

WATER STRESS MODIFIES INTRASPECIFIC INTERFERENCE BETWEEN RUST (*PUCCINIA LAGENOPHORAE* COOKE)-INFECTED AND HEALTHY GROUNDSEL (*SENECIO VULGARIS* L.)

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SUMMARY

Populations of groundsel (*Senecio vulgaris* L.) were grown in the field in bottomless containers which allowed roots to penetrate freely into the natural soil profile. The 36 plants within each population (equivalent to 1250 m⁻²) were either all inoculated with the rust *Puccinia lagenophorae* Cooke, all rust free, or were a 1:1 mixture of the two. Rain was excluded from all populations by small shelters. Half the populations were subjected to mild drought, whilst remaining populations were well-watered. Rust significantly reduced shoot dry weights, especially in droughted populations. The frequency distributions of shoot dry weight showed significant inequality (were strongly skewed) in all treatments and populations. Inequality of the frequency distribution of shoot dry weight was increased in rusted populations because infection increased the proportion of suppressed individuals. Again the effect of rust was most pronounced under conditions of drought and particularly in mixture. Rust significantly lowered mean shoot water potential (ψ) in dry monocultures and in both wet and dry mixtures. Values of ψ at harvest in suppressed, rusted individuals in mixtures were often highly negative. Compared with dry monocultures, water stress in mixtures was ameliorated in the healthy, but exaggerated in the rusted, components. The more negative values of ψ in rusted populations were the result of changes in frequency distributions as well as in mean values. Under dry conditions status in the dry weight hierarchy was closely correlated with ψ . These changes are interpreted as reflecting the reduced ability of the root systems of rusted plants to compete for limited water.

The competitive ability of control over rusted groundsel, as measured by relative crowding coefficient (K_{cr}), was 1.09 under well-watered conditions but increased to 1.51 under drought. In both well-watered and droughted populations, the greater impact of rust on the population hierarchy of mixtures was reflected in the inverse relationship between the status of sub-classes, based on shoot weight and class K_{cr} . It is concluded that water stress probably plays a crucial role in determining the impact of rust on mixed populations in the field.

Key words: Rust disease, water stress, competition.

INTRODUCTION

Infection by pathogens, including rust fungi (Uredinales), can reduce the ability of the host to compete in mixture with either uninfected plants of the same species (Burdon, Groves & Cullen, 1981; Burdon *et al.*, 1984) or with other non-host species (Groves & Williams, 1975). We reported previously that the rust *Puccinia lagenophorae* Cooke substantially reduced the ability of infected groundsel (*Senecio vulgaris* L.) to compete in mixture with uninfected groundsel when grown in tubs under glasshouse conditions (Paul & Ayres, 1986a). Morphological changes in rusted plants in mixture suggested that these were suffering both root and shoot competition. The nature of the limiting factors for which plants compete may be

crucial in determining the magnitude of any pathogen-induced inhibition of competitive ability. Whilst it may be undesirable to seek to isolate specific factors as the basis of competitive interactions between plants (Harper, 1977), our knowledge of rust-induced changes in host physiology (see, for example, Ayres & Paul, 1986) suggests that variations in the availability of soil water may be particularly significant in determining the impact of infection on competition.

Rusts may be particularly injurious under drought conditions in the field (Wapshere *et al.*, 1974; Ayres, 1978). Under laboratory conditions rusted plants have consistently been found to be more susceptible to drought than uninfected controls. This vulnerability has been attributed partly to increased water loss from infected shoots, and partly to the reduced ability of root systems to obtain water (Ayres, 1985). Results of most pot-based studies of the rust/drought interaction have been influenced by the small volume of soil available for root growth. Under these conditions, soil water deficits are often more extreme and arise far more rapidly than is the case in the field. The effects of such stress may differ from those occurring when comparatively mild water deficits develop relatively slowly and concurrently with plant growth, as may often occur in the field. Under such conditions total water loss from the whole plant may be little changed by rust, despite increased loss per unit leaf area, because of the inhibition of leaf growth which also results from disease (Paul & Ayres, 1984). However, the maintenance of water flux depends upon the rusted plant having access to water as soil drying progresses. Access to soil water in the field will be subject to the effects of rust on the capacity of the root system to exploit water present deep in the soil profile, and on interference from neighbours.

In this study, populations of groundsel were grown in the field under conditions which did not limit the downward growth of roots and which allowed water stress to develop slowly. Monocultures and equiproportional mixtures of control and rusted plants forming a DeWit replacement series (DeWit, 1960) were grown under well-watered and drought conditions with the aim of determining the effect of drought on intraspecific competition between rusted and control plants.

