

# Effects of interactions between nutrient supply and rust infection of *Senecio vulgaris* L. on competition with *Capsella bursa-pastoris* (L.) Medic.

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(Received 11 August 1989; accepted 29 November 1989)

## SUMMARY

*Senecio vulgaris* L., either healthy or inoculated with rust (*Puccinia lagenophorae* Cooke), was grown in monoculture or in mixture with *Capsella bursa-pastoris* (L.) Medic. under high or low nutrient conditions. At harvests made 7, 9, and 11 weeks after sowing, uninfected *S. vulgaris* progressively outcompeted *C. bursa-pastoris* under nutrient-rich conditions. Rust infection eliminated the competitive advantage of *S. vulgaris* over *C. bursa-pastoris* under high nutrient conditions. In contrast, under low nutrient conditions *C. bursa-pastoris* outcompeted uninfected *S. vulgaris* and infection with *P. lagenophorae* resulted in no additional competitive disadvantage to its host. The reduced competitiveness of rusted *S. vulgaris* under high nutrient conditions was associated with reductions in root growth in mixtures that were greater than those caused by rust in monocultures.

The effects of nutrient supply, rust infection and competition on tissue concentrations of nitrogen, phosphorus and potassium were complex and often influenced by interactions between these factors. Increasing the nutrient supply increased nitrogen concentrations ([N]) in *S. vulgaris*, as did rust infection, but the effects of infection were confined to monocultures. In general [N] in *C. bursa-pastoris* showed rather less variation. Phosphorus concentrations ([P]) in *C. bursa-pastoris* increased with nutrient supply but under nutrient-rich conditions were reduced by competition. In *S. vulgaris* [P] increased with increasing nutrient supply and with infection but in both cases responses were confined to monoculture. Potassium concentration ([K]) in *S. vulgaris* was increased by rust, especially in mixtures. In *C. bursa-pastoris* [K] under high nutrient levels was higher in mixtures than in monoculture.

The mechanisms by which the effects of rust on host competitiveness differed under high and low nutrient conditions are considered and the implications for our understanding of the role of rusts in natural vegetation are discussed.

Key words: *Senecio vulgaris*, *Puccinia lagenophorae*, rust, competition, nutrient supply.

## INTRODUCTION

Infection by the host-specific rust fungus *Puccinia lagenophorae* Cooke reduces the ability of *Senecio vulgaris* L. (groundsel) to compete with uninfected plants of the same species (Paul & Ayres, 1986a, 1987a), with lettuce (*Lactuca sativa* L.) (Paul & Ayres, 1987b) and with *Euphorbia peplus* (Paul, 1989a). The reduced competitiveness of rusted *S. vulgaris*, especially under drought conditions (Paul and Ayres, 1987a), is consistent with the deleterious effects of infection on carbon fixation and water relations (Paul & Ayres, 1984). Thus, it is of interest that rates of nutrient uptake per unit root dry weight were higher in rusted *S. vulgaris* than in uninfected

controls (Paul & Ayres, 1988a, b; Paul, Laxmi & Ayres, 1990). The tendency for nutrient acquisition to be increased in rusted plants suggests that the deleterious effects of rust on the competitiveness of *S. vulgaris* might be less severe in nutrient deficient media than under more fertile conditions. (Paul, 1989b). Here we report an experimental test of this hypothesis. The effect of rust infection of *S. vulgaris* on competition with *Capsella bursa-pastoris* (L.) Medic. (shepherd's purse), another weedy annual, was compared under nutrient-rich conditions, similar to those used in our previous investigations of competition (Paul & Ayres, 1986a, 1987a, b; Paul, 1989a), and in an unfertilised field soil (Paul, Laxmi & Ayres, 1990).

## MATERIALS AND METHODS

*Cultivation and inoculation*

Seeds of uniform lines of the two species were sown in seed trays kept in an unheated glasshouse. *C. bursa-pastoris* was sown on 14 June 1988 and *S. vulgaris*, which germinates more quickly, seven days later. Uniform seedlings were pricked-out into plastic tubs (17 × 17 × 15 cm deep) on 5 July 1988, when both species were at the two leaf stage. All tubs were immediately transferred to the field and sunk so that their rims were level with the soil surface. This ensured that soil temperature within the tubs was close to that occurring naturally in the field and prevented excessive water-loss.

