PLANT RESISTANCE TO INSECT PESTS

A General Review with Reference to New Zealand Grassland Farming

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INTRODUCTION

THE UTILIZATION of plant resistance against insect pests is not a new phenomenon in New Zealand, but until the present decade it has been largely concerned with resistance in horticultural (Lamb, 1953a; Smith *et al.,* 1960; Cottier, 1948), cereal (Morrison, 1938) and fodder crops (Lamb, 1953b; Palmer, 1956, 1965; Palmer and Smith, 1967). Cockayne suggested in 1911 that it may be possible to breed grasses resistant to grass grub and Flay and Garrett (1942) observed that lucerne (*Medicago sativa*) and cocksfoot (*Dactylis glomerata*) pastures were less susceptible than perennial ryegrass swards to grass grub (*Costelytra zealandica*) attack. Undoubtedly attempts to develop resistant pasture plants against pests were adversely affected by the successful use of DDT and dieldrin between 1950 and 1970. Since the restrictions placed on their use, entomologists in New Zealand have been faced with the problem of finding alternative control procedures including the development of resistant pastures.

Resistance, if isolated and incorporated into new varieties, is largely a community rather than farmer expense. In low profit margin pastoral farming, where better to attack phytophagous pests than through the component legumes and grasses, which in contrast to other control procedures are maintained permanently in the system?

For convenience the remainder of this paper is divided into four sections:

(1) Plant resistance — the general concept and theories.

(2) Plant resistance — its place in pest control.

(3) Plant resistance — its utilization in insect control programmes.

(4) Pasture resistance — in New Zealand.

PLANT RESISTANCE — THE GENERAL CONCEPT AND THEORIES

Resistance of plants to insects is genetically controlled. A basic tenet of evolution is the adaptability of orgaaisms to overcome adverse conditions. This is evidenced by the ability 04 plants to withstand the depredations of insects and diseases, because selective pressures on the gene pool result in dominance of resistant plants. This process of natural selection can be manipulated by man. One of the earliest records of plant resistance to insects occurred in 1831 when the apple variety Winter Magetin was found to be resistant to apple woolly aphis, *Eriosoma lanigerum*. Degrees of resistance occur and are expressed as: immunity, high or low resistance, and low or high susceptibility. Apparent resistance may occur in crops or pastures through induced or chance escape and need to be recognized before undertaking extensive research programmes.

The ability of insects to attack plants is also genetically controlled and expresses itself in the form of biotypes, which develop by selection pressure from resistant plant varieties — particularly varieties with low or moderate levels of resistance. These biotypes survive, multiply and re-establish the species as a pest again.

Painter (1951) defined resistance as "the relative amount of heritable qualities possessed by the plant which influence the ultimate degree of damage doae by the pest". He recognized three major mechanisms 0% resistance, namely:

(1) Non-preference or preference, by the insect for such requirements as food, shelter, and oviposition.

(2) Antibiosis, which results in adverse effects on the insect's biology.

(3) Tolerance, which' is the ability of the plant to withstand, repair, and recover from infestation.

Preference or non-preference operates by insects first finding food plants (dispersal is important here) and then accepting or rejecting them according to the presence or absence of particular stimuli to which the pest is conditioned, The following types of stimuli are involved: Visual (light and colour) ; mechanical (e.g., angle of leaf contact, hairiness of surfaces, and stem solidity)) ; olfactory (smell) ; and gustatory (taste) .

Antibiasis, which can only be separated from preference and non-preference by experiment, results from: the deleterious effects of toxic (insecticidal) compounds present in some plants; lack of specific food materials; differences in the quality and quantity of food materials; and plant growth responses which isolate the pest from food material by galling, cork formation and necrosis. Antibiosis may result in: death of early instars of insects; delayed development; reduced size and fecundity of offspring; or, changed behaviour of the insect and consequently its attraction to host plants.

Tolerance differs from antibiosis and preference in that the dominant part is played by the plant, and no active response is made by the insect. It is the ability of a variety or species to withstand attack better than another variety or species which is subjected to the same level of pest infestation. A plant is more tolerant than another because it has better ability to repair injury, make new (replacement) growth under the prevailing environmental conditions, and/or is able to withstand injury better. Consequently, tolerance is more subject to environmental variation than preference or non-preference. In addition, the age and size of plants are important in determining, the level of tolerance obtained. The following plant characteristics may be associated with tolerance:

(1) Presence or absence of adventitious buds.

(2) Ability to produce growth hormones.

(3) Ability to withstand moisture deficit or extremes in temperatures.