MATERIALS AND METHODS

Propagation and inoculation

Seed of a uniform line of groundsel (*Senecio vulgaris* L.) was sown in seed trays containing a 1:1 mixture of sharp sand and 'Shamrock' peat compost (Irish Peat Development Authority) in an unheated glasshouse on 27 June, 1986. Seedlings were pricked out into their final containers (see below) on 16 July, when they possessed one to two leaves. Each container held a population of 36 plants in a uniform 6 × 6 grid, each plant being 3 cm from each of its neighbours (equivalent to approximately 1250 m⁻²). On 21 July, plants were inoculated with an aqueous suspension of aeciospores of *Puccinia lagenophorae* Cooke applied using a camel hair brush. After inoculation all populations were covered with black polythene sheet for 24 h to provide conditions of darkness and high humidity necessary for infection (Paul & Ayres, 1984). Inoculation was repeated on 29 July and 4 August to ensure high and uniform levels of infection. Within populations either all plants, or alternate plants on the grid, were inoculated (rusted monoculture and 1:1 mixture, respectively) or all plants were left uninoculated (control monoculture). There were 10 replicates of each population, half of which were subjected to drought (see below), giving a 2 by 2 by 2 factorial design with five replicates.

Inevitably, some cross-infection of controls occurred, although in practice it proved a minor problem, perhaps because rain shelters (see below) minimized the periods of leaf wetness required for rust infection. The technique was conservative in that cross-infection served to reduce the magnitude of differences between inoculated and control plants. We consider this preferable to the unknown consequences of using either genetically different lines, or large amounts of fungicides to protect controls (Paul & Ayres, 1986a).

Site preparation and imposition of water deficits

The final containers were bottomless plastic tubs (17 × 17 × 20 cm deep) sunk into the field until their rims were level with the soil surface and back-filled with soil from the site. This permitted root penetration into the natural soil profile below the base of the tubs. The field site was situated on a slight, south-facing, slope at the University of Lancaster Field Station. It was prepared by treating existing vegetation with glyphosate ('Tumbleweed', Murphy plc) followed 10 d later by rotovating twice to a depth of approximately 20 cm. Tubers were placed in position immediately following the final rotovation and soil was allowed to settle for 7 d before groundsel seedlings were pricked out (see below). In order to reduce problems from the germination of naturally occurring weed seeds and to provide a favourable medium for the quick establishment of the experimental plants the natural soil surface was covered with a layer of John Innes No. 2 compost, approximately 1 cm deep.

Droughted and well-watered treatments were assigned to separate but adjacent plots. Plots were covered by identical shelters (2 × 3 m), each constructed of sheets of transparent Perspex ('Novolux', ICI plc) supported on a metal frame approximately 1 m above the soil surface. In order to prevent lateral movement of soil water into the droughted plot, a ditch was excavated to a depth of approximately 20 cm around its perimeter. Populations in the well-watered plots were freely watered twice each week: droughted plots received no water after the shelters were put in place (21 July). Temperatures under shelters were normally less than one degree higher than in an adjacent uncovered site (although this difference increased up to approximately 4 °C on sunny, windless days) and irradiance was reduced by less than 5 %.

Harvest procedures

All populations were harvested on 26 August after severe storms on the previous night had damaged the shelters and filled with rain the ditches surrounding the experimental plots. At the time of harvest the plants were almost 9 weeks old and the initial inoculation had taken place approximately 6 weeks earlier. Plants were excised at soil level and shoot water potential (ψ) in all plants in one tub each of wet and dry monocultures and two populations of each mixture were determined immediately using a Scholander pressure bomb. While the surface soil of the unwatered plots was not wetted by the storm, it seemed possible that water draining down the slope within the soil profile would soon have become available to stressed plants, so allowing some recovery from negative ψ . Under these circumstances it was decided that measurements should be confined to 1 d, before any recovery became pronounced, so measurement of ψ from all replicate populations was rendered impractical. As a result, only 36 values of ψ were obtained per treatment and, in the case of monocultures, these were from only one replicated population. Thus, while the distribution of ψ could be compared between treatments using the Mann–Witney *U* statistic (see below) caution is

necessary in interpretation in view of lack of replication at the population level. The frequency distribution of ψ within populations could, however, be established and related to plant status as measured by shoot dry weight. Individual shoots harvested from all populations were dried to constant weight before dry weights were determined.

