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Seasonal Effects on Rust Disease (*Puccinia lagenophorae*) of *Senecio vulgaris**

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Abstract

The impact of phytopathogens upon their hosts, and hence their potential effectiveness in weed control, depends intimately on environmental conditions which affect both pathogen epidemiology and, through stress, the physiological state of the host. The effects of rust (*Puccinia lagenophorae*) on groundsel (*Senecio vulgaris*) have been studied in summer and under the more stressful conditions prevailing overwinter. Field grown groundsel, infected with rust in autumn, showed 70% mortality by spring whereas in controls mortality was only 40%. Rust-infected plants were more liable to die, both as seedlings, due to hypocotyl infections, and during severe winter weather. However, since the pathogen failed to overwinter, surviving plants were able to produce abundant seeds, so reducing the net effect of autumn inoculation. During summer rust caused little mortality but its cumulative effects throughout host development resulted in a substantial reduction in seed output.

The contrasting effects of rust in winter and summer are discussed in terms of maximizing the effectiveness of phytopathogens in weed control.

Keywords: Groundsel, *Senecio vulgaris*, rust disease, *Puccinia lagenophorae*, biocontrol, mycoherbicide

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1. Introduction

In the context of weed control by chemicals, Gressel and Segel (1982) distinguished 'knockdown', the initial kill soon after herbicide application, from 'effective kill' (E.K.) which is the overall effect of treatment on seed production. Even where knockdown approaches 100%, the capacity of a few surviving plants to make compensatory increases in seed production may reduce E.K. substantially below that due to the initial knockdown.

In naturally occurring epidemics, few phytopathogens, least of all obligate biotrophs such as rusts, cause sufficient injury to their host to result in its death; their knockdown effect is negligible. However, even in the absence of mortality the accumulated effects of infection throughout host development may substantially inhibit seed production. Hence, phytopathogens, unlike chemical herbicides, may cause E.K.s substantially greater than their initial knockdown. Large E.K.s over successive generations may substantially reduce weed populations, as seen in such successful examples of the 'classical' biocontrol tactic (Templeton et al., 1979) as the Chondrilla — *Puccinia chondrillina* interaction. However, substantial E.K.s without pronounced knockdown do not achieve weed-free, 'clean', crops comparable to those achieved by chemical herbicides. If the mycoherbicide approach is to compete with chemi-herbicide treatments, the absence of knockdown, albeit partly cosmetic, may be a major disadvantage.

Various strategies might be expected to improve knockdown without diminishing longer term effects on the growth of survivors. Massive inoculation densities are one possibility. An alternative is to exploit interactions between phytopathogens and abiotic environmental stresses. We have investigated the role of a range of environmental stresses in the ecology of groundsel (*Senecio vulgaris* L.) infected with rust (*Puccinia lagenophorae* Cooke). While our studies have not been directed specifically towards weed control, our results may be relevant in devising strategies for optimizing the efficiency of phytopathogens in biocontrol. We report here two experiments conducted in the field in summer and in the more stressful conditions of winter. While stresses occurring during winter are complex, water stress may be an important component. We have investigated water stress induced by both drought and soil freezing in greater detail in controlled environments (Paul and Ayres, 1984; 1985).

Table 1. Key differences between the summer and winter field experiments, (see Paul and Ayres, 1986a, b).

	Sowing Date	Pricking-out Date	Inoculation Date	Transfer to field Date	Planting density m^{-2}	Harvest interval (weeks)
Winter	14 Sept 81	12 Oct 81	19 Oct 81	19 Oct 81	400	4
Summer	24 May 82	18 June 82	23 June 82	25 June 82	200	1

2. Materials and Methods

Experiments were conducted at the same field site in summer and winter, using similar techniques. Key differences between the two experiments are listed in Table 1; the following methods were common to both.