Plants were grown in a 1:1 mixture of field soil and sharp sand which at the beginning of the experiment contained 21.7 mg N, 16.1 mg P and 162 mg K per tub (NO<sub>3</sub> was extracted in distilled water, NH<sub>4</sub> in 6% NaCl and P and K in 2.5% acetic acid: Allen *et al.*, 1974). A low nutrient treatment received no additional fertiliser and for the high nutrient treatment 9.6 g N, 5.9 g P and 15.9 g K were added as John Innes Base Fertiliser, and in addition 83 mg N, 36 mg P and 69 mg K were supplied in 500 ml of a dilute fertiliser solution (Maxicrop, Maxicrop Garden Products, Cambridge) at weekly intervals from 4 weeks after pricking-out. On these occasions 500 ml of distilled water was added to low nutrient tubs. All tubs were freely watered throughout the experiment. Plants were supported and confined within the area of the tub (290 cm<sup>2</sup>) by 0.5 cm plastic mesh.

A simple replacement series design was used (DeWit, 1960) consisting of monocultures of the two species and a 1:1 mixture at a single planting density of 16 plants per tub (c. 560 plants m<sup>-2</sup>). In half of the *S. vulgaris* monocultures and mixtures all plants of *S. vulgaris* were inoculated with an aeciospore suspension of *P. lagenophorae* (see Paul & Ayres, 1987a) on 14 and 19 July. Weather conditions throughout the experiment were cool with frequent rain and these conditions allowed severe natural rust-infection to occur after the initial inoculations. In order to prevent serious cross-infection of control populations the systemic fungicide Plantvax (75% oxycarboxin w.p., Applied Horticulture, U.K.) was applied at weekly intervals from 9 August. At the rate of application used (0.75 g a.i. l<sup>-1</sup>) this compound has been found to have no direct effects on the growth of either *S. vulgaris* or *C. bursa-pastoris* (Paul & Ayres, unpublished). Oxycarboxin treatment did not wholly prevent rust-infection of controls, especially later in the course of the experiment, but such infection was very slight compared with the severe and uniform infection of inoculated plants that was evident from 21 July.

*Harvest procedures and nutrient analyses*

Four replicate tubs of each treatment were harvested 3, 5 and 7 weeks after the initial inoculation with rust. At harvest the root ball was removed from the tub and the roots carefully washed free of soil. Once clean the root systems of individual plants were separated and shoots excised at soil level. Roots and shoots were blotted dry, and dry weights determined after drying to constant weight in a forced draught oven at 80 °C.

After weighing, the roots and shoots of all plants of each species taken from a replicate tub were combined and ground using a hammer mill with a 0.2 mm mesh. Ground material was digested and analysed for phosphorus and potassium utilising the methods of Allen (1982) modified as we described previously (Paul & Ayres, 1988a). Briefly 10–30 mg of dried, ground plant material was digested in 5:1 perchloric: nitric acid under reflux. Digests were made up to a known volume, subsamples taken and the concentration of phosphorus (as phosphate) determined spectrophotometrically using the vanadomolybdate method (Allen, 1982), and that of potassium by flame photometry. For nitrogen analysis 20–40 mg of ground, dried tissue was subjected to Kjeldahl digestion with a selenium catalyst. The concentration of nitrogen (as ammonia) was determined spectrophotometrically by the indophenol reaction (Allen *et al.*, 1974).

*Analysis of competition and statistics*

Competitive interactions between species were determined by the relative crowding coefficient of *S. vulgaris* over *C. bursa-pastoris* ( $K_{SC}$ , DeWit, 1960):