Statistics and analysis of interference

Previous studies of groundsel rust have shown that infection results in substantial changes in population structure (Paul & Ayres, 1986a, b). Inequality in the distributions of shoot dry weights and ψ were determined using the Gini Coefficient, G (Weiner & Solbrig, 1984). The distribution of G remains unclear (Weiner & Solbrig, 1984). However, values of G from the five replicates of each of the eight third-order treatments were compared pairwise using the distribution-free Mann-Whitney U statistic (Sokal & Rohlf, 1981). Since it was clear from Gini coefficients that shoot dry weight and ψ were far from normally distributed (see results), the U statistic was used in the same way to compare these parameters. Some measure of the effects of rust, water deficit, competition and their interactions, both on G and harvest data, was made by pairwise comparisons of first- and second-order treatments, again using the Mann-Whitney method. Data for total shoot dry weight per population were more normally distributed and were compared using standard factorial analysis of variance.

Interference was analyzed using the methods of DeWit (1960). Relative yields and relative crowding coefficients of control over rusted (K_{cr}) were determined for well-watered and unwatered populations. In the light of possible changes in population structure and because previous experience suggested that these might be more pronounced in mixture than in monocultures (Paul & Ayres, 1986a), variation in competitive interactions with status within the population hierarchy was examined. This was achieved by dividing all populations into six equal sub-classes on the basis of increasing shoot dry weight and K_{cr} was calculated for each sub-class within each replicate and water-stress treatment.

RESULTS

Interference

Dry weight yield per population [Fig. 1(a), (b)] was substantially reduced both by rust infection ($P < 0.001$) and, more especially, by soil water deficit ($P < 0.001$). There was some evidence of an interaction between rust and drought, but this was not statistically significant ($0.1 > P > 0.05$). Under well-watered conditions relative yields of control and inoculated plants were 0.450 and 0.426, respectively. The difference between control and inoculation plants was not significant but the value for rusted populations was significantly less than 0.5 ($0.05 > P > 0.01$). In contrast, when mixtures were subjected to drought the relative yield of controls was 0.516 whilst that for inoculated populations was 0.401, significantly less than 0.5 and also lower than relative yields of rusted populations under well-watered conditions.

If well-watered and water-stressed treatments are considered together, the overall effect of infection was to cause a significant ($0.05 > P > 0.01$) reduction in relative yields. This was reflected in the reduced competitive ability of infected plants as measured by relative crowding coefficients [Fig. 1(a), (b)]. Under well-watered conditions the mean value of K_{cr} , 1.06, was not significantly greater

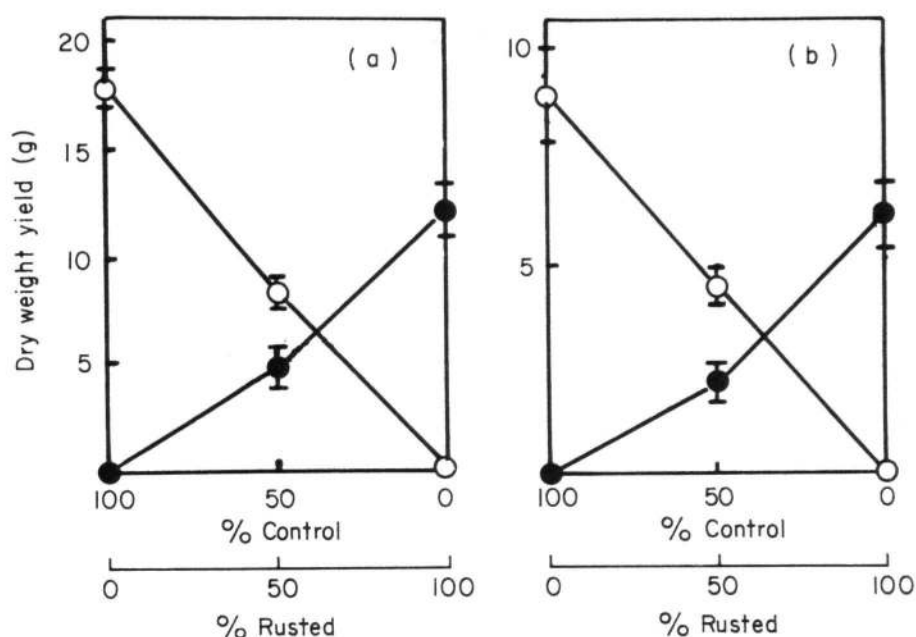


Fig. 1. Replacement series diagram for (a) well-watered and (b) droughted populations of control (○) and rust-infected (●) groundsel. Points are means of five replicates \pm standard errors. The significance of the relative crowding coefficient of control over rusted groundsel (K_{cr}) relative to $K_{cr} = 1$ is shown (*, is significant at $P = 0.05$). (a) $K_{cr} = 1.06$ nsd; (b) $K_{cr} = 1.51$ *

than 1. However, under drought conditions K_{cr} increased to a mean of 1.51, significantly greater than 1 ($0.05 > P > 0.01$) but not when compared with the value obtained in the absence of drought ($0.1 > P > 0.05$). There appeared to be an underlying tendency for infected plants to compete less well in mixture with controls under drought than under well-watered conditions.

