

HOST RESISTANCE AND BIOLOGICAL WEED CONTROL

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The development of disease-resistant populations of target weeds from resistant individuals under control pressure by an introduced pathogen is theoretically a possible deterrent to phytopathogenic weed control. A wild host population would be expected to display some degree of variability in susceptibility to a given pathogen, i.e., a rust fungus. Because of their relatively greater heterogeneity, variability in disease reaction within wild populations would exceed that experienced by separate crop plantings. Hence, all else being equal, some individuals would be less heavily infected than others by a disease agent released in the control area. Such individuals could theoretically out-reproduce their more susceptible counterparts and, with a continuing selection pressure differential, eventually reach a position of dominance within the population, both in terms of numbers and of survival equipment.

Because phytopathogenic weed control is in its infancy, it is difficult to predict the effect this resistance factor would have in practice. The effect would certainly vary, depending upon the level of heterogeneity in the population, the variability of the inoculum and capacity or opportunity of the pathogen to acquire new genetic material and the environmental conditions. In populations with a narrow range of variability, the more resistant individuals may be reduced along with those having a higher degree of susceptibility, especially in instances of high inoculum density, for although the effect of single infections may be reduced by resistance factors, the weight of numbers alone could conceivably reduce host vigour to a point where the individual could no longer actively compete in association with individuals of other, more economically desirable, plant species surrounding it. The wider the range of variability within the population, the less would be the reducing effect of a high inoculum density on the more resistant individuals.

In greenhouse studies of the disease reaction of separate selections of *Rumex crispus* L. from the United States inoculated with urediospores of the rust fungus, *Uromyces rumicis* (Schum.) Wint. collected in Europe, wide ranges of disease reaction have been observed in "populations" composed of but 40-70 plants each. It is not known how representative these "greenhouse populations"

are of their respective natural populations, but it stands to reason that the natural populations would be no less variable than the sample representatives removed from them, and in all probability would contain a wider range of variability.

As regards the variability of inoculum and the capacity or opportunity of the pathogen to exchange genetic material in order to better cope with developing host resistance, *U. rumicis* may again be used as an example. The life-cycle of this rust involves *Ranunculus ficaria* L. as an alternate host. Classically, it is upon the alternate host that the greatest opportunity exists for the pathogen to exchange or acquire new genetic material, for it is here, during the development of the pycnial and aecial stages, that sexual recombination occurs and different physiologic races most frequently develop. Thus, in situations where both the primary host (*R. crispus*) and the alternate host occur within a functional radius of each other, the pathogen has both the capacity and the opportunity to develop new races pathogenic to resistant lines of the host, and the significance of resistance factors in the primary host population is correspondingly reduced. In situations where the alternate host is absent, the opportunity for the development of new pathogenic races is decreased considerably. In such a situation host resistance factors would acquire added significance.

It should be pointed out here that new races can develop by other mechanisms than through sexual recombination. Mutations, and anastomoses of vegetative hyphae from different races, are both known mechanisms whereby genetic material of a rust clone can be altered, although it is not known how frequently these mechanisms operate in *U. rumicis*. Nor is the alternate host necessary for the rust to survive from season to season, as long as winter conditions are mild enough for the repeating, or urediospore, stage to overwinter on the primary host. It is likely, however, that the primary mechanism of variability in *U. rumicis* is sexual recombination on the alternate host, and that mutation and vegetative anastomosis play minor roles.

Should *U. rumicis* be introduced into the United States as a prospective control agent, the questions of host resistance and presence of the alternate host must be considered. According to available floral survey literature the rust is not present in the U.S. and its alternate host is restricted to the eastern part of the country. Should a control programme be initiated in an area where the alternate host is absent and where the pathogen would

have to rely upon secondary mechanisms to provide for a variable inoculum, the spectre of population resistance, or selection toward resistance, may emerge as a deterrent to control. The introduction of a mixed inoculum, consisting of urediospores of several races differing in pathogenicity, would be considered advantageous in this instance.

It might be interesting at this point to speculate upon certain comparative aspects of phytopathogenic and phytophagous weed control regarding the possible role of resistant individuals as control deterrents. In one case, certain individuals would be resistant, in varying degrees, to infection by a pathogen; in the other case resistance to feeding or oviposition by insects would be encountered. In both cases the specific resistance factors carried by the individual plants would be largely unknown, and could be referred to only in general terms.