$$K_{SC} = \frac{S_x}{C_x} \div \frac{S_M}{C_M}$$

where  $S_x$  and  $C_x$  are the mean yield per plant of *S. vulgaris* and *C. bursa-pastoris* respectively in mixture and  $S_M$  and  $C_M$  are mean plant yields in monocultures. Values of  $K_{SC}$  greater than 1.0 indicate that *S. vulgaris* outcompetes *C. bursa-pastoris* while values less than 1.0 show that the second species is the more competitive. The growth of each species in mixture was related to that in monoculture by the expression of relative yields (i.e. yield per tub of the species in mixture/yield in monoculture). The mechanisms by which rust-infection might modify competition between *S. vulgaris* and *C. bursa-pastoris* were considered using the techniques of Hall (1974) who stated that 'As, by definition the value for the relative crowding coefficient ( $K$ ) gives an indication of the intensity of competition taking place, a comparison of  $K$  for dry matter yield with  $K$  calculated for any other growth factors... could give an indication as to the limiting factor in competitive interference'. Thus, the resource which is limiting

competition will have the value of  $K_{sc}$  most different from unity.  $K_{sc}$  was calculated for total plant contents of N, P and K as well as for dry weight.

Data for  $K_{sc}$  values and relative yields were analysed using a two-way (nutrient  $\times$  disease) factorial analysis of variance; those for dry weights and nutrient concentrations by three way (nutrient  $\times$  disease  $\times$  competition) analysis of variance (Sokal & Rohlf, 1981).

## RESULTS

### Competition and dry matter production

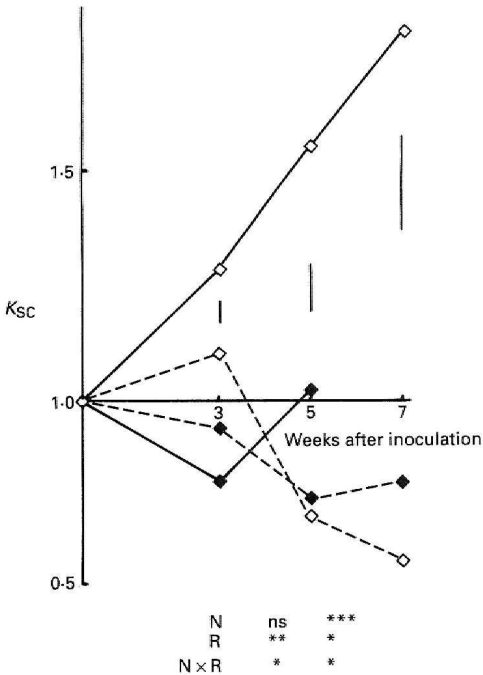
In the high nutrient treatment  $K_{sc}$  for control *S. vulgaris* was significantly greater than 1.0 at the first harvest and increased progressively with time (Fig. 1). The competitive advantage of *S. vulgaris* over *C. bursa-pastoris* was eliminated by rust infection: 3 weeks after inoculation  $K_{sc}$  was significantly less than 1.0, showing that *C. bursa-pastoris* outcompeted *S. vulgaris*, while 5 weeks after inoculation the two species appeared to compete almost equally ( $K_{sc} = 1.03$ ). The relative crowding coefficient for high nutrient rusted populations was not calculated at the final harvest due to substantial die-

back of groundsel, especially in monocultures (see below).

At the first harvest nutrient supply did not greatly alter competitive balance between *C. bursa-pastoris* and *S. vulgaris*, but values of  $K_{sc}$  tended to differ less from unity under low nutrient conditions. Hence, the effect of infection on the competitiveness of *S. vulgaris* was less under low than high nutrient conditions (Fig. 1) and there was a significant ( $P = 0.05$ ) rust-nutrient interaction. By 5 weeks after inoculation the balance of competition was reversed under low nutrient conditions with *C. bursa-pastoris* having a significant competitive advantage over both control and rusted *S. vulgaris* (Fig. 1). The interaction between the effects of nutrient supply and rust was also significant at the second harvest as infection did not significantly change host competitiveness under low nutrient conditions. Similarly, at the final harvest *S. vulgaris* was at a significant competitive disadvantage versus *C. bursa-pastoris* at low nutrient levels but rust infection caused no additional reduction in competitive ability (Fig. 1).

The nature of competitive interactions is considered in detail for the second harvest (the pattern of differences between treatments was similar but less pronounced at the first harvest, while at the final harvest interpretation of the effects of rust were confused by the premature senescence of infected plants).