Population structure

The distribution of shoot dry weight tended towards positive skewness in all populations. This inequality was reflected in the values of Gini coefficients [Fig. 2(a) to (d)]. The overall effects of competition and water stress on population inequality, as determined by Mann–Whitney comparisons of Gini coefficients, were non-significant (Table 1). In contrast, rust infection caused substantial and highly significant increases in Gini coefficients: rust increased inequality. However, the magnitude of the effect of rust was highly dependent on interactions with other treatments, being significant only in mixtures and more so in water-stressed than well-watered mixtures (Table 1). Inequality increased in rusted populations, or rusted components of mixtures, because plants of low dry weight were even more frequent in proportion to the total population than in the less unequal control populations. In addition, infection consistently reduced the dry weights of the few large plants [Fig. 2(a) to (d)]. Water stress also reduced maximum shoot dry weights within populations, by some 50% in rusted and control monocultures and in controls in mixture, but by almost 70% in the rusted component of mixtures [Fig. 2(a) to (d)].

The effects of rust on population structure were apparent in the variation in relative crowding coefficients between classes of different shoot dry weight. Both under well-watered and water-stressed conditions K_{cr} showed a consistent inverse relationship to shoot dry weight, so the impact of infection on competitive ability was more pronounced on plants of lower status in the hierarchy (Fig. 3). In five of the six dry weight classes this relationship was little changed by water stress: the increase in the value of K_{cr} under dry as opposed to wet conditions was almost

