Induced resistance to rust diseases and its possible role in the resistance of multiline varieties

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(Accepted 21 February 1975)

Summary

Inoculation of wheat seedlings with a non-virulent race of *Puccinia striiformis* delayed the onset of sporulation of a virulent race and also decreased the spore mass produced. Similarly, the sporulation of a virulent race of *Uromyces appendiculatus* on bean seedlings was reduced by application of a weakly virulent race.

We suggest that these effects of induced resistance could retard the development of rust diseases in the field particularly in multiline varieties.

Introduction

The use of multiline varieties for rust disease control in inbreeding cereal crops was proposed by Jensen (1952) for oats and by Borlaug (1953) for wheat. Such varieties consist of a mixture of lines with similar agronomic phenotypes but with differing genes for race-specific resistance to rusts. Where some of the lines are susceptible, disease develops more slowly on the susceptible plants than in pure stands of the susceptible lines (Leonard, 1969).

Reviewing the proposed mechanisms by which disease incidence is reduced in multiline varieties, Browning & Frey (1969) suggested that a proportion of the initial inoculum falls on to lines which are resistant, thus reducing the effective level of inoculum. Of the spores produced by the infected susceptible lines, only a proportion will land on other susceptible plants, the remainder landing on resistant plants and reducing the effective rate of increase of the pathogen. In addition, the resistant plants may act as a mechanical barrier to dispersal; this would become less effective as the level of inoculum increased but might persist through a short season of infection. Browning & Frey stated, however, that the mechanism of control might be more complex in the case of the multiline wheat cv. Miramar 63 which remained relatively resistant to *Puccinia striiformis* Westend. and *P. graminis* Pers. through the long growing season in Colombia with yellow and black rust continuously present.

We suggest that resistance induced by infection with a non-virulent race of a rust pathogen and effective against subsequent infection with a virulent race may be a
further factor contributing to resistance in multiline varieties (Johnson & Taylor, 1974). Induced resistance might occur when any line was resistant to spores from some infected lines in the variety but susceptible to spores from other sources.

Induced resistance was demonstrated by Cheung & Barber (1972) in wheat to a virulent race of *Puccinia graminis* after inoculation with a non-virulent race, resulting in a reduction of 80% in the number of pustules. Yarwood (1956) described induced resistance in beans to *Uromyces phaseoli* (Pers.) Wint., now accepted as *U. appendiculatus* (Pers.) Ung., and in *Antirrhinum majus* L. to *Puccinia antirrhini* Diet. & Holw. Prior inoculation of beans with a non-virulent strain of *U. appendiculatus* reduced the number of pustules of a virulent strain by 33%. Littlefield (1969) demonstrated reductions in both number and size of pustules in similar experiments with flax (*Linum usitatissimum* L.) and *Melampsora lini* (Ehrenb.) Lev.

To be effective in reducing the spread of disease in the field we considered that induced resistance would have to cause delayed or reduced sporulation of virulent races of the pathogens. We therefore weighed spores produced by virulent races in the presence and absence of non-virulent or weakly virulent races using yellow rust (*Puccinia striiformis*) on wheat (*Triticum aestivum* L.) and bean rust (*Uromyces appendiculatus*) on beans (*Phaseolus vulgaris* L.).

**EXPERIMENTAL**

*Experiment 1: Puccinia striiformis on wheat*

Seedlings of wheat cv. Maris Templar were grown singly in plastic tubes in a glasshouse and were inoculated, when the primary leaf was fully expanded, with a mixture of talc and uredosporas of *P. striiformis*. They were placed in a refrigerator at 10°C and 100% r.h. for 48 h to encourage infection and were then returned to the glasshouse. The inoculated leaves were inserted into glass tubes for the entire period of sporulation and the accumulated spores were then weighed on an electrical microbalance. This technique is described in more detail elsewhere (Johnson & Bowyer, 1974).

Eighteen primary leaves of Maris Templar were inoculated with spores of race 104 E9 (Johnson, Stubbs, Fuchs & Chamberlain, 1972) of *P. striiformis* which causes a non-virulent, grade 0 infection type (Gassner & Straib, 1932). Another eighteen were dusted with talc alone. After 5 days, nine seedlings from each group were inoculated with spores of a virulent race, 41 E136 (susceptible grade 4 infection type). The remaining seedlings were inoculated with a 1:1 mixture, by weight, of spores of races 104 E9 and 41 E136 adjusted so that the virulent inoculum (41 E136) was at the same density as in the previous treatments in which it was used. The plants were arranged in nine randomized blocks, each of four treatments, for collection of spores.