Replacement series diagrams reveal that under high nutrient conditions the shoot dry weight yield of control *S. vulgaris* in mixture was higher than expected from that in monoculture (i.e. the relative yield of *S. vulgaris* exceeded 0.5, Figure 2a). Rust infection substantially reduced shoot dry weights (Fig. 2b) but had little effect on the balance of competition based on this measurement, reducing the relative yield of *S. vulgaris* shoots from  $0.64 \pm 0.05$  to  $0.59 \pm 0.06$ . By contrast, infection reduced relative yields based on root dry weight to  $0.41 \pm 0.001$  compared with  $0.55 \pm 0.06$  in controls (Fig. 2c, d). Under nutrient-rich conditions, the relative yields of *C. bursa-pastoris* were less than 0.5 for shoots but were unaffected by rust infection of *S. vulgaris* (Fig. 2). The competitive advantage of *C. bursa-pastoris* over *S. vulgaris* under low nutrient conditions was evident in relative yields of both roots and shoots which in all mixtures exceeded 0.5 for *C. bursa-pastoris* and were below 0.5 for *S. vulgaris* (Fig. 2e-h).

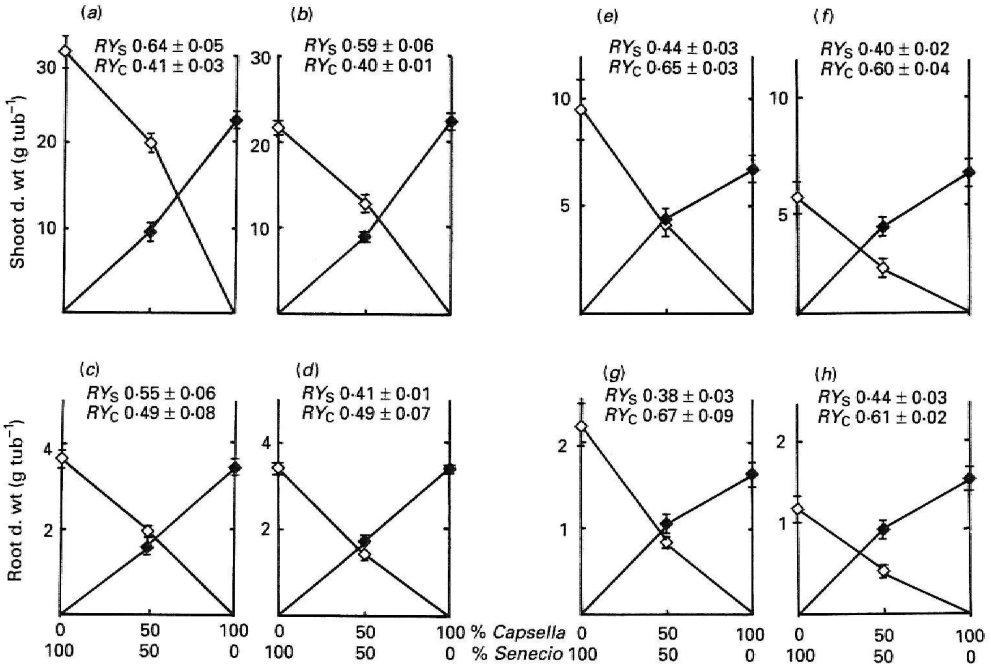


**Figure 1.** The relative crowding coefficient of control (open symbols) or rust-infected (closed symbols) *Senecio vulgaris* over *Capsella bursa-pastoris* at successive harvests under nutrient-rich (solid lines) or nutrient-poor conditions (dashed lines). Points are means of four replicates and bars are least significant differences at  $P = 0.05$ . The significance of the effects of nutrient supply ( $N$ ), rust infection ( $R$ ) and their interaction ( $N \times R$ ) as determined by 2-way factorial analysis of variance are shown.

\*  $P = 0.05$ ; \*\*  $P = 0.01$ ; \*\*\*  $P = 0.001$ .

