MECHANISMS OF RESISTANCE IN CEREALS TO PESTS

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ABSTRACT

A research programme to detect resistance to pests in a crop should ideally address at the outset the following questions: How wide a genetic range of plant material should be screened? Should the mechanisms of resistance be investigated? Should the biological components (antibiosis, antixenosis, tolerance) be studied? At what point should plant breeders be involved? An alternative to the above approach is the crude but rapid screening of large numbers of plants by releasing pests and assessing plant survival after an interval. Examples of both approaches are given, concentrating on cereals, with a discussion of the advantages and limitations of each strategy.

INTRODUCTION

Host plant resistance to insects has the potential, acting alone, or with insecticides and/or with natural enemies, to keep pest numbers below economic thresholds and thereby reduce pesticide inputs. Pesticides are not always used rationally on U.K. cereals, for instance; economic losses (Wratten & Mann, 1988; Wratten *et al.*, 1990) and undesirable side-effects can occur even when products are applied in response to spray thresholds (Vickerman & Sunderland 1987; Vickerman *et al.*, 1987; Sotherton *et al.*, 1987; Wratten *et al.*, 1988). In addition to the above economic and environmental advantages, simple cost-benefit analysis relating research and development costs for a new resistant cultivar to its economic value following release can be 1:300 (Luginbill, 1969). The development of a typical new pesticide, however, may incur an expenditure of $50m, with little prospect of recouping this outlay for many products before patent expiry (Finney, 1988). Because of these high costs, return on investment has been delayed, raising doubts in some companies about long-term investment in agrochemical R & D (Finney, 1988). Against this must be weighed the limitations of host-plant resistance as a major pest-control method. These limitations will be discussed in this paper, which will use case studies of cereal pests to illustrate prospects for the use of host plant resistance.

APPROACHES TO THE INVESTIGATION OF RESISTANCE

Screening via crude bioassays

The simplest way of searching for useful levels of resistance is to inundate a wide range of replicated plant material in the laboratory, glasshouse or field, with large numbers of the pest and leave the system for a few days or weeks. All that need be assessed after the chosen interval has elapsed is the condition and number of surviving plants. In theory, this method can identify highly resistant lines which survive the high pest pressure and has been used for aphids by Reinink & Dieleman (1989) in a glasshouse screen of lettuce cvs., by Birch (1989) for turnip root fly (Delia floralis) in brassicas, and by Dunbier, Kain & McSweeney (1977) in New Zealand; the latter led to the release of a new, aphid-resistant lucerne cultivar within three years of initial screening. Although this method is intuitively attractive, it does have potential drawbacks, especially if the initial screening is not conducted under realistic conditions. The main limitation is that no information on the classical components of resistance (antibiosis, non-preference, tolerance; Painter, 1951) is obtained, or on resistance mechanisms. This also means that screening has to be based on bioassays using the pest, rather than via a short-cut involving screening for cuticular hair density, levels of secondary plant compounds, etc. Also, should the resistance break down in the field, the lack of a detailed understanding of its nature means that an explanation for the breakdown is unlikely to be found. Because of this method's broad approach, however, it has the advantage that it is not biased in favour of only one component; some laboratory screens concentrate on antibiosis only, for instance the work by Bohidar et. al., (1986) and Spiller & Llewellyn (1987) on seedling resistance in wheat to aphids.