In order to minimize genetic variation, uniform selected lines of both *S. vulgaris* and *P. lagenophorae* were used. Both were selected from a natural population on the campus of the University of Lancaster. Seeds were sown in trays of Levington compost (Fisons plc) which remained in an unheated glasshouse until the first true leaf appeared. Seedlings were then pricked-out into large tubs (45.8×30×13.2 cm deep) filled with John Innes No. 2 compost. Tubs were transferred to a field site, on the University campus, at a height of 25 m above sea level. In order that temperatures in the tubs should be similar to those of undisturbed field soil, each tub was sunk into the ground until its top was at the same level as the surrounding soil. All plants in half the tubs were inoculated by an aeciospore suspension applied to all leaf surfaces using a camel-hair brush. Plants in the remaining tubs served as rust-free controls. In winter plants were infected *in situ* but in summer, because conditions were less suited to infection, all tubs were transferred to a controlled environment more favorable for infection (Paul and Ayres, 1984). Tubs were returned to the field two days later. In both experiments mortality was assessed weekly and destructive harvests were made at regular intervals (see Table 1).

Interactions between rust and soil necrotrophs

Pots, each containing 25 groundsel seedlings, were held at 10°C under a photon flux density of 200μmole quanta $m^{-2}s^{-1}$ for a 10 hr day. Humidity was kept near saturation by frequent watering to encourage damping-off. Seedlings either remained uninoculated or were inoculated

(a) with *P. lagenophorae*; (b) with soil necrotrophs (from soil at the field site); or (c) with rust and necrotrophs together. All plants in a pot received the same treatment. Mortality was assessed after 4 weeks.

3. Results

The effect of rust on groundsel during summer

During summer, environmental conditions were consistently favorable to the growth and development of both host and pathogen. Indeed, inoculated plants became very severely rusted. Little mortality was observed in either control or inoculated populations until after plants had commenced flowering, when mortality in both treatments was associated with the rapid senescence of plants which had begun to set seed (Fig. 1). In inoculated populations senescence occurred from 5 weeks after the date of inoculation (5 w.a.i.), that is some 3 weeks earlier than in control populations. However, once senescence had commenced, rates of mortality were similar in both control and rusted populations. One consequence of the earlier onset of senescence and mortality of rusted plants was a reduction in the duration of reproduction. This factor, together with reduced vegetative growth earlier in development, substantially inhibited capitulum production in inoculated populations (Fig. 2). Reduced capitulum production was the primary factor limiting the potential reproductive output of populations, which was approx. 25,000 florets m^{-2} in rusted stands, some 60% lower than that of controls (64,000 florets m^{-2}).

The effects of rust on overwintering groundsel

Growth of both host and pathogen populations was slower in autumn than in summer. Nonetheless, the frequency of infection showed a typical sigmoid increase (Fig. 3) reaching a mean intensity of c.1.5 pustules per cm^2 leaf by 12 w.a.i. However, rust was not distributed uniformly between plants in the inoculated population. As rust spread after the initially uniform inoculation, a relatively small proportion of host plants came to support much of the pathogen population (Fig. 4). Variation in the distribution of infection within populations and within tissues of individual plants became crucial in determining the effects of rust on its host population.

In autumn, rates of seedling mortality in the first 2 weeks following inoculation were substantially increased by rust infection. At the end of this period, 30% of all inoculated seedlings had died compared with only 4% of those in control populations (Fig. 5). However, during this initial phase, mortality of seedlings with infections confined to the leaves was only slightly higher (6%

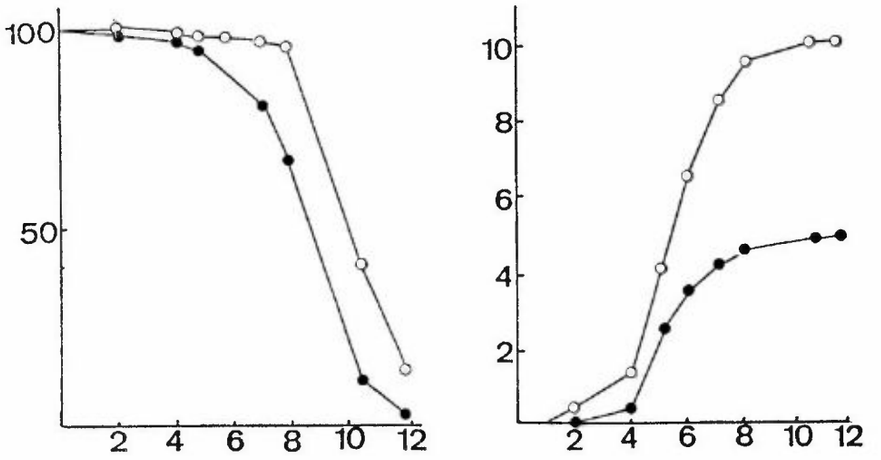

Figure 1. Mortality of control (o — o) and rust-infected (• — •) groundsel plants grown in the field during summer (From Paul and Ayres, 1986c).