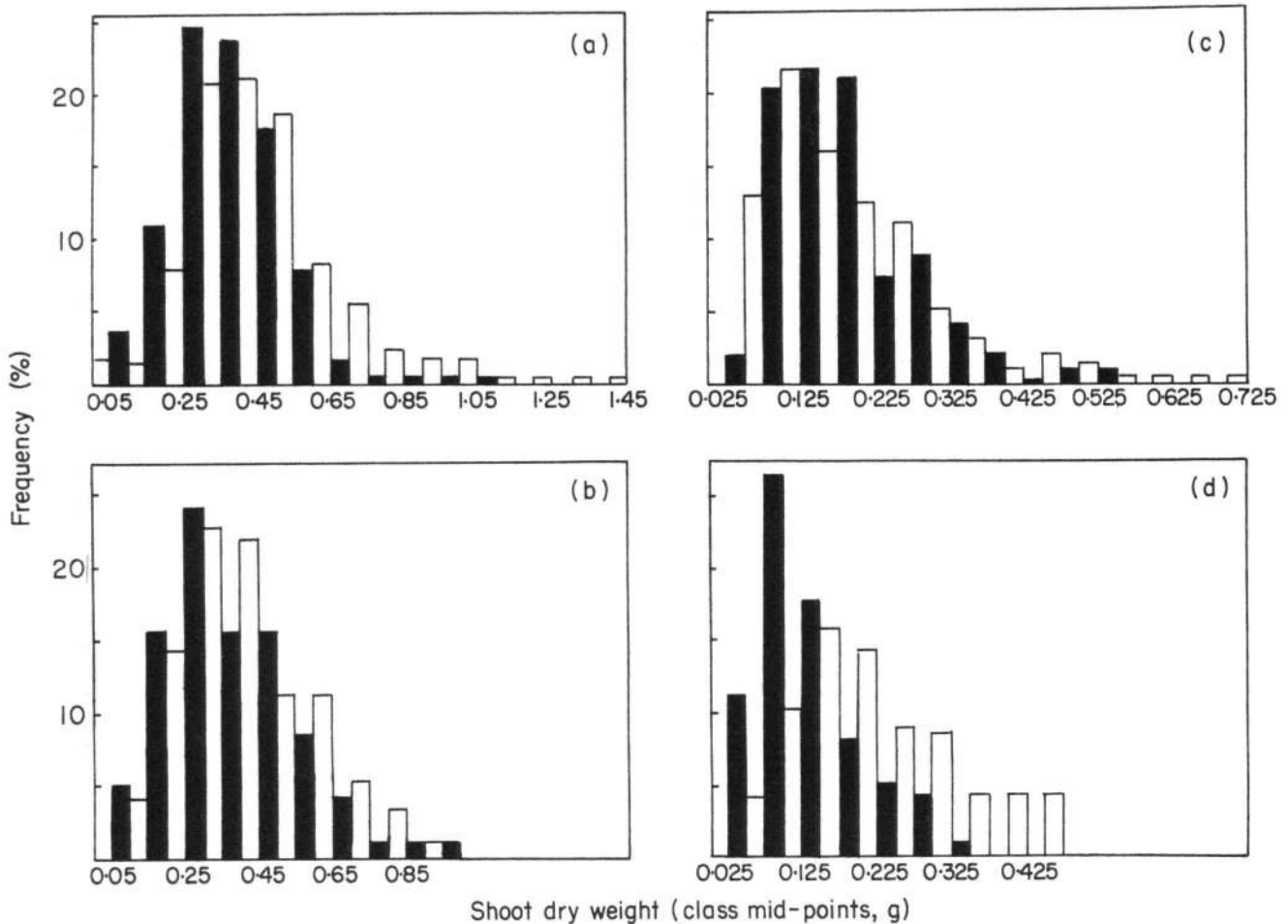


Fig. 2. Frequency distributions of shoot dry weights of control (open bars) and rusted (filled bars) groundsel grown in (a) well-watered monocultures, (b) well-watered mixtures, (c) drought-treated monocultures and (d) drought-treated mixtures. Data are combined from five replicate populations giving total sample sizes of 180 for monocultures and 90 for mixtures. The range of values of the Gini coefficient for the five replicates are shown. (a) Control, 0.349–0.477; rusted, 0.411–0.563; (b) control, 0.383–0.457; rusted, 0.369–0.645; (c) control, 0.297–0.476; rusted, 0.463–0.671; (d) control, 0.369–0.645; rusted, 0.403–0.873.

constant (0.32 to 0.39: Fig. 3). Values of K_{cr} for the class containing plants with lowest shoot dry weights were higher than expected from the trend evident in classes of higher weight, especially under well-watered conditions. Indeed, this class was exceptional in that K_{cr} was greater in well-watered than well-stressed populations (3.32 and 1.94, respectively; Fig. 3).

Water potential of the shoots

Plants in unwatered plots showed evidence of water stress within 2 weeks of the imposition of drought. Both control and rusted plants showed greatly reduced leaf expansion and stem elongation under drought. Conditions were not sufficiently severe to cause wilting in control plants, but rusted plants lost turgor when daytime temperatures were high. Wilting was especially evident in rusted individuals in mixtures but even these plants appeared to recover overnight and were not visibly wilted early in the day.

Under well-watered conditions the frequency distributions of shoot water potential in both monoculture and mixture showed little tendency towards inequality and Gini coefficients were low [Fig. 4(a), (b)]. Rust infection had little effect on either the range or distribution of ψ in monoculture. In mixture, infection resulted in slightly more negative values of ψ ($0.05 > P > 0.01$) but appeared to have no effect on its distribution.

Table 1. The effects of interference, drought and rust infection and their principal interactions on the Gini coefficients of shoot dry weight distributions

(a) Main effects of interference, drought and rust infection combined over all second-order and third-order treatments

	z	P
Interference	0.271	nsd
Drought	1.109	nsd
Rust infection	4.274	***

(b) Two-way interactions between rust and water supply and between rust and interference

Overall significance of rust in:	z	P
Wet (monocultures and mixtures)	2.796	**
Dry (monocultures and mixtures)	3.326	***
Monoculture (wet and dry)	0.756	nsd
Mixture (wet and dry)	3.024	**

(c) Three-way interactions (i.e. pairwise comparisons of third-order treatments. Only statistics relevant to rust and its interactions are presented)

Effect of rust in:	Wet	Dry
Monoculture	nsd	**
Mixture	*	***

* Significant at $P = 0.05$; ** significant at $P = 0.01$; *** significant at $P = 0.001$. nsd, not significantly different. Comparisons were made by the non-parametric Mann-Whitney U test using the large sample approximation (z) in (a) and (b) and the Mann-Whitney statistic (U_s) in (c) (Sokol & Rohlf, 1981). The range of values of the Gini coefficient is shown for each treatment in Figure 1.