(4) Amount of suberin and wound callus produced.

(5) Level of resistance to disease organisms which invade injuries caused by insects.

(6) Ability to replace damaged root systems.

(7) Length of straws and stems.

(8) Strength of stem tissues.

(9) General vigour associated with heterosis.

Even though it does not reduce pest populations, tolerance of plants could be important in pest control because:

(1) Tolerant plants probably exist in all populations and can be used as the basis for breeding new strains.

(2) Plant tolerance, if utilized, can effectively raise the economic threshold level.

(3) Tolerant plants maintain normal pest populations and consequently do not interfere with the action of natural enemies.

In New Zealand, tolerance appears to be the basis for Ariki and Ruanui ryegrasses being able to withstand Argentine stem weevil attack better than Manawa and Paraa ryegrasses (Pottinger, 1961b) . Tolerance has been only accidentally exploited in New Zealand but from an insect control point of view offers to play an increasingly important role in our low profit margin grassland farming, Tolerance is often difficult to recognize, and, because tolerance may not hold from one region to another (because of environmental changes), its development should be by multidisciplinary teams of agriculturalists.

As in most scientific disciplines, workers closely involved with resistance have been coacemed with more precisely defining plant resistance to pests and have erected- hypotheses to explain the mechanisms involved. Beck (1965) took a more fundamental view than Painter and emphasized the inherent biological relationships. He defined resistance as "the collective heritable characteristics by which a species, race, clone, or individual may reduce the profitability of successful utilization of that plant as a host by an insect species, race, biotype, or individual". Because of its loose biological relationships, Beck excluded tolerance from this definition. Such a suggestioe may be theoretically valid but from an agricultural point of view tolerance must be considered together with preference and antibiosis. In fact, Palmer and Smith (1967) who appear to follow Painter, proposed that a plant is resistant when it suffers less economic damage than a susceptible one under conditions which would be normally injurious.

Beck considers that the principal mechanism of plant resistance is linked with host preference. Considerable controversy surrounds the processes involved, with some workers (Fraenkel, 1959) emphasizing the "token stimuli theory" (namely, the role of nutritionally inert chemicals) and some (Thorsteinson, 1960) the role of nutrient substances for host selection. There is evidence for both viewpoints and Kennedy (1958) has attempted to overcome the shortcomings by proposing a "dual discrimination theory", which utilizes both points of view. This implies ability of insects to selectively discern compounds of differing nutrient status, but feeding and oviposition can play a part in host selcctioa as well as preference. Plant resistance is manifested by both biochemical and biophysical factors. As much of the work supporting the ideas outlined above has been done on a restricted number of plants, it is difficult to make generalizations on the applicability of these concepts.

The fact that we can develop plants resistant to pests without knowledge of the mechanisms is an advantage rather then a weakness. In a country such as New Zealaad with limited scientific and monetary resources, whilst it may be theoretically desirable to understand the mechanisms of all plant resistance to insects, it is probably more expedient to emphasize tbe location of sources of resistance, the development of resistant swards and their integration with other control procedures, rather than to let research become dominated by identification of the more fundamental mechanisms involved.

PLANT RESISTANCE — ITS PLACE IN PEST CONTROL

Palmer and Smith (1 967) have listed several advantages associated with the utilization of plant resistance for pest control. These points and others are briefly discussed below:

(1) Resistance is already existent and only requires to be revealed by screening and in some cases the level of resistance concentrated by a recurrent breeding programme. The resulting resistant varieties might be sown as special-purpose swards or mixed with other pasture species and assessed as "resistant pastures". If such pastures ace easily managed and have high stock carrying capacity, they could provide a profitable means of pest control acceptable to farmers.

(2) The'ccst of development of insect resistant plants may be less than the cost of insecticide development. Because the latter costs are usually spread over an international market, however, it is difficult to argue or generalize on this point, as definitive data are lacking for both situations.

(3) Control is automatic, without recurring costs to the grower.

(4) Extensive farmer education may not be required in order to utilize plant resistance to pests as a control procedure.

(5) In many cases resistance to pests has shown a high degree of permanency. For example, resistance to apple woolly aphis has lasted over 140 years and resistance of grapes to phylloxera (*Viteus vitifoliae*) for a century. In cases of low or moderate resistance, however, selection of new biotypes of the pest can eliminate the advantage, as occurred in New Zealand with the breakdown of rape resistance to the cabbage aphid, *Brevicoryne brassicae.*

(6) Quite often resistant plants can be developed rapidly. This depends upon the genes involved, the breeding sys-

tem of the plants and ease of crossing, the agronomic value of the parental material, and the length of each plant and pest generation. In the U.S.A., strains of lucerne resistant to stem nematode, *Ditylenchus dipsaci*, have been developed and marketed within three years (Sprague and Dahms, 1972) .