### Nutrient concentrations

Nitrogen concentrations ( $[N]$ ) averaged for whole plants of *S. vulgaris* were significantly ( $P = 0.001$ ) altered by nutrient supply, rust infection and by competition from *C. bursa-pastoris* but general conclusions about the main effects of nutrients, rust



**Figure 2.** Replacement series diagrams for shoot (a, b, e, f) and root (c, d, g, h) dry weights of *Senecio vulgaris* ( $\diamond$ — $\diamond$ ) and *Capsella bursa-pastoris* ( $\blacklozenge$ — $\blacklozenge$ ) at Harvest 2, (5 weeks after initial inoculation with rust). Plants were grown either at high (a–d) or low (e–h) nutrient and were either inoculated with rust (b, d, f, h) or uninoculated (a, c, e, g). Note that the dry weight scales differ between graphs. Values of relative yields for *S. vulgaris* ( $RY_S$ ) and *C. bursa-pastoris* ( $RY_C$ ) are also shown. All values are means of four replicates  $\pm$  standard errors.

and competition must be made with caution since the three-way interaction between these factors was also significant ( $P = 0.05$ ). However, increasing nutrient supply consistently increased [N] (Fig. 3a, b). Rust infection increased [N] in monocultures, especially under nutrient-rich conditions, but had no significant effects in mixtures. Thus, under high nutrient conditions competition from *C. bursa-pastoris* significantly reduced [N] of rusted but not control *S. vulgaris*. Variations in [N] of *C. bursa-pastoris* were less pronounced than those in *S. vulgaris* although increasing nutrient supply again caused significant increases (Fig. 3). Competition from control *S. vulgaris* had no effect on [N] of *C. bursa-pastoris*. However, in mixtures with rust-infected *S. vulgaris*, [N] in *C. bursa-pastoris* increased compared with monoculture in the nutrient-rich treatment but decreased in the nutrient-poor treatment.

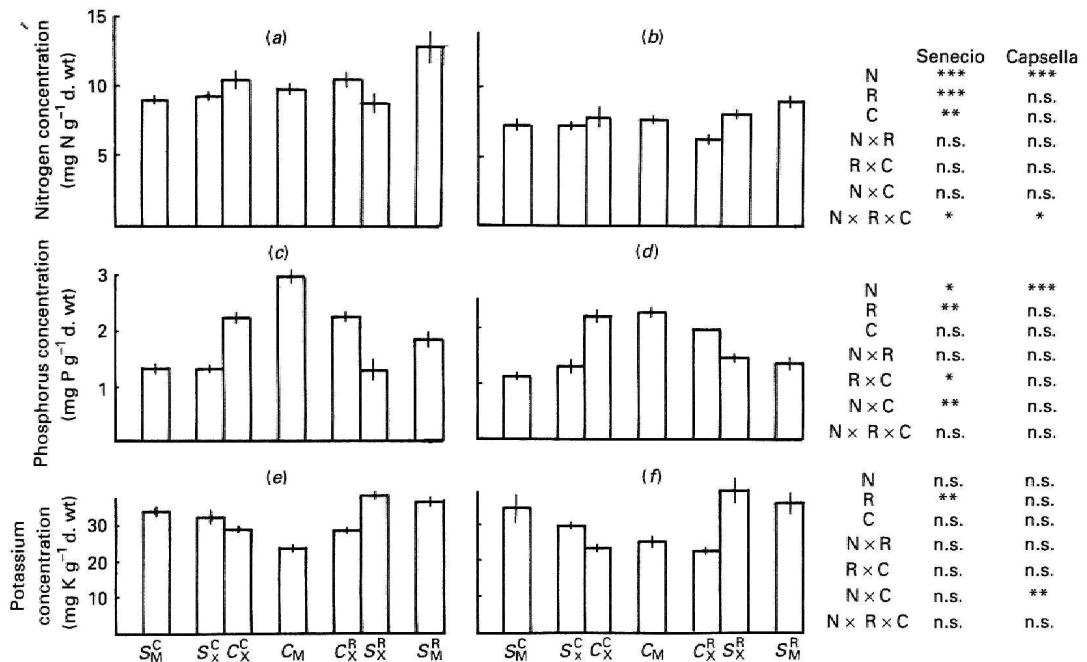
Whole plant phosphorus concentrations ([P]) were rather higher in *C. bursa-pastoris* than *S. vulgaris* but under high nutrient conditions competition from both control and rusted *S. vulgaris* reduced [P] in *C. bursa-pastoris* (Fig. 3c, d). Increasing nutrient supply significantly ( $P = 0.001$ ) increased [P] in both *C. bursa-pastoris* and *S. vulgaris* ( $P = 0.05$ ) but in the latter the effect of nutrient supply was modified by a significant ( $P = 0.01$ ) interaction with competition and responses were largely confined to monocultures

(Fig. 3c, d). Rust infection also increased [P] in *S. vulgaris*, principally under nutrient-rich conditions but these effects were confined to monocultures and the interaction between rust and competition was statistically significant ( $P = 0.05$ ; Fig. 3c, d).