There is a major difference between the system used by phytophagous insects to spread through a population and that by which spores of a pathogen come to be dispersed. The spread of the insect is largely *active*. That is, an insect actively seeks its host, utilizing a sense of selection which, in many cases at least, is mediated by its reaction to certain feeding attractants or oviposition stimulants, or inhibitors to the same, which are natural, chemical or morphological characteristics of the plants concerned. Hence, an insect may either accept or reject an individual, depending upon the presence or absence of certain host features. If an individual is rejected, the insect will seek a neighbouring plant with preferred or favourable characters. The dispersal of a pathogen, on the other hand, is passive (excepting cases of plant viruses spread by insect vectors, a system which might be described as "pseudo-active"). Having no auto-locomotive or sensory capacity, a pathogen is entirely dependent upon random spore dispersal via physical environmental factors such as wind or water. (Certain Phycomycetes do produce flagellate, swimming zoospores, however.) Once deposited upon a plant surface, a fungus spore can neither accept nor reject the individual. If the plant provides a suitable substrate for infection, infection occurs. If the plant is resistant, or has some degree of resistance, infection is either prevented or maintained at low levels. The pathogen is compensated for its lack of an active dispersal system by its capacity to produce a large number of propagules. This insures effective dispersal, and in instances of high inoculum density it can be presumed that most of the host population will come under infection pressure.

Let us now consider this difference in dispersal systems in relation to the possible significance of resistance in biological control. Control depends upon high levels of significant host damage, which in turn depends upon a rapid, extensive numerical build-up of the control agent. How many resistant individuals within the population be affected by this massive build-up? On a hypothetical basis, we can visualize a target population subjected to control pressure by an introduced phytophagous insect. Variability within this population surely exists, and certain individuals, either because of a lack or insufficient titre of attractant, or excessive level of inhibitor (in general terms), can be designated as hosts of secondary preference. Under normal circumstances, when the host population is in balance with that of the insect, such individuals would suffer less damage and could be classed as resistant. But what happens when an imbalance is purposefully provided in favour of the insect? Essentially, all hosts of primary preference are rapidly colonized and the number of progeny soars. As the insect population increases and the host population declines, the scarcity of preferred host material becomes critical. The insect population becomes crowded to the extent that a certain segment may be forced to accept individuals of secondary preference, "distasteful" as they may be . . . plants which would have otherwise been rejected, or resistant. The result could be a reduction of so-called resistant plants along with the more susceptible, or preferred, plants.

In the case of pathogen build-up, however, no crowding effect occurs, as such. Certainly the situation evolves in which the susceptible or preferred element in the population is reduced to critical levels and the pathogen population, or inoculum density, reaches astronomical proportions, but in such instances the pathogen does not react by accepting resistant individuals. This is not to say that the weight of numbers has no significance (see above). Under conditions of high inoculum density the resistant individual is subjected to a high infection pressure. If its resistance is of a low level it may be materially damaged by the preponderant weight of a myriad of minor infections. The higher the resistance, the less the extent of material damage.

In the final analysis, based largely upon hypothetical grounds, it appears that phytophagous insects would have a slight advantage over phytopathogens in their ability to cope with host resistance in a biological weed control programme if the genetic potential of the pathogen is restricted. The major ingredient of this advantage is

the insect's ability to maneuver. An insect is an animal with a brain and, as such, is capable of a certain amount of determinant action. However low-based or primitive this capacity may be, it still emerges as an advantage in parasitism. In a large sense, the question of whether or not an organism will attack a resistant plant may be paraphrased either of two ways, depending on whether an insect or a pathogen is to be the assailant. In the case of the insect, the question, simply stated, is, "Will it, or won't it"? In the case of the pathogen, "Can it, or can't it"? This is an over-simplification, to be true, and ignores the many exceptions and gradations that will apply in practice, but it denotes a major difference between the two categories of control agents, and in so doing provides an interesting point of comparison for discussion.

The problem of host resistance in biological weed control is still largely a hypothetical one. It was interesting to note that, among the several entomologists present at this symposium, no instance, past or present, could be recalled of resistance developing in populations under control pressure by phytophagous insects. The problem may yet arise, however. The field of phytopathogenic weed control can list few principles and fewer precedents, excepting those derived from the basic science of plant pathology, which can be used as distinct guideposts. The question of host resistance, therefore, looms as a potential problem, demanding considerable thought and investigation on the part of the proponents of this field.