Maximum spore production occurred on wheat seedlings inoculated with the virulent race of *P. striiformis* only (Table 1a). The onset of sporulation was delayed by 7 days on seedlings which had also been inoculated with the non-virulent race (104 E9) at the first inoculation; total spore production was significantly reduced in these seedlings. Sporulation was not significantly reduced or delayed when virulent and non-virulent inoculum were applied together without prior application of the non-virulent race.
Table 1. Weight of spores (mg) collected from leaves of Triticum aestivum inoculated with virulent (V) (41 E136) and non-virulent (NV) (104 E9) races of Puccinia striiformis and from Phaseolus vulgaris inoculated with virulent (V) (025) and weakly virulent (WV) (041) strains of Uromyces appendiculatus

<table>
<thead>
<tr>
<th>Inoculation sequence</th>
<th>L.S.D. P ≤ 0.05</th>
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<tr>
<td>(a) Expt 1. Triticum</td>
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<td>Day 1</td>
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<td>Day 6</td>
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<td>mg spores/100 cm²</td>
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<td>Upper leaf surface</td>
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<td>Lower leaf surface</td>
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<td>(b) Expt 2. Triticum</td>
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<td>(c) Expt 3. Phaseolus</td>
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<td>Day 1</td>
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<td>Day 2</td>
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<td>mg spores/four leaves</td>
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<td>1st collection</td>
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<td>2nd collection</td>
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<td>Total</td>
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Experiment 2: Puccinia striiformis on wheat

This experiment was designed to allow almost simultaneous application of non-virulent inoculum, but to avoid interference due to blocking of stomata, by application of the two types of inoculum to opposite surfaces of the leaf.

Fourteen seedlings of Maris Templar were placed on a Formica surface with the upper (adaxial) surface of the seedling leaf upwards and a further fourteen with the lower (abaxial) surface upwards. The leaves were held in position with narrow strips of transparent adhesive tape and inoculated with spores of the non-virulent race (104 E9) dispersed in talc. A further twenty-eight seedlings, half with the upper and half with the lower surface of the leaves upwards were dusted with talc alone. All fifty-six were then placed with their undusted surface upwards and immediately inoculated with a mixture of talc and spores of the virulent race (41 E136). The seedlings were arranged in fourteen randomized blocks, each of four treatments and all the spores produced were collected in glass tubes and weighed.

From Table 1b it can be seen that virulent inoculum alone resulted in greater spore production when applied to the upper surface of the leaf than when applied to the lower surface. Similarly non-virulent inoculum significantly (P < 0.05) reduced sporulation of the virulent race when applied to the upper surface but not significantly when applied to the lower surface of the leaf.

Experiment 3: Uromyces appendiculatus on beans

Seedlings of the bean cv. Brown Kentucky Wonder (USDA 814) were grown singly in 7.5 cm diameter plastic pots in a controlled environment chamber (12 h dark at
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14 °C and 12 h with 8600 lux at leaf level at 26 °C). The primary leaves of 112 seedlings at 20 days old were wetted with water containing a wetting agent (Tween 80). Half the seedlings were then dusted with talc and the other half with a mixture of talc and spores of *U. appendiculatus* (Ugandan isolate 041) weakly virulent to Brown Kentucky Wonder, giving a grade 3 infection type (Crispin & Dongo, 1962). All seedlings were incubated for 24 h in sealed black polyethylene bags; half the seedlings from each group were then (day 2) inoculated with a mixture of talc and spores of a virulent isolate of *U. appendiculatus* (Ugandan isolate 025, grade 4-5 infection type). The remaining twenty-eight seedlings previously inoculated with talc alone were inoculated with a 1:1 mixture, by weight, of isolates 025 and 041 dispersed in talc, adjusted so that the concentration of spores of isolate 025 was equal to that in the previous treatment in which it was used. The remaining twenty-eight seedlings, previously inoculated with isolate 041, were dusted with talc alone. After incubation in polyethylene bags the plants were placed in seven randomized blocks each with four treatments, each plot containing four seedlings. Spores were collected 19 and 22 days after the second inoculation, using a cyclone spore collector (Tervet & Cassell, 1951) and weighed.

Sporulation of the virulent race (025) of *Uromyces appendiculatus* on Brown Kentucky Wonder beans was reduced by prior or simultaneous inoculation with a weakly virulent race (Table 1c). Between the first and second spore collections the sporulation declined on plants inoculated with virulent inoculum only, but that on plants inoculated with weakly virulent inoculum did not. Because not all spores were collected in this experiment it is not known whether total sporulation was reduced by application of weakly virulent inoculum, but there was undoubtedly a delay in reaching maximum spore production.

**DISCUSSION**

Our results show that resistance induced by application of non-virulent races can delay and reduce sporulation resulting from infection with virulent races. This occurred even when virulent and non-virulent inocula of *P. striiformis* were applied almost at the same time (Expt 2) and when a weakly virulent rather than a completely non-virulent race was used to induce resistance (Expt 3). An application of non-virulent *P. striiformis* to the upper surface also reduced sporulation of the virulent race on the lower surface of wheat leaves thus confirming the finding of Cheung & Barber (1972) that induced resistance includes an inducible active process and is not solely due to blocking of stomata. All these factors would increase the chances of induced resistance affecting disease development in the field.

Multiline varieties with a mixture of resistant and susceptible lines could provide a suitable environment for the occurrence of induced resistance and we suggest that this probably constitutes one of the mechanisms contributing to the resistance of such varieties. Several authors have reported that resistance to rust fungi can be induced by inoculation with rust spores from another species (Yarwood, 1956; Johnston & Huffman, 1958; Littlefield, 1969). We suggest that such resistance could also limit the development of disease where different crops are grown in mixtures as with dredge
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corn, or in some of the intercropping systems which are commonly practised in tropical agriculture.

We are carrying out trials designed to detect effects of induced resistance in the field and intend to publish the results in a subsequent paper.

REFERENCES


