

Summative address: One

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In a college, there is a large temptation to browse in other people's book-cases. I found, thus, that Jules Verne quoted Linnaeus with the catchy sentence 'Nature did not make fools'*. This states, bluntly, what John Harper tried to get across in more polished form in the Keynote paper, emphasizing that the behaviour of plants is determined by considerations of individual fitness and that there is nothing in the process of evolution that has any aspect of community behaviour as a goal. Hence, the most noted ecologist at the Symposium argues that ecology does not exist, and this may be a blessing in disguise for two reasons. In the first place, it justifies the existence of agricultural and environmental scientists with their human and perhaps foolish goals of productivity, yield, efficiency, diversity, stability and beauty and, in the second place, it justifies the approach of simulation, the art of building models that bridge the gap or eliminate the discord between analyst and holists, as noticed by Harper.

The basic elements of simulation models are, then, more or less formulated in accordance with the opinion of the analyst, whereas the understanding, or lack of understanding, of the problems of the holist is evaluated by qualitative and quantitative comparison of the behaviour of the real system and the model. There are many analysts in biology, and those engaged in model building according to the 'bridge concept' are often leaning over backwards in the attempt to remain on speaking terms with as many people as possible. This leads to models of considerable complexity, the tragedy being that complexity usually does not pay for the holist. Perhaps good examples are the production, transpiration and photosynthesis models mentioned by Ludlow, and Stern and Rhodes. The more sophisticated models are indispensable in their attempt to summarize the knowledge of the plant physiologist, the micrometeorologist and the soil scientist, and to compare the relative importance of the contributions of these various fields. However, often the holist may be satisfied with a simple model that assumes a simple Blackman type of photosynthesis response, a random arrangement of leaves, 30 per cent root growth and a respiration rate that is governed by the composition of the structural material in terms of carbohydrates, proteins and fats. Even this model may frequently be replaced by the simple statement that closed canopies of C₃-type plants, during their grand period of growth and when well supplied with water and nutrients, will accumulate dry matter at a rate of about 200 kg ha⁻¹ day⁻¹.

'But who wants dry matter only?' was shouted from the back benches during the discussion. Certainly not our holist *par excellence*, the grazier. He wants a reasonable quantity and quality of fodder throughout the year from persistent pastures that are heterogeneous in time and space — and this with the least effort possible. Whether advantageous or not for plant species, farmer or naturalist, this means

*'Twenty Thousand Leagues under the Sea'

that plants occur in pastures under a situation of competitive interference and this exerts its influence on the botanical composition of the stand and the gene population within species themselves. One of the highlights of this Symposium was indeed Antonovics's paper, in which the rapid genetic changes that occur in competitive situations were illustrated and their importance emphasized.

On the other hand, the phenomenon that differences between species are often magnified when they are grown in competitive situations largely escaped attention. For instance, Turner and Begg, illustrating the difference in response of species towards increasing water potential, remark during their paper that they could not judge the importance of their observations. However, with their data, and that of others, it is possible to classify plant species as *spenders* or *savers*. Plants are *savers* of water if they react sensitively to even relatively slight water stresses with decreased foliage growth and closure of stomata. Being a *saver* may be advantageous under relatively dry conditions because the plants can mature and form seed within a developmental period of normal duration, so that they may profit from late showers. *Spender* properties, on the other hand, are advantageously associated with rapid development. In many situations, both types of plants have the same limited amount of water available, and since transpiration coefficients (within either the C₃ or C₄ group of plants) are not very different, yields of *spender* and *saver* are then about the same. However, when grown in competition, the water saved by the *saver* for future use is rapidly consumed by the *spender*, so that the latter has a very pronounced competitive advantage. The analogy with human society is noticed, but unintended on my part.

Another example is the barley-oats mixture, mentioned by Snaydon (Chapter 17) to illustrate the advantage of mixtures. The explanation is known. Within a wide range, the growth of oats is hardly affected by the pH of the soil, but root growth and, thus, the early development of barley, is hampered on soils that are on the acid side. Hence, when barley is grown with oats, the competitive advantage of the latter increases drastically with decreasing pH. In large parts of Jutland (Denmark) and in parts of Great Britain there were fields on which the pH varied erratically from place to place. When sown with barley only, this resulted in an uneven stand. But, sown with oats, barley takes over on those parts of the field with near neutral pH, and oats claim the acid parts, so that the yield of the mixture is higher than of barley alone. Sowing only oats is no solution, since barley is the better money-maker. The best solution would be to sow barley in the parts of the field with normal pH and oats in the parts with low pH, but either advance knowledge of the pH is not available or it could lead to an over complicated sowing pattern.