Infection by rust was the only factor to significantly alter whole plant potassium concentrations ([K]) in *S. vulgaris* ( $P = 0.01$ ; Fig. 3e, f). [K] was significantly greater in rusted than control plants under both high and low nutrient conditions. However, under both treatments rust-induced increases in [K] were pronounced only in mixtures with *C. bursa-pastoris* (Fig. 3e, f). Competition from *S. vulgaris* had no significant effects on [K] in *C. bursa-pastoris* under nutrient-poor conditions. However, when nutrients were freely available [K] was significantly ( $P = 0.01$ ) greater in *C. bursa-pastoris* growing in mixture with *S. vulgaris*, whether control or rusted, than in monocultures (Fig. 3e, f).

*Relative crowding coefficients for different resources*

Values of  $K_{SC}$  calculated for different resources showed comparatively little variation (Table 1). When nutrients were freely available rust-infection appeared to reduce the ability of *S. vulgaris* to compete for all the resources investigated, but  $K_{SC}$  was significantly reduced only for plant dry weight and plant nitrogen content (Table 1). By contrast, in



**Figure 3.** Whole plant concentrations at Harvest 2 of nitrogen (a, b), phosphorus (c, d) and potassium (e, f) of control and rust-infected *Senecio vulgaris* and *Capsella bursa-pastoris* under nutrient-rich (a, c, e) and nutrient-poor (b, d, f) conditions. All values are means of four replicates and bars are  $\pm$  standard error at  $P = 0.05$ . The significance of the effects of nutrient supply (N), rust (R), competition (C) and their interactions are shown: symbols as in Figure 1.

Key to columns.  $S_M^C$ , control *S. vulgaris* monoculture;  $S_X^C$ , control *S. vulgaris* in mixture;  $C_X^C$ , *C. bursa-pastoris* in mixture with control *S. vulgaris*;  $C_M$ , *C. bursa-pastoris* monoculture;  $C_X^R$ , *C. bursa-pastoris* in mixture with rusted *S. vulgaris*;  $S_X^R$ , rusted *S. vulgaris* in mixture;  $S_M^R$ , rusted *S. vulgaris* monoculture.

**Table 1.** Relative crowding coefficients, at harvest 2, of healthy and rusted *Senecio vulgaris* over *Capsella bursa-pastoris* under high and low nutrient conditions and calculated for different resources. Means of four replicates  $\pm$  standard errors. \* show that values for control and rusted are significantly different at  $P = 0.05$  as determined by paired *t*-tests

Nutrient supply	Basis of measurement	Basis of measurement			
		Dry weight	N content	P content	K content
High					
Control		1.55 $\pm$ 0.20	1.36 $\pm$ 0.23	1.45 $\pm$ 0.34	1.30 $\pm$ 0.21
Rusted		1.03 $\pm$ 0.29*	0.84 $\pm$ 0.19*	1.13 $\pm$ 0.17	1.22 $\pm$ 0.19
Low					
Control		0.65 $\pm$ 0.08	0.68 $\pm$ 0.09	0.77 $\pm$ 0.15	0.63 $\pm$ 0.11
Rusted		0.68 $\pm$ 0.05	0.71 $\pm$ 0.07	0.76 $\pm$ 0.09	0.83 $\pm$ 0.09*

the low nutrient treatment the only significant effect of rust was to increase the capacity of *S. vulgaris* to compete for potassium,  $K_{SC}$  for all other resources were unchanged by infection (Table 1). The competitive advantage of *C. bursa-pastoris* over *S. vulgaris* was evident in that  $K_{SC}$  was substantially less than 1.0 in all cases.

