

rhabdom. In this configuration the eye acts as an ordinary apposition eye (like that of a bee, for example) with each rhabdom having its private optical system. When the screening pigment retracts in the dark the reflected, superposition rays take over, forming a much brighter image directly on the rhabdom layer. From a taxonomic point of view these eyes also represent an interesting compromise, being a clear intermediate between the reflecting superposition eyes of the long-bodied decapods (shrimps and crayfish) and the other crabs with pure apposition eyes. In some ways this is sad. A short while ago we could say that "X could not evolve into Y because the eye of the intermediate

form would not work". Now we cannot; Nilsson's eye links apposition eyes to both other types of superposition eye, acting as a kind of universal taxonomic glue.

It is too early to tell whether the parabolic superposition principle will be of value in optical technology. I have failed to find anything like it in optics textbooks. Its cousins have been useful: refracting superposition mechanisms have influenced inhomogeneous lens design, and the reflecting mechanisms have found a use in X-ray telescopes. The trick is to find a problem to which this eye is the solution. □

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Agriculture

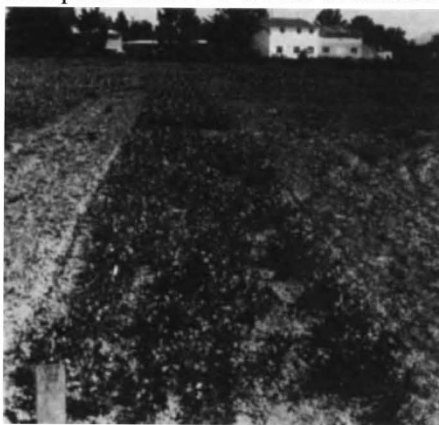
Models of crop growth

Gareth Hughes

THE first step in appraising the effect of a pest or disease on crop yield is usually to characterize the relationship between severity of attack and loss in yield¹. Most people have used an empirical regression equation to couple crop yield to pest and disease dynamics, even in cases where relatively realistic models of the latter are available. Recently, however, interest has grown in developing simulations of crop growth driven by plant physiological processes in relation to the physical environment, and which include mechanistic models of pests and diseases to enable the assessment of losses². But such models can often be too demanding in terms of input data requirements to be useful in practice³. Waggoner and Berger now suggest⁴ that the effects of pests and diseases can be modelled in a similar way to the effects of agronomic factors such as plant population density and nutrient and water supply on crop growth and yield.

The paradigm for crop-growth models is Monteith's analysis⁵ of biomass (W) as the time-integrated product of the photosynthetically active radiation (PAR) incident on the top of the leaf canopy (R), the fraction (f) of PAR intercepted by the canopy and the amount of dry matter produced per unit PAR intercepted (e). Many analyses have shown that, at least under good conditions, W is almost proportional to the amount of intercepted PAR ($W = \int f.R.dt$), where e is the proportionality constant and t time⁶. In such cases, crop yields depend on the growth and duration of the leaf canopy in relation to the seasonal pattern of irradiance. Recent data show⁷ that physical environmental stresses can reduce crop yields by their effects on both f and e . The question raised⁴ by Waggoner and Berger concerns the nature of the effects of biotic stresses on these variables. They reanalysed data

from four crops — peanut, potato, maize and wheat — under pathogen attack, with the objective of characterizing relationships between W and the amount of radiation intercepted by healthy foliage. These relationships all seemed to be linear, and no differences were apparent for cases where data were also available for a comparison of the slopes (estimates of e) of relationships for diseased and manually defoliated crops. Haverkort and Bica-mumpaka reached a similar conclusion⁸



The aftermath of pest disturbance of an experimental crop of peas at Finca Zamadueñas, Spain.

from experiments in which they grew potato crops with or without control measures against *Phytophthora infestans*. They could account for practically all the differences in yield by differences in radiation interception by healthy leaves. Both diseased and healthy crops had the same value of e .

Two aspects of these results^{4,8} are particularly noteworthy. First, bearing in mind differences in photosynthesis that have been detected in healthy and diseased plants⁹, it is interesting that no differences in e between healthy and diseased crops were detected. This is good news for those

who develop crop-loss assessment models using manual defoliation to simulate the effects of pests and diseases, although examples of variation in e in attacked crops will surely emerge.

The second interesting feature of the new results is the apparent insensitivity of the underlying analysis of crop growth to changes in the spatial pattern of the crop. Most pests and diseases have patchy spatial patterns, and thus can disrupt the more-or-less regular patterns in which crops are sown, in addition to inflicting plant injury (see figure). This is recognized as a problem in both conventional¹ and crop-growth-based² loss-assessment modelling, because the spatial pattern of plants can influence the level of intra-crop competition. Some recent results¹⁰ show how patchiness in a crop can influence yield, independent of plant population density (and pests and diseases).

Waggoner and Berger's analysis⁴ suggests that the function relating f to green-area index in healthy crops can also serve for diseased crops. They do not account for any differences in radiation interception resulting from the spatial patterns of the foliage of healthy and diseased crops. Haverkort and Bica-mumpaka⁸ estimate f directly, rather than as a function of green-area index, but this cannot account for changes in the level of intra-crop competition for resources other than PAR resulting from patchiness in attacked crops.

Neither analysis includes a crop response to plant spatial pattern, and results from studies¹¹ in which the effects of spatial pattern as well as severity of crop injury are incorporated into conventional loss-assessment models demonstrate the importance of including both. There are new models relating crop growth and yield to plant spatial arrangement and resource capture^{12,13} which, although they do not deal directly with the problem of patchiness arising from pest or disease disturbance, may provide a framework for the development of crop-growth-based loss-assessment models that include responses to the spatial pattern of crop injury. □

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