Evaluation of the biological components and mechanisms of resistance

The advantage of investigating all potential resistance components is that there is less likelihood that a key insect-plant interaction will be overlooked. If, in addition, a major mechanism of resistance is identified, the possibility exists for a rapid biochemical or physical (e.g. leaf hairs) screen of a very large range of plant material without the time-consuming elements of insect culturing and bioassays. Of the three components proposed by Painter (1951), antibiosis (defined in this case as an effect on the performance of the insect, via fecundity, mortality, development rate, etc.) is the commonest in the literature, especially among laboratory studies. It often involves the caging of single insects on plants, and in the case of aphids on cereals, of recording such parameters as intrinsic rate of increase (r_m; Birch, 1948), relative growth rate (van Emden, 1969), rate of honeydew production (Spiller & Llewellyn, 1987), number of embryos in the adult parthenogenetic female (Bintcliffe & Wratten, 1982), adult weight (Lee, 1983) etc. Host non-preference (= antixenosis) is a less relevant measurement for laboratory screening since it is likely to be greatly influenced by environmental conditions in the field, including the crop's agronomy and the areas of monoculture over which it is grown. The relevance of simple laboratory choice experiments involving cereal aphids (e.g. Leather & Dixon, 1982; Dent, 1986; Dent & Wratten, 1986) to single-cultivar monocultures is questionable. Tolerance, whereby certain cvs. yield better than do others per unit pest number, is a realistic measurement only under field conditions. Even then, unless it operates below or near the pest's economic threshold, it would be unlikely to replace or even supplement pesticide use. Although tolerance is unlikely to promote the development of resistance - breaking pest biotypes, if employed as the major component it could lead to high pest levels on a regional basis, leading to future problems.

Screening of a wide genetic range of plant material

Concentration on commercial cvs. has the potential disadvantage that they may have low levels of resistance compared with their ancestors and wild relatives. This decline in resistance with cultivation history is well illustrated by the black bean aphid, Aphis fabae on Vicia (Fig. 1). The disadvantage of screening plant material which is genetically remote from commercial cultivars is that crosses may be difficult to make, due to 'premating' and/or 'postmating' problems (Stalker, 1980).

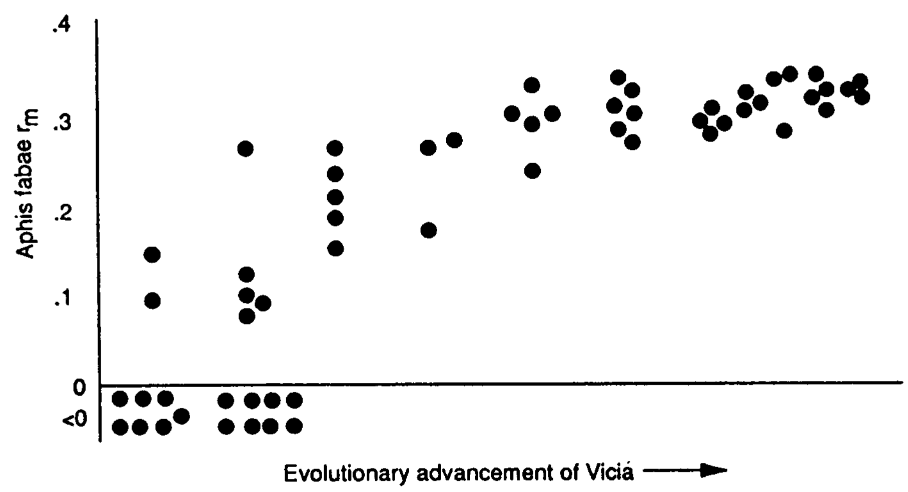

FIGURE 1. Performance of Aphis fabae in relation to evolutionary advancement of Vicia hosts (from Holt & Birch, 1984)

CASE STUDIES OF RESISTANCE IN CEREALS

The role of hydroxamic acids in conferring resistance to Lepidoptera and aphids

The structure of hydroxamic acids (Hx) is similar to that of amides with a hydroxyl group rather than a hydrogen atom attached to the nitrogen atom. Hx from cereals are benzoxazinone type cyclic Hx, i.e. benzene ring is fused to a 6-membered ring containing an oxygen atom besides the hydroxamic acid function. They share much of their biosynthetic pathway with tryptophan. DIMBOA (2, 4-dihydroxy-7-methoxy-1, 4-benzoxazin-3-one) is the most abundant compound among the Hx which have been isolated from maize, wheat and several related wild Gramineae. They are found in the plant as glucosides which are enzymically hydrolysed to the corresponding aglucones when the plant tissue is injured (see review by Niemeyer, 1988).