## DISCUSSION

The substantial reduction in the ability of *S. vulgaris* to compete with *C. bursa-pastoris* that resulted from

rust-infection under high nutrient conditions (Fig. 1) corroborates published studies which have consistently shown that rust infection reduces host competitiveness. These studies have, however, invariably used nutrient-rich media for plant growth. Thus, previous investigations of the effects of *P. lagenophorae* on the competitiveness of *S. vulgaris* (Paul & Ayres, 1986a, 1987b; Paul, 1989a) utilised John Innes No. 2 compost (the high nutrient treatment in the current study), Potter (1987) used John Innes No. 3 compost in studies of the effect of *P. coronata* on competition in *Lolium* spp., while

weekly applications of full-strength Hoagland's solution were used in investigations of *P. chondrillina* on *Chondrilla juncea* (Burdon, Groves & Cullen, 1981; Burdon *et al.*, 1984). In a previous study where we grew *S. vulgaris* in unfertilised field soil, infection by *P. lagenophorae* significantly reduced the competitiveness of its host only under drought conditions (Paul & Ayres, 1987*b*). In that experiment, as here in the low nutrient treatment (Fig. 2), the lack of rust-induced reductions in host competitiveness occurred despite substantial growth reductions in monoculture.

The absence of any rust-induced reduction in competitive ability in *S. vulgaris* under low nutrient conditions in an earlier experiment (Paul & Ayres, 1987*b*) suggests that this effect is not specific to the interaction between *S. vulgaris* and *C. bursa-pastoris*. Nonetheless the particular nutrient requirements of these species may well have influenced the trends observed. In particular, the switch in competitive advantage from *S. vulgaris* under high nutrient to *C. bursa-pastoris* under low nutrient conditions is itself of interest. With increasing nutrient supply shoot:root ratio (S:R) increased by *c.* 60% in *C. bursa-pastoris* but by 90–120% in *S. vulgaris*. The greater investment of dry weight in leaves under high nutrient conditions may have allowed *S. vulgaris* to compete strongly for light. As well as decreasing S:R, nutrient deficiency may also result in substantial increases in specific root length (SRL, root length per unit root dry weight) in *S. vulgaris* (Paul & Ayres, 1986*c*). Rust infection also increases SRL in *S. vulgaris* (Paul & Ayres, 1986*c*; Paul *et al.*, 1990). SRL was not measured here but in populations grown under the same nutrient regimes, but later in autumn, SRL was increased by rust infection, especially in nutrient-rich conditions. *C. bursa-pastoris* showed substantially greater values of SRL which changed little with nutrient supply. Similar changes in SRL occurring here during the summer and combined with the observed changes in dry weight partitioning would have had the result that in low nutrient mixtures the length of *C. bursa-pastoris* root per unit soil volume was 2.5–3.5 times greater than that of *S. vulgaris*. This much more intensive exploitation of the soil mass by *C. bursa-pastoris*, achieved with a comparatively low investment of dry matter because of the high SRL, may have conferred a competitive advantage to this species under nutrient-deficient conditions.

Under low nutrient conditions the increased SRL observed in rusted populations in autumn (see above) was greater in mixture than monocultures. Since there was no marked increase in S:R in rusted plants, such increases in SRL may have allowed rust-infected *S. vulgaris* to exploit soil resources in mixtures relatively more efficiently than controls. In controlled environment studies we showed specific absorption rates (SARs) for N, P and K were higher