(7) Comparison of plant and animal production between resistant and susceptible swards and crops, is one of several ways in which the significance of pests can be assessed.

(8) The side-effects of breeding for plant resistance can be beneficial, particularly if genes to increase yield, palatability, and other desirable agronomic characteristics can be incorporated during the breeding programme.

(9) Screening programmes generally yield new data pertinent to insect behaviour, fecundity and loagevity, which may have bearing on understanding of infestation processes and development of new controls.

(10) There, are no adverse environmental side-effects or residue. problems associated with the usc of plant resistance.

(11) Use of even partially resistant plants, on a large scale within regions, may reduce the incidence of specific pests by adding to existing generation mortality over a period of time. In California, use of wheat varieties with high immunity has elminated Hessian fly, *Mayetiola destructor* as a pest (Sprague and Dahms, 1972).

Despite these advantages it is amazing how little effort has been devoted throughout the world to the development of insect-resistant clovers and grasses. It is interesting to note:

(1) That white clover (*Trifolium repens*) cultivars developed in New Zealand and unwittingly exposed to pest infestations have been found to have a higher level of resistance to clover eelworm, *Heterodera trifolii* (Kuiper, 1960) .

(2) That Corkill (1952) found slug damage was often more severe in New Zealand on glucoside-free white clover plants, but was not detectable on plants with high cyanogenetic glucoside content. Records such as this point to the potentiality of a more systematic screening and research programme aimed at developing insect resistant plants in New Zealand.

As in all control programmes, there are disadvantages associated with the use of plant resistance.

(1) Use of resistance is dependent on finding suitable mutant plant forms, but even where resistance is not obvious recurrent breeding programmes and rigorous selection can develop partially or moderately resistant lines (Hunt et al., 1971).

(2) Unlike the use of broad-spectrum insecticides, plant resistance is selective to specific pests. Problems can arise in this regard as found by P. D. King (pers. comm.) and R. East (pers. comm.) with black bzetle and white-fringed weevil populations. Where such conflict occurs reliance on other controls, such as insecticides, becomes a necessity for the least troublesome or most easily controlled of the pests.

(3) Deleterious genes which lower yield or palatability to stock may be present 'in insect-resistant plants, although further breeding can reverse this situation.

(4) Resistance is not always permanent and may be modified or lost by changes in the plants, the pest species or changes in agricultural practice.

(5) Lack of understanding of plant-insect inter-relationships. Selections made in the laboratory do not necessarily behave the same under field conditions, and it is important that the pest is present throughout plant breeding programmss.

Recently, the genetic inter-relationships that exist between the host plant and insect have been studied for some pests (Gallun, 1972) . This has resulted in a better understanding of how to control insects by resistant varieties. Plant breeding programmes can utilize biotypes of pest species to locate new sources of resistance, distinguish between sources of resistance and determine the inheritance of resistance. It is essential that a thorough knowledge of pests and host plants is available in order to fully evaluate cultivars for insect resistance (Dahms, 1972). There is a need in New Zealand for a much closer integration of MAF and DSIR research in plant breeding programmes aimed at developing insect-resistant or tolerant plants; and more specifically, to incorporate insect physiologists, insect ecologists, agricultural entomologists, general agriculturalists, and animal nutritionalists within the more traditional plant breeding teams of geneticists, agronomists, plant breeders, and plant pathologists.

. It is imperative that cultivars of the main and potentially interesting pasture plants be obtained from all possible sources and screened for resistance by subjecting them to adequate and uniform pest infestations. There is a need to return to severely damaged swards and select material from them, as well as extension of the search overseas. Resistance discovered can be transferred to usable cultivars by selection or hybridization. In development of breeding programmes it is important to base selections on germ plasm obtained from as wide a genetic base as possible, as this tends to ensure a more permanent and higher level of resistance.

UTILIZATION IN INSECT CONTROL PROGRAMMES

Plant resistance can be used in the following situations against pests:

(1) As the principal control measure — e.g., the use of aphid-resistant rape and various swede varieties against cabbage aphid, *Brevicoryne brassicae,* and long-rotation ryegrass varieties against Argentine stem weevil in New Zealand (Pottinger, 1973).

(2) When low levels of resistance to a pest are involved, it can be used as an adjunct to other measures. This situation probably applies to the wheat varieties used in New Zealand in relation to Hessian fly control.