Apart from this, the 1000 kernel weight of the oats in the mixture is also slightly higher because the earlier-ripening barley leaves some water and light solely for use by oats during the last week of ripening. As potato-eaters, we tried in Wageningen to exploit this difference in time of growth by mixing early and late potatoes. However, it appeared that the total yield was too often mainly governed by the total amount of water and nutrients available during one season, so that the mixture hardly outyielded the monocultures.

As emphasized by Trenbath, in Chapter 10, the possible advantage of mixture over monoculture is conveniently judged in a replacement series. Species are

grown in monoculture and in mixtures of various composition, but so that the sum of their relative frequencies equals one (relative frequency is defined as the seed rate of one species in the mixture over the seed rate of the same species in monoculture). There is no advantage in using the mixture when it appears that the relative yield total (R_{YT}) (defined as the yield of one species in the mixture over the yield of this species in monoculture plus the same ratio for all other species in the mixture) equals one.

There has been some confusion at the Symposium about the interpretation of the results of such series. Rossiter, for instance, assumes that there is no competition when the yields of both species in a replacement series are proportional to their seed rates (e.g. as in Chapter 11, Fig 2f). But this is only true when the relation between yield and seed density is also linearly related in a simple density-of-sowing experiment within the range covered by the replacement series, or, in other words, for replacement series at low overall seed densities. Since the yields of the monocultures and the slope of the yield lines are not the same, this implies that one species could still gain on the other when the harvested seed from the mixture is resown or, in other words, that natural selection is operative even when there is no struggle for life (i.e. competition). In general, there is a diminishing return in yield with increased density of sowing of a species, and then a linear relation between yield and seed rate in replacement series shows that both species competed with equal strength for the complex of water, nutrients and light involved in their growth.

Another problem of interpretation, illustrated in Snaydon's lecture, concerns the importance of the yield of a diallel mixture being higher or lower than mid-parent yields, i.e. the average of the monocultures. The first situation occurs when the highest yielding species in monoculture crowds most effectively for the complex of growth essentials, so that its yield function shows diminishing returns in the replacement series; the second situation applies when the reverse occurs (e.g. Chapter 11, Figs 2e and d, respectively). With $R_{YT} = 1$ the yield of any mixture is intermediate between the two monocultures. In both situations it is possible to sow one part of a field with one species and the other part of a field with the other in such a way that the yield of both species is the same as in the diallel mixture sown on the whole field. Obviously, it is of no practical importance whatsoever, whether diallel yields are higher or lower than mid-parent yields. One may argue that it is not known *a priori* how the field has to be divided between both species to achieve a certain yield of each species but, in that case, the composition of the harvested diallel mixture is not known either.

When $R_{YT} > 1$, it is still possible to obtain, for one of the species, the same yield as in the mixture by sowing part of the field with that species only. But then it appears that a larger part than the remainder has to be sown with the other species for it to achieve the same yield as in the mixture. Obviously, only where $R_{YT} > 1$, and the yield of both species in monoculture is about the same, will the mixture yields be higher than either monoculture.

Relative yield totals are often > 1 in grass/legume mixtures, which have been discussed at length at this Symposium. With these mixtures a stable equilibrium may be reached: with little grass and much legume in the mixture, the grass is well supplied with nitrogen and may be strong enough to replace the legume, but with

much grass and little legume the reverse may occur. Unfortunately, the equilibrium situation is, in general, not the situation where the highest yield is obtained, which is in agreement with Harper's conclusion that there is nothing in nature that has productive efficiency as its goal. Where monocultures of the legumes yield the most, we should question, with Rossiter, why grasses are desirable at all in legume/grass mixtures. Apart from aspects related to the quality of the food, a main argument seems to be that grasses are necessary to keep weeds out. However, if the grass is allowed to grow so vigorously that it can do this job, it is likely to suppress the legume towards a too low percentage in the sward. In passing, I want to be somewhat provocative by remarking that I am less impressed by the performance of grass/legume mixtures than are many Australians, but I would go far beyond my time and space limit in an attempt to work out my doubts

Relative yield totals may also be > 1 , when the species are growing at different times of the season or when the field is non-uniform, examples being given at an earlier stage in this talk. It is sometimes assumed that this is also the case when the roots of one species grow more rapidly and more deeply downwards than the other. However, this situation is closely analogous to that of one species being taller than the other, and leads only to a competitive advantage of the taller-growing and deeper-rooting species.