in rusted than control plants (Paul & Ayres, 1988*b*; Paul *et al.*, 1990). However, it proved difficult to calculate comparable data from the field studies. Senescence of *S. vulgaris*, particularly of older, rusted leaves, was far more rapid than in the growth room and, combined with frequent heavy rain, this apparently caused substantial losses of acquired nutrients, resulting in large variation in SAR data. However, it seemed that SARs in the field were generally lower than those for pot-grown individuals under comparable nutrient levels but that the effects of infection were broadly similar. Furthermore, the tissue concentrations of N, P and K found in *S. vulgaris* in the field (Fig. 3) were in the same range as in the growth room (Paul *et al.*, 1990). Thus, the responses in nutrient uptake observed in individuals grown in a controlled environment were, in this case, valuable in predicting the effects of *P. lagenophorae* in the field. For *S. vulgaris* growing in the field under low nutrient conditions, SARs for potassium (SAR<sub>K</sub>) between 3 and 5 weeks after inoculation increased from  $47.0 \pm 4.6$  mg K g<sup>-1</sup> week<sup>-1</sup> in control mixtures to  $57.1 \pm 4.1$  mg K g<sup>-1</sup> week<sup>-1</sup> in rusted while comparable figures in monocultures were  $51.7 \pm 4.5$  and  $55.0 \pm 2.6$  mg K g<sup>-1</sup> week<sup>-1</sup>. These changes in SAR<sub>K</sub> will have contributed to the significantly increased ability of rusted *S. vulgaris* to compete for potassium under low nutrient conditions (Table 1). Whether this result can be further attributed to the more efficient exploitation of soil discussed above remains unclear.

The increased ability of rusted *S. vulgaris* to compete for potassium under low nutrient conditions was not reflected in any change in the overall balance of competition with *C. bursa-pastoris*. Hall (1974) noted that the total content of a nutrient element may be a poor indicator of whether sufficient has been acquired to allow normal functioning. This *caveat* may be especially apt for rust-infected plants where an unknown proportion of nutrients will be sequestered by the pathogen (Walters, 1989). Indeed, it may be unwise to attempt to attribute the effects of infection on host competitiveness to any single resource. Certainly in the low nutrient treatment, where growth was clearly nutrient limited, no resource could be identified as having a dominant role and the lack of rust-induced reductions in the capacity of *S. vulgaris* to compete with *C. bursa-pastoris* may well have reflected both the efficient exploitation of soil nutrients and the absence of any inhibition of carbon fixation by rust under these conditions (Paul & Ayres, 1986*b*). In the high nutrient treatment there may be greater justification for attributing the reduced competitiveness of rusted *S. vulgaris* to a depressed ability to compete for light, and for relating this observation to the reduced leaf expansion and photosynthetic rates of infected plants (Paul & Ayres, 1984, 1986*b*). Nevertheless the data is by no means unequivocal and more detailed physio-

logical measurements on competing stands are required before the mechanisms underlying the effects of rust on host competitiveness can be stated with any confidence.

Whatever the underlying mechanisms, the absence of any rust-induced reduction in host competitiveness under low-nutrient conditions may be important when considering the possible effects of these pathogens in natural vegetation. In many habitats plant growth may frequently be more limited by nutrient deficiencies than by light (e.g. Field & Mooney, 1986) and root competition may often be more important than shoot competition in determining the balance between species (Bastow-Wilson, 1988). Hence, the effect of rust infection on competitive interactions under field conditions might be expected to be less than those recorded in nutrient enriched media (see above). The low nutrient treatment used here is not unrealistically impoverished and natural populations of *S. vulgaris*, growing in dunes for example, may well experience lower nutrient concentrations (e.g. Ernst, 1983). In the field the effects of rust on host competitiveness will be influenced by interactions not only with nutrient supply but also *inter alia* by drought (Paul & Ayres, 1987*b*). It is also possible that the reduced effect of *P. lagenophorae* under low-nutrient conditions depends on rust-induced physiological dysfunctions being the primary injury resulting from infection. This may not always be the case, for example rust infection may render the host more vulnerable to infection by secondary necrotrophic pathogens (Hallett, Paul & Ayres, 1990), which resulted in the pronounced die-back of rusted monocultures late in this experiment, or to frost injury (Paul & Ayres, 1986*d*). Such effects might substantially modify rust-nutrient interactions in the field. Equally such interactions may be very different in a ruderal species, such as *S. vulgaris*, than in a host species adapted to nutrient deficient habitats (Paul, 1989*a*, 1990). Nonetheless, in view of the substantial interactions between *P. lagenophorae* and nutrient supply that we have reported here, it would appear advisable that in future investigations of the influence of pathogens on competitive interactions account should be taken of the possible effects of using artificially nutrient-rich media, such as have generally been used to date.

#### ACKNOWLEDGEMENTS

We thank K. A. Laxmi for invaluable technical assistance and R. D. Blackwell for advice on nitrogen analysis. NDP is grateful to NERC for continued financial support.

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