Figure 2. Cumulative production of mature capitula in control (o — o) and rusted (• — •) groundsel populations during summer.

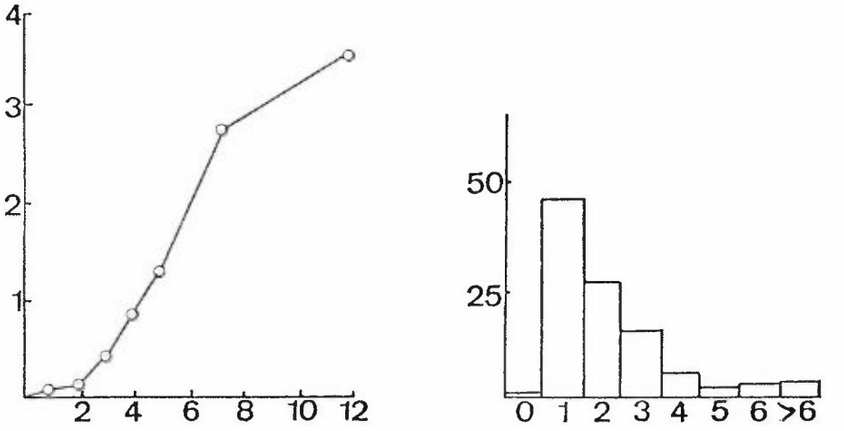

Figure 3. Frequency of rust infection within groundsel populations inoculated early in autumn.

Figure 4. Frequency distribution of the intensity of rust infection (pustules $plant^{-1}$) within inoculated groundsel populations in autumn.

week^{-1}) than that of uninfected controls (2% week^{-1}). The increased mortality in inoculated populations was attributable to the occurrence of rust infections on the hypocotyl which resulted in a very high risk of mortality (up to 57% week^{-1}). Rates of mortality in inoculated populations declined from 3 w.a.i. This did not appear to be due to any decline in damage caused by rust pustules on the hypocotyls but rather because fewer new hypocotyl infections occurred. Indeed, from c. 6 w.a.i. (when plant dry weight was approx. 40 mg), hypocotyl infections were exceptional although rust continued to increase in frequency on the leaves.

Hypocotyl rust-infections often caused symptoms closely resembling those produced by necrotrophic 'damping-off' pathogens, i.e. browning and water soaking of the tissues which eventually girdled the hypocotyl and killed the seedling. Under controlled environment conditions, inoculation with rust alone, or with soil pathogens alone, caused increases in mortality compared with uninoculated controls (Fig. 6). Rust and soil-borne pathogens together caused 76% mortality, substantially more than would be expected from the effect of either factor alone, suggesting that a greater than additive interaction may occur between *P. lagenophorae* and soil-borne necrotrophs.

Rates of seedling mortality were similar in rusted and control populations from 3 w.a.i. until the onset of severe winter weather (12 w.a.i.). While mortality of control plants increased during severe conditions, controls appeared consistently less vulnerable to winter injury than were inoculated plants (Fig. 5). The risk of mortality was not equal for all plants in inoculated populations; the smallest plants were most susceptible to winter-kill. However size *per se* was not the determining factor since control plants suffered substantially less injury than infected plants of comparable dry-weight or leaf area. Within inoculated stands it was small plants which sustained the highest intensities of infection, and, particularly early in winter, injury was closely correlated with the intensity of infection (Fig. 7).

By the onset of regrowth in spring (16–20 w.a.i.) only 40% of inoculated plants survived, compared with 70% of controls (Fig. 5). Furthermore, surviving inoculated plants were significantly smaller than controls: for example mean leaf areas were only 1.98 cm^2 per plant, approximately half that of controls (3.80 cm^2). Leaf area per unit ground area was some 70% lower in inoculated than in control stands. Even when rusted plants survived into winter, infected tissues proved exceptionally vulnerable to injury with the result that no infections survived overwinter. Thus, in spring all plants, including those infected during autumn, were free of rust. A proportion of