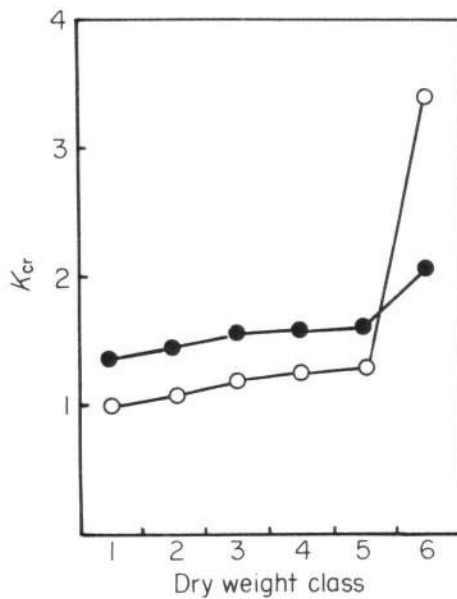


Fig. 3. The relationship between the relative crowding coefficient of control over rusted groundsel (K_{cr}) and status in the population hierarchy, based on shoot dry weight, under well-watered (\circ) and drought (\bullet) conditions. Class 1 contains plants of greatest shoot dry weight, class 6 plants of lowest weight.

Drought induced a pronounced lowering in ψ in all treatments (Fig. 4). Water deficit caused only slight changes in the inequality of the frequency distributions of ψ in monocultures; there was a small decrease in controls and a small increase in rusted shoots [Fig. 4(a), (c)]. However, these small but opposing changes were sufficient to result in a considerable difference in the values of G between control and infected monocultures under drought, which contrasted with the negligible effect of rust in well-watered monocultures. This rust-induced change in the distribution of ψ under water-stressed conditions had the result that, even though