Early work on Hx concentrated mainly on resistance in maize. Klun, Tipton & Brindley (1967) reported significant correlations between resistance to the European corn borer (Ostrinia nubilalis) and levels of benzoxazolinones (hydroxamic acid breakdown products) in maize extracts and followed this with bioassays using artificial diets which showed hydroxamic acids to be the most active plant component. Robinson, Klun and Brindley (1978) demonstrated feeding deterrent effects both in field and laboratory tests. In the 1980's, recurrent selection based either on DIMBOA levels or on insect damage led to improved first-brood resistance.

Long, Dunn, Bowman & Routley (1977) reported a highly significant negative correlation (r = 0.72) between the level of infestation of the corn leaf aphid (Rhopalosiphum maidis) and the concentration of DIMBOA in maize tissue. Argandona, Luza, Niemeyer and Corcuera (1980) found similar relationships for the rose-grain aphid Metopolophium dirhodum on wheat. In addition hydroxamic acids have been implicated as resistance factors in several wheat cultivars to the aphids Schizaphis graminum and R. maidis (Corcuera, Argandona & Niemeyer, 1982). S. avenae was investigated in this context in preliminary work by Bohidar et. al. (1986) who found that 96% of the variance in the resistance of six Chilean wheat cultivars was explained by Hx levels. Although Hx levels decline as plants age (Thackray et. al. 1990), the youngest leaves of seedlings had high Hx levels, while the levels in young flag leaves were similar to those of some seedlings. The latter data are important as S. avenae causes yield loss when feeding on flag leaves and ears of mature wheat plants (Wratten, 1978) and is not a seedling pest in the U.K. other than as a BYDV vector in N. England (McGrath & Bale, 1989). Leszczynski et. al. (1989) demonstrated a highly significant negative correlation ($r = -0.905$) between S. avenae intrinsic rate of increase (r_m) and Hx concentration in flag leaves of wheat. Screening mature plants for Hx or via an insect bioassay is time-consuming, however, as at least two months are needed to obtain wheat in ear under U.K. glasshouse conditions. If there was a correlation between seedling Hx or aphid resistance and their values in mature plants, this would be of value in accelerating a screening programme. In a series of papers by Lowe in the 1980s (e.g. Lowe, 1984 a,b,c) aphid bioassays were used to rank a large number of cvs. of winter wheat in relation to their resistance as semi-mature plants to the grain aphid. When these were evaluated as two-leaf seedlings for DIMBOA content, using high performance liquid chromatography (Fig. 2 a,b; see Niemeyer et. al., 1989 for methods), a wide range of DIMBOA content was obtained (Fig. 3). Resistance to the grain aphid was measured in six of these cvs. which showed the greatest range in Hx concentration and the correlation was very high ($r= -0.94$; Fig.4). However, there was no significant correlation between the rankings of these cvs. as seedlings, based on Hx levels and aphid relative growth rate, and the rankings of Lowe(loc. cit. There was also no significant correlation between the Hx ranking of all 36 cvs. as seedlings and their ranking in Lowe's mature plant bioassays. Hydroxamic acids can therefore explain a high proportion of the variation in resistance to S. avenae in wheat, but plants need to be screened for Hx levels and resistance at the same growth stage. The effect is mainly via antibiosis, although the fact that inverse relationships exist between DIMBOA levels in aphids feeding on wheat p lants and DIMBOA levels in the plants themselves suggest that feeding deterrency may be involved (Niemeyer et. al., 1989).