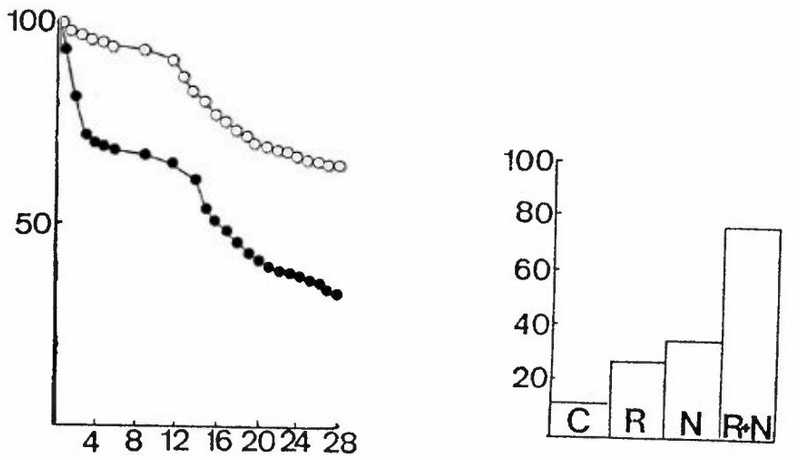

Figure 5. Mortality of control (o — o) and rusted (• — •) groundsel plants following inoculation early in autumn (from Paul and Ayres, 1986a).

Figure 6. Mortality of groundsel seedlings in controlled environments. Seedlings were either uninoculated (C), or inoculated with rust along (R), soil pathogens alone (N) or with both rust and soil pathogens (R+N).

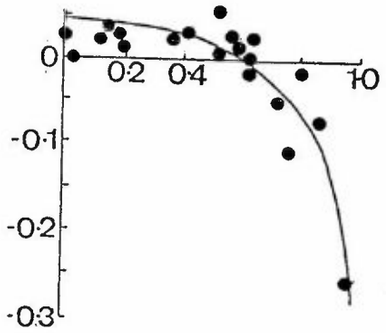

Figure 7. Relationship between the severity of rust infection (pustule weeks cm^{-2} leaf area) and winter injury 12 w.a.i. (from Paul and Ayres, 1986a).

plants in inoculated populations was able to exploit the exclusion of rust and grew vigorously throughout spring. In terms both of vegetative growth and seed production per unit area, this regrowth compensated for earlier winter injury. Thus, the overall effect of rust infection in autumn was to reduce seed production per unit area by some 60% compared with controls.

4. Discussion

In summer rust infection resulted in an E.K. of 60% despite the absence of any knockdown mortality. In the winter experiment the initial knockdown was 30% within 3 weeks, and 70% following winter-kill, but E.K. was again 60% because surviving plants showed compensatory increases in reproduction. The procedures used in these experiments, particularly the low inoculation intensity, were not designed to control groundsel but nonetheless resulted in quite substantial E.K.s. The results also suggested a variety of methods by which E.K. and especially knockdown might be increased.

Firstly, young seedlings were prone to rust-induced mortality. Thus, applying the pathogen at this brief critical stage is more likely to be effective in autumn than in summer when growth is most rapid. Inoculation in autumn also exploits the greater vulnerability of infected plants to winter-kill. The cool, damp conditions of autumn may also have favored the 'damping-off' symptoms associated with hypocotyl infection. It seems possible that these may have resulted because infected hypocotyls were susceptible to infection by necrotrophic pathogens. Dimock and Baker (1951) showed that the necrotroph *Fusarium roseum* could colonize and kill *Antirrhinum majus* but that this pathogen infected the host only via sporulating pustules of *Puccinia antirrhini*. Such interactions between rusts and necrotrophs raise the interesting possibility of 'dual' application of phytopathogens as a mycoherbicide strategy.

The potential of this initial knockdown could be most fully exploited if rust could be reintroduced to surviving plants in spring. Since the occurrence of rust at this time was limited by the absence of inoculum, not conditions unfavorable to infection, artificial inoculation would be expected to result in a rapid increase in disease. Severe infection, by limiting host production, should increase E.K. above the level of the knockdown effect. Within crops, competition between the crop and rusted groundsel would further increase E.K. since infection reduces the competitive ability of this host (Paul and Ayres, 1986d). The strategy of autumn inoculation with rust might prove effective in perennial fruit crops, such as blackcurrant, where groundsel, particularly simazine resistant races, often poses severe problems.

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