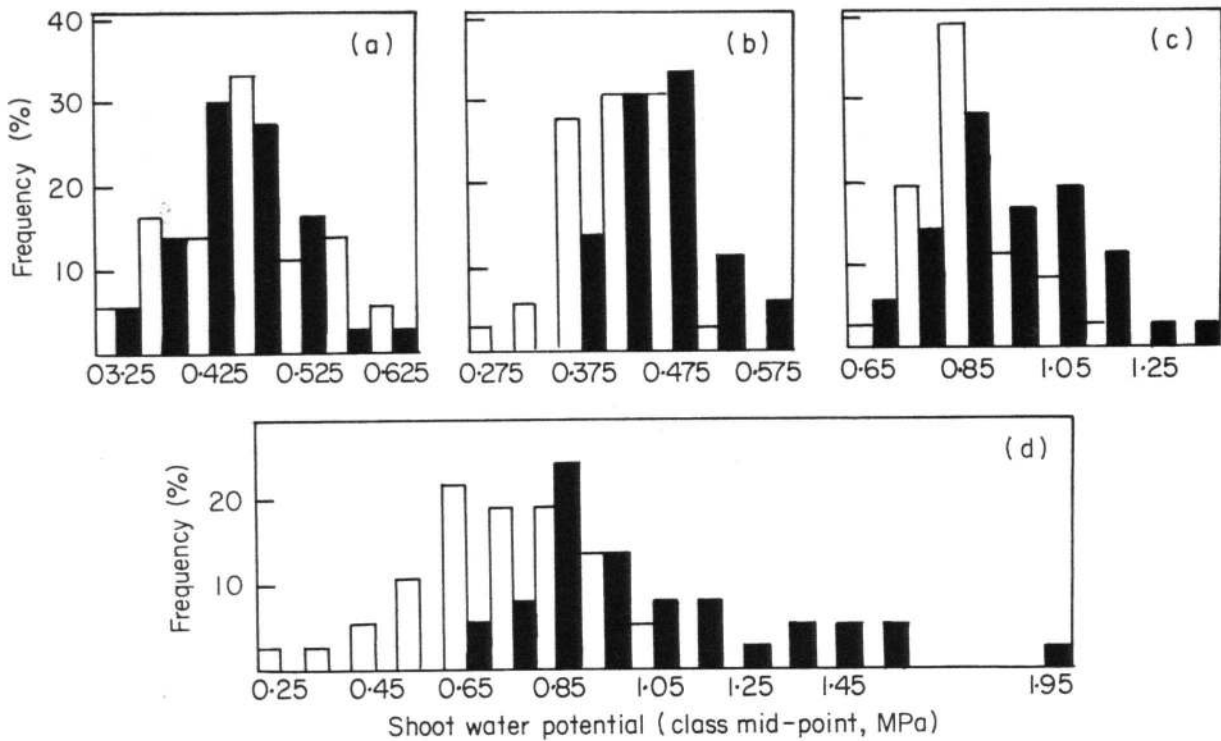


Fig. 4. Frequency distributions of shoot water potentials (ψ) of control (open bars) and rusted (filled bars) groundsel grown in (a) well-watered monocultures, (b) well-watered mixtures, (c) drought-treated monocultures and (d) drought-treated mixtures. Total sample size is 36 in all populations. Values of the Gini coefficient (G) and of mean ψ are shown for each population. (a) Control G , 0.177 (mean, 0.458); rust G , 0.168 (mean, 0.445). (b) Control G , 0.141 (mean, 0.416); rust G , 0.114 (mean, 0.456). (c) Control G , 0.153 (mean, 0.864); rust G , 0.201 (mean, 0.931). (d) Control G , 0.254 (mean, 0.725); rust G , 0.313 (mean, 1.063).

infection reduced mean ψ by only 0.07 MPa, the effect of rust was significant as determined by the Mann-Whitney test ($P < 0.001$).

The value of G for ψ in rusted components of stressed mixtures (0.31) was the highest recorded in any population. The frequency distribution was distinctly positively skewed: in the majority of plants ψ was near -0.80 MPa but in some values of ψ were far more negative, the lowest being -1.92 MPa [Fig. 4(d)]. The distribution of ψ in the control component of dry mixtures also showed substantial inequality ($G = 0.254$) but, in contrast to the rusted component, this resulted from negative skewness [Fig. 4(d)]. Whilst the values of ψ in many control and rusted plants in stressed mixtures were in the range -0.60 to -1.00 MPa, in remaining individuals they were very different. Overall, in droughted mixtures rust resulted in decreases in ψ , which were significant as determined by the Mann-Whitney U test ($P < 0.001$), although the mean value changed by only 0.34 MPa [Fig. 4(c), (d)].

Under well-watered conditions there was no significant correlation between shoot water potential and status in the dry weight hierarchy in any population [Fig. 5(a), (c)]. By contrast, in water-stressed populations there were highly significant negative correlations in all cases [Fig. 5(b), (d)]. In both dry monocultures and the control component of mixtures the relationship between ψ and shoot dry weight appeared to be approximately linear (Fig. 5). By comparison, this relationship appeared to be curvilinear in the infected component of mixtures, individuals of low dry weight status having exceptionally negative water potentials.