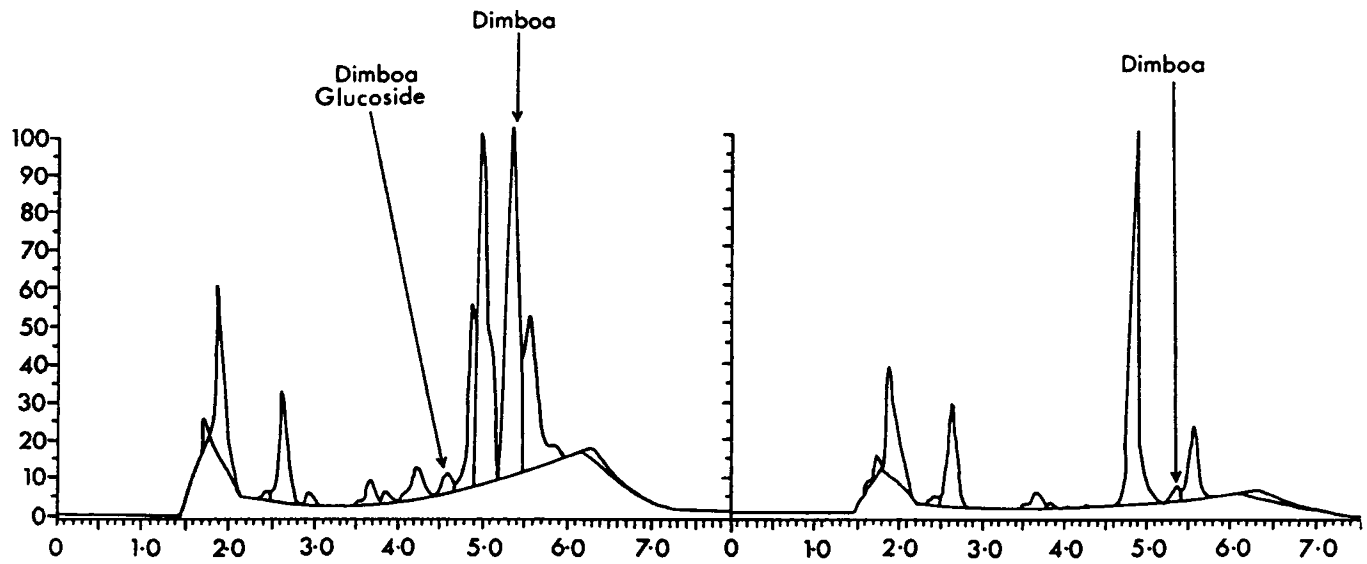

FIGURE 2. HPLC analyses of high and low DIMBOA wheat cultivars.

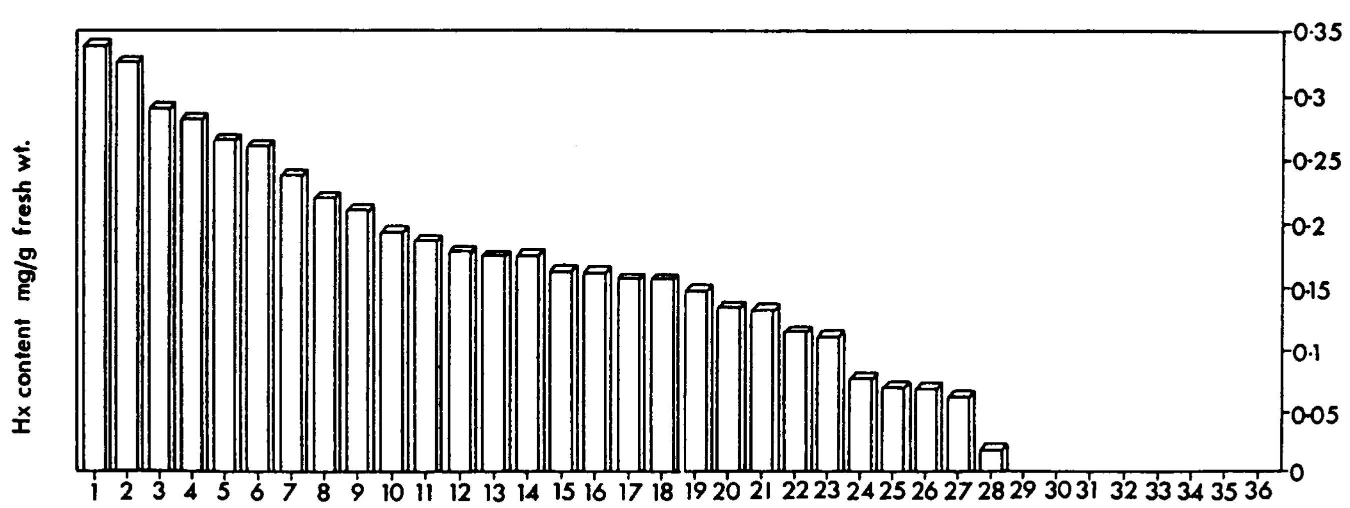

FIGURE 3. Range of DIMBOA concentrations in seedlings of cultivars screened by Lowe as mature plants via aphid bioassays.