During the discussion of Trenbath's paper it was remarked that it does not mean much that, in the published literature, the RYT in more than 95 per cent of cases was *c.* 1, because most experiments were done with selected pasture and crop species grown with a reasonable supply of water and nutrients. For this reason, van den Bergh, of the Wageningen group, executed a field experiment on poor health soil, in which 10 species (which were assumed to be adapted to poor conditions) were grown in monoculture and in mixtures. Under these conditions, the RYTs of mixtures in which dicots (*Chrysanthemum*, *Rumex* and *Plantago*) dominated were appreciably higher than one. Since the main growing periods of the species coincided, and the soil was uniformly poor, this result cannot be readily explained.

However, it has been argued by Trenbath that species may differ in their minimum requirement for necessary elements and, by Hall, that the relative competitive ability of species may differ for different elements. Based on similar observations, Braakhekke, of the Wageningen group, is analysing the extent to which the RYT of a mixture is > 1 because of species differing in their minimum requirement for certain elements and/or in their ability for preferential uptake of elements that are most needed. Based on these theoretical arguments he is setting out to show that, even in water culture and in a controlled environment, combinations of species using elements supplied at minimal levels may be found that result in a RYT > 1 . Of course the reverse may occur as well: preferential uptake of the element least needed and a RYT < 1 . It is hoped that these theoretical and experimental studies may throw new light on the discrepancy between current theoretical analyses that suggest, too often, dominance of one species, and the field observation that many species and genotypes coexist for long periods. When I discussed the problem with Harper, he remarked that it should be possible to find, side by side, species with symptoms that point to deficiency of different elements and, since several scientists with sharp eyes and suitable field oppor-

tunities are at the Symposium, it seems worthwhile to suggest a close look for such species.

Recently, several reports, especially from agricultural experimental stations in developing countries, suggest that surprisingly often there is considerable advantage in growing mixtures of species. However, too many experiments are done in which the seed rate of each species in the mixture is the same as in monoculture. The sum of the relative seed frequencies is then two instead of one, which means that the seed density in the mixture is twice that of the monoculture. Since both species respond, in general, to higher seed rates, the RYT is thus > 1 . So far so good, but a mistake is made when it is then concluded that it is advantageous to grow the species in a mixture rather than to grow them at higher density.

In proper replacement series, the RYT may be > 1 under poor conditions, on non-uniform soil, with species that have partly overlapping growing periods or respond differently to diseases and with mixtures that contain legumes. It is, therefore, certainly worthwhile to pursue the possibility of mixtures in situations where yields are low and labour costs are of minor concern, but this should be done on a proper basis.

It may be remarked here that competitive phenomena are illustrative of the general agricultural principle that heterogeneity has to be exploited in low yielding situations, and uniformity in high yielding situations. This principle is related to the S or sigmoid-shaped yield response to most growth factors. The diminishing return at the higher-yield end means that the average of a situation where part of the field is treated sub-optimally and the other supra-optimally is lower than in the case of optimal treatment of the whole field. But at the lower end, it is often better to concentrate the scarce resource on only part of the available surface. Water supply is perhaps the most illustrative example. A winter rainfall of 150 mm, uniformly distributed over the soil surface, leads often to no herbage yield at all, be it only because there is never water enough for germination and early establishment. However, heterogeneous distribution of the same rainfall by local runoff/run-on may lead to germination, establishment and growth of reasonable amounts of herbage on part of the surface — amounts that are worth conserving and sometimes worth exploiting.

The excellent lecture of Rovira (Chapter 7), on the complexity of the rhizosphere, started the usual discussion between believers and disbelievers in allelopathic effects, which was so heated this time that I feel obliged to take a stand. Since replacement series became the fashion, the Wageningen group has been chasing situations in which $RYT > 1$ on the argument that this is sufficient proof of allelopathy. The phenomenon was found to occur in mixtures of *Anthoxanthum* and *Lolium*, the first one being the producer of the allelopathic material, in this case probably a virus carried over to the healthy *Lolium* in the mixture, but not in the monoculture. A more genuine example has been thoroughly analysed by Eussen (BIOTROP, Bogor, Indonesia), who showed that the RYT of mixtures of alang-alang (*Imperata cylindrica*) and maize or sorghum in containers with soil may run as low as 0.65, the growth of alang-alang being the same, but that of the crop plant being much lower than in spacing experiments. Moreover, it was shown that the leachate from the soil on which alang-alang had grown did not affect the growth of alang-alang, but hampered the growth of soil-grown maize. Bio-assay

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and chromatographic techniques have detected the active substance but the chemical formula is not known. Together with field observers who regard alang-alang as a weed, I consider these series of experiments convincing proof of the existence of allelopathy under field conditions. And although I try to establish the custom of giving summative addresses without literature references, in this case I refer the reader to *Biotrop Bulletin*, **10** (1976) and to a forthcoming issue of *Oecologia*, for further information.