(3) As one of several components in integrated control programmes. It is conceivable that resistant pastures or crops (as is the case for lucerne grown to resist grass grub in some regions) for practical reasons are feasible for only part of the farm.

(4) As a safeguard (or screening procedure) to prevent the release of more susceptible varieties from plant breeding programmes.

PASTURE PLANT RESISTANCE — IN NEW ZEALAND

Research on the resistance of pasture plants to pests is at a very early stage of development in New Zealand. The following studies are of pertinence in this field:

(1) Tolerance and resistance of grasses to Argentine stem weevil *(Hyperodes bonariensis)* (Kelsey, 1958; Pottinger, 1961a, b).

(2) Grass grub-host plant inter-relationsips (Radcliffe, 1970, 1971).

(3) Measurement of the effects of lucerne and pasture swards on grass grub populations (Kain and Atkinson, 1970).

(4) Screening of pasture legumes and grasses for resistance to the major pasture pests, namely:

(a) Grass grub (Farrell and Sweney, 1972, 1974a, b; Kain et al., 1975) .

(b) Porina (*Wiseana cervinata*) (Farrell et al., 1974).

(c) Black beetle (*Heteronychus arator*) (King et al., 1975) .

(d) White-fringed weevil (*Graphognathus leucoloma*) (R. East, pers. comm.).

(e) Soldier *fly* (*Inopus rubriceps)* (P. J. Gerard, pers. comm.).

(f) Argentine stem weevil (S. L. Goldson, pers. comm.).

(5) Understanding the chemical basis of specific resistances (Sutherland and Hillier, 1974).

(6) Development of resistant pasture swards, acceptable to the farming community (Kain et al., 1975).

Space does not allow a full discussion of this work. Screening by all the workers involved has been undertaken to distinguish intergeneric, interspecific, and intraspecific differences in resistance, and assessment of the levels of resistance ,either to assist plant breeders or isolate varieties for field evaluation and use. Sutherland and Hillier's (1974) long-term' studies cn the chemical mechanisms, which will be of assistance to plant breeders, could assist the development of chemically based controls and should lead to an understanding of the mechanisms of resistance involved.

Farrell and Sweney (1972, 1974a, b) and Kain *et al.* (1975) have shown that white clover, New Zealand's most important pasture legume, favours development of grass grub more than any other pasture plant. Both groups of workers have shown that varying levels of resistance exist in both grasses and legumes. Plants with potentially utilizable resistance include, lotus, *Poa pratensis,* ryegrass and *Phalaris tuberosa.* Lucerne is already being widely used in grass grub infested areas. Studies of Kain and his fellow workers suggest that resistance of lotus and lucerne to grass grub are of a preference non-preference type, but that resistance of phalaris is antibiotic. Their studies have shown that it is possible to mix susceptible and resistant plants and develop resistant swards; and their research on the development and management of agronomically worthwhile, grass grub resistant pastures, to encourage resistant species at critical times to minimize damage, offers the most immediate application of resistance in grass grub control programmes.

The research of Farrell et *al.* (1974) has revealed considerable potential for the use of both grasses and legumes to combat porina. The interesting features are that, despite the difference between grass grub and porina feeding habits and the mechanism of resistance (0. R. W. Sutherland, pers. comm.), lotus and *Phaiaris tuberosa* strongly resist porina, whilst cocksfoot appears to have a moderate level of resistance. It has been known for some time that black beetle does not thrive on clovers. Research by King et *al.* (1975) has shown that lucerne is highly resistant to larvae and. as a consequence, offers a method to farmers to alleviate the effects of this summer-active pest.

Several other studies have been initiated to find resistance to other pasture pests, but none is at a far enough stage to comment on in this paper.

CONCLUSION

Development of overall (both legume and grass components) immunity of pastures to New Zealand major pasture pests must be our primary goal. Even if this becomes a reality, New Zealand will need to rely on and must not neglect research on the development of alternative control procedures. Kain and Atkinson (1970), Farrell and Sweney (1972, 1974b) and Kain et *al.* (1975) have demonstrated the high resistance of lucerne, Lotus *pedunculatus,* 'Grasslands Maku' and phalaris to grass grub. This level of resistance may not always be possible for other pests, but a low or moderate level of resistance, if utilized in conjunction with other procedures, could provide a useful base for improvement. It can be fairly concluded that, even though an active research programme to develop pasture species resistant to pasture pests is less than five years old, it is now firmly established. The programme can be improved by an increase in scientific and monetary resource and the establishment of more broadly based research teams.

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