The role of physical factors in aphid resistance in wheat

Lowe *et al.* (1985) demonstrated a role for antixenosis in wheat against *S. avenae*, with the possibility that non-glaucous cvs. may be avoided by the aphid. Acreman & Dixon (1986) examined six genotypes of awned spring wheat and showed that aphids were up to 22% less fecund, and were more likely to be dislodged than aphids feeding elsewhere on an ear. These two factors reduced aphid population growth to one third of that on awnless plants. Population modelling by Acreman (1984) revealed that with the regular reductions in aphid numbers of cereals by 85% which are feasible via host plant resistance, the three outbreaks recorded over a five-year study period would not have occurred.

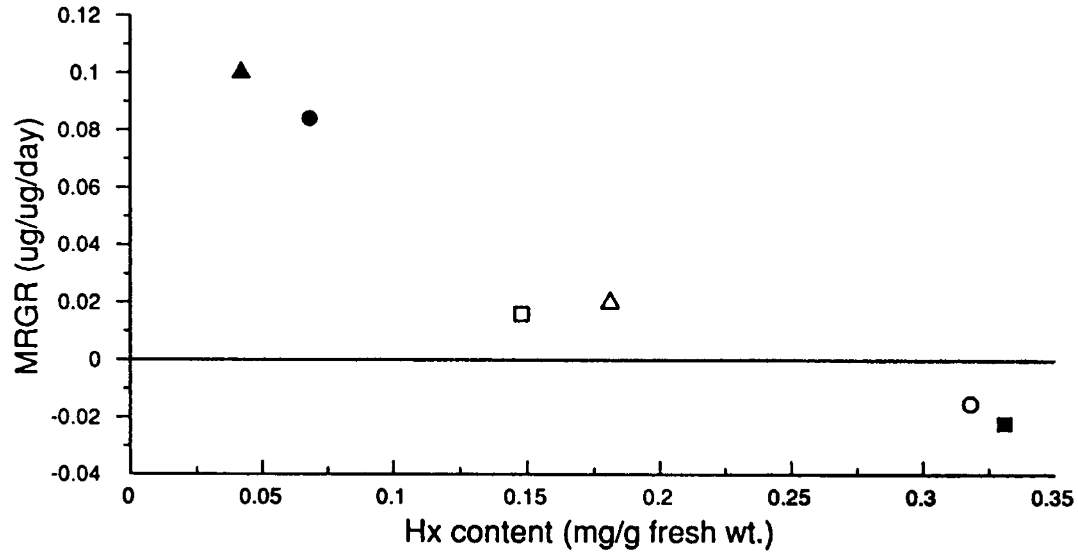

FIGURE 4. Relationship between mean relative growth rate of Sitobion avenae and seedlings selected from those in Fig. 3 representing a high range in hydroxamic acids.

Resistance to aphids as virus vectors

This is usually biologically less tractable than is the production of resistance against direct-damaging pests as resistance is usually only partial and thresholds for virus vector control are usually low. However, Givovich & Niemeyer (1991) showed that in wheat seedlings with high DIMBOA levels, fewer plants were infected with BYDV by R. padi than on low DIMBOA cvs. Fewer aphids reached the phloem on the high DIMBOA cvs. and those which did reach the phloem took longer on high DIMBOA cvs. In W. Europe, R. padi feeds low down on wheat and barley seedlings, often on the leaf sheaths at or below ground level. In view of the above results for S. avenae (Fig. 4; which showed the importance of evaluating the appropriate growth stage, it is relevant to examine leaf sheath Hx levels in seedling wheat. This was done for R. padi on a range of Triticum material, using relative growth rate and HPLC analysis of DIMBOA, as described above. A correlation coefficient of - 0.794 was obtained (Fig. 5). This evidence, and that of Givovich & Niemeyer (1991) suggests that Hx levels may be a good indicator of pest performance in plant breeder's screening, not only for direct-damaging pests such as S. avenae but for virus-vectors such as R. padi.

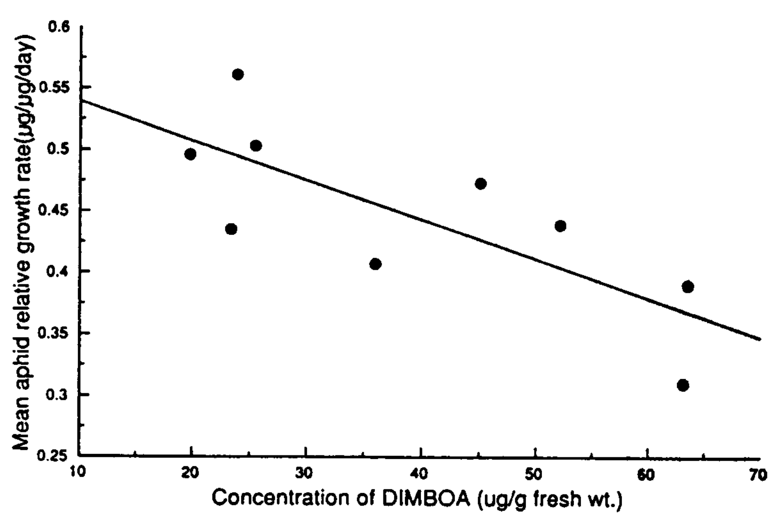

FIGURE 5. Relationship between mean relative growth rate of Rhopalosiphum padi and seedling sheath hydroxamic acid levels.

Resistance to other cereal pests

Silica has been implicated in the resistance in grass to frit fly (Oscinella frit) attack (Moore, 1984), and the distribution and quantity of silica within the plant may make a major contribution to control of this fly in grassland (Clements & Henderson, 1983). Silica was also implicated in resistance in oats and wheat to Hessian fly (Mayetiolia destructor; Miller et. al., 1960), and in rice resistance to mollusc grazing (Wadham & Wynn-Parry, 1981). The addition of sodium silicate to host plants reduced growth rates of populations of frit fly and S. avenae (Hanisch, 1981). The structure and persistence of the coleoptile (in oats) and colour (in ryegrass) determine levels of oviposition by the frit fly.

CONCLUSIONS AND PROSPECTS

Even a relatively small increase in resistance can reduce the probability of a pest outbreak, especially in combination with the action of natural enemies with or without insecticide use (see van Emden, 1987 and van Emden & Wratten, 1990 for reviews). However, Burn (1987) in a review of integrated pest management in cereals, concluded that for most insect pests in these crops the ' ... use of varietal resistance seems remote, and will remain so while so little attention is given to it in plant breeding programmes'. This is in contrast to resistance to fungal pathogens, where varieties exist which offer some resistance to eyespot, powdery mildew, Septoria and yellow and brown rust. It is interesting to speculate whether the absence of aphid-resistance breeding programmes leading to the growing of aphid-susceptible cvs. (such as Maris Huntsman in the 1970s) over large areas, may have influenced grain aphid abundance at field or regional 'meta-population' (Hanski, 1989) scales. The reason for this lack of progress in insect resistance is likely to be a combination of a) arable pests are easily controlled chemically, with no serious insecticide resistance in cereal pests b) there has been no suitable biochemical or physical factor in cereals which could be used as an indicator of pest performance, to speed up the screening process c) bioassays were often laboratory based and concentrated on modern cvs. which did not reveal large differences in resistance for use in breeding programmes d) environmental awareness of insecticide side-effects has been much higher recently than in the 1970s, leading to moves in some European countries to reduce these inputs substantially.
e) some plant breeding concerns have been taken over by agrochemical companies; this may make it less likely that pest-resistant cvs. will be produced from this source as insecticide sales may suffer as a consequence.

Despite the above five partly historical reasons, in the 1980s and 1990s a general desire to reduce pesticide inputs has arisen alongside the demonstration that some physical (e.g. awns) and biochemical (e.g. DIMBOA) factors can explain high proportions of the variation in aphid numbers on wheat. It seems that it is now timely to exploit this information in directed screening and plant breeding programmes, possibly via technological development agencies such as the British Technology Group in the U.K. or via agrochemical companies.

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