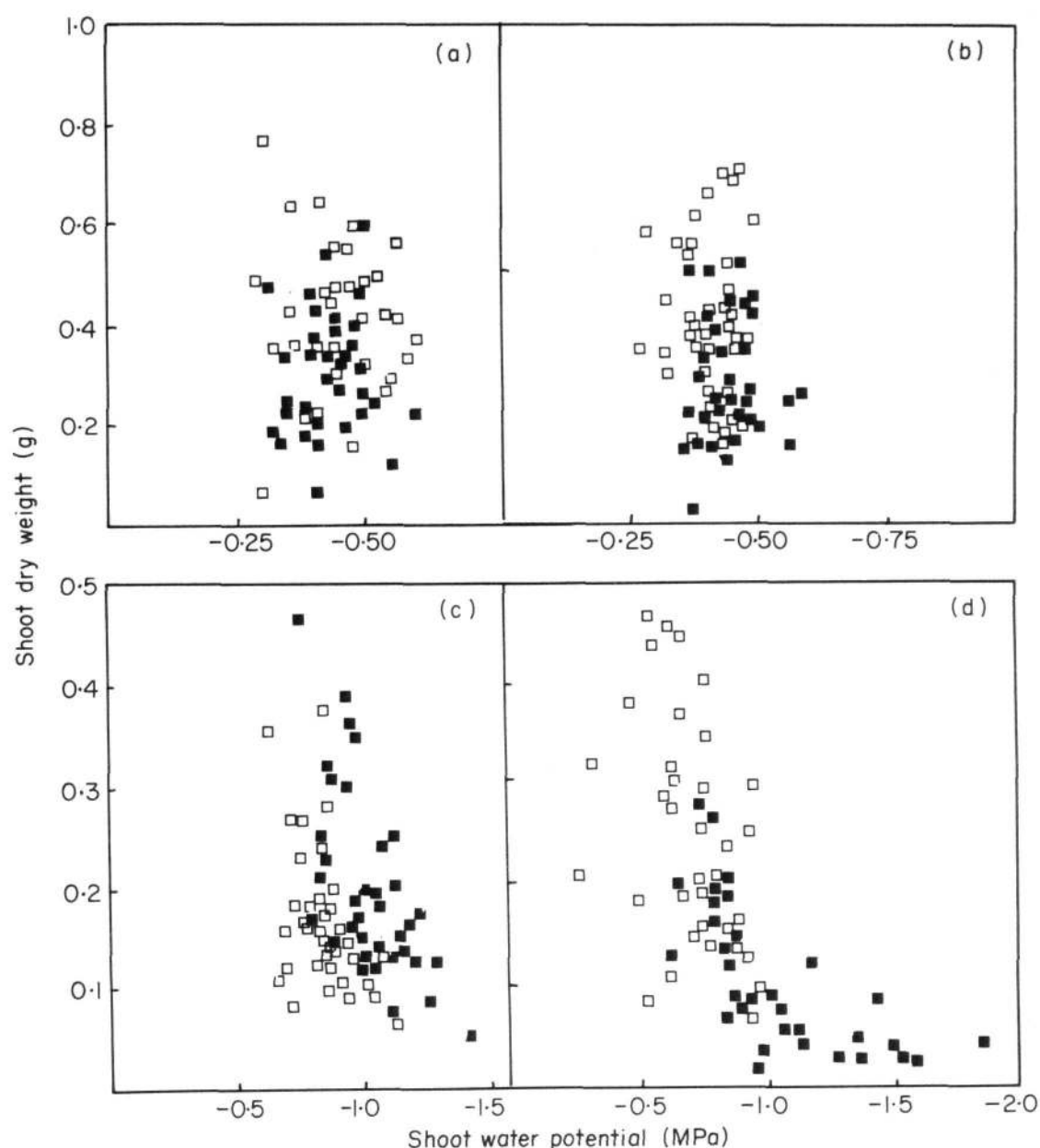


Fig. 5. The relationship between shoot dry weight and shoot water potential of control (\square) and rust-infected (\blacksquare) groundsel in (a) well-watered monocultures, (b) well-watered mixtures, (c) drought-treated monocultures and (d) drought-treated mixtures. The value of Spearman's coefficient of rank correlation (r_s) and its significance are shown for each population (**, significant at $P = 0.01$; ***, significant at $P = 0.001$). (a) Control r_s , -0.155 nsd; rusted r_s , 0.131 nsd. (b) Control r_s , 0.011 nsd; rusted r_s , 0.159 nsd. (c) Control r_s , 0.559 ***; rusted r_s , 0.589 ***. (d) Control r_s , 0.456 **; rusted r_s , 0.810 ***.

DISCUSSION

Despite the unfavourable weather conditions, the shelters were successful in maintaining the drought-stress treatment for some 5 weeks. The effects of the drought treatment were evident in the growth of groundsel within the first 2 weeks after watering ceased. The deleterious effects of rust infection on the growth of groundsel were consistently more pronounced under water stress than under well-watered conditions. Indeed, although rust significantly reduced the shoot dry weight of well-watered plants, its effect on competitive ability and shoot water potential were marginal. The absence of change in ψ contrasts with the results of pot experiments in which rusted groundsel (Paul & Ayres, 1984) and other species (Tissera & Ayres, 1986) had lower water potentials than controls under well-watered conditions. This contrast may be attributable to a variety of mechanisms.

For example, transpiration under the cool, damp conditions of the field is likely to have been low compared with that in growth chambers where higher temperatures are often combined with low humidity and turbulent air movement. Such reduction in the driving force for transpiration may have allowed rusted plants in the field to maintain a near-normal water balance despite reduced leaf resistances to water loss. In addition, water-balance may have been maintained in rusted plants by the unrestricted growth of roots in the field which would have allowed exploitation of relatively large soil volumes for water. Whilst infection has been shown consistently to reduce root dry weight and to increase the shoot:root ratio (Ayres, 1985; Paul & Ayres, 1986b), compensatory mechanisms exist (Paul & Ayres, 1986c; Tissera, 1986) which may allow water uptake to be maintained. The greater effect of rust on ψ in mixture than in monoculture indicates the importance of competition between roots for water. It may be that controls exploited water deep in the profile which was less available to rusted individuals. However, the relief of stress in controls and its exaggeration in rusted plants in mixtures suggests direct competition for the same water reserves. Limited excavations showed that roots from rusted as well as control monocultures had penetrated into wet soil deep in the profile but did not allow the quantity of roots from the two to be compared, nor roots from control and rusted plants in mixtures to be distinguished. In general, differences in the size of root systems (Thomas, 1984) and in gross root morphology (Martin & Snaydon, 1982) may be significant in competitive interactions in the field, and the morphology and spatial distributions of the root system of rusted plants under field conditions clearly merit further investigation.

Correlations between growth and physiological parameters at final harvest require cautious interpretation