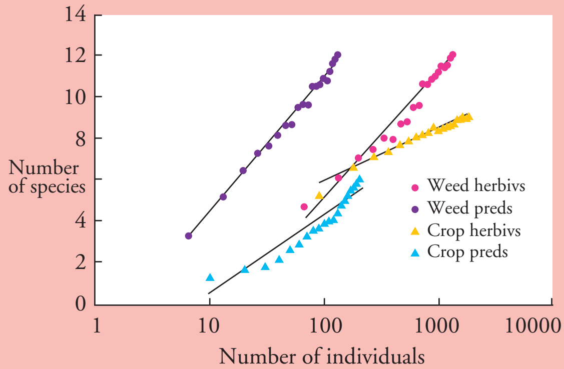

Figure 2 Figure showing greater diversity (steeper slope of the species-accumulation curve and higher intercept) in insect herbivores and predators associated with weed flora (heterogenous structure) compared to those insects associated with the crop vegetation (homogenous structure, OSR)

depending upon the dispersal characteristics of the pathogen and its population structure.

The structure of a crop canopy has the potential to influence the invasion, establishment and spread of insects through a field. Homogeneous canopy structures that have high levels of connectivity between stems and leaves may allow a rapid spread of herbivorous insects, thereby increasing the likelihood of pest populations reaching threshold levels. In addition, the dynamics between pests and their predators may be destabilised by this rapid population growth due to the lag in development of predator populations relative to their prey. If heterogeneity in canopy structure causes a reduction in the apparency of the plants to the herbivores, the plants have a refuge from insect attack and the population growth of the pest may be reduced. Introduction of sufficient heterogeneity in canopy architecture to impede the movement of herbivores without significantly affecting that of the predators may enhance the potential for natural biological control.

Within-field heterogeneity is not only an important consideration for management of pest populations, but also for management to increase plant and invertebrate diversity. Increased canopy heterogeneity can result in greater diversity of associated herbivores and their natural enemies through the provision of a range of niches where direct competition for resources can be avoided. We have shown that the diversity of insects associated with the weed flora was greater than that associated with crop plants, and the diversity of predators was greater than that of their prey. In general, weed plants hosted up to ten times as many invertebrates per gram of plant material compared to the crop. Within-field plant diversity is therefore important for management of pests and to enhance diversity at higher trophic levels. This may be achieved either by allowing the development of the weed community to within acceptable limits according to the competitive ability of the weed population, or by creating a mixture of a range of different crop genotypes.

Below ground, soil resources of water and nutrients are very patchily distributed. As much variation is often reported within the root system of a single plant as exists across a small field. Plants compete with their neighbours for these resources, and their effectiveness in doing so depends on their ability to grow a root into the resource patch, and the relative sink strength of the root for the resource. Hence, the interaction between root distribution, soil resource distribution, and the uptake efficiency determines the ability of plants to uptake water and nutrients, resulting in effects on the above ground canopy environment. We are studying both the genetic variation in root traits (Forster et al., 2003), and modelling the effect of root distribution and soil structure on uptake. There is potential to choose appropriate complementary root systems within a crop mixture to give a robust yield, whilst minimising nutrient loss.

In the context of agriculture, compromises have to be reached between environmental or ecological considerations and the economics of food production. A yield of the quantity and quality required by end-users must be delivered in a timely and cost-effective way. However, the customer is not always right, and in some instances a compromise in some of their requirements may give them unforseen benefits in other areas whilst also satisfying the requirements of others further up and down in the supply train. We addressed an example of this in a previous article (Newton & Swanston, 1998) showing how better malt can be produced from barley mixtures. Another example is illustrated by the difficulty of combining desirable traits within a single cultivar. The yield of alcohol obtainable from a sample of malt is determined by two factors, extract (the total soluble material) and fermentability (the proportion that yeast can convert into alcohol). Both factors are controlled by a number of genetic factors and, on one chromosome segment, desirable expressions for the two characters were shown to be linked in repulsion (Meyer et al., 2001). In this case, selection for optimal levels of extract could mean inheriting a gene that adversely affects fermentability whereas they can be combined in mixtures. This also illustrates the potential value of trait-associated markers in the the design of mixture.

In conclusion, heterogeneity in canopy structure should be seen as an asset to be exploited to achieve practical, sustainable agriculture. As long as variation around an acceptable mean for the harvested product is comparatively small, end-users will not detect significant problems and if the buffering effects of mixtures reduce the environmental component of variation, acceptable levels of homogeneity should be readily obtainable. The reduction in requirements for pesticides from more balanced crop ecology, and the productivity gain from better resource utilisation, are self-evident benefits.

References

Meyer RC, Swanston, JS, Young GR, Lawrence PE, Bertie, A, Ritchie, J, Wilson A, Brosnan, J, Pearson, S, Bringhurst, T, Steele, G, Aldis, PR, Field, M, Jolliffe, T, Powell, W, Thomas, WTB, 2001. A genome-based approach to improving barley for the malting and distilling industries. Project Report No.264, Home-Grown Cereals Authority.

Forster BP, Bengough G, Ellis RP, Thomas WTB, Clark S, Gordon D, El-Menaie H, Keith R, Waugh R, Hedley P, 2003. Genomics of the root-soil interface. Scottish Crop Research Institute Annual Report for 2001-2, pp. 154-154.

Newton AC, Swanston JS, 1999. Cereal variety mixtures reducing inputs and improving yield and quality - why isn't everybody growing them? Scottish Crop Research Institute Annual Report for 1998/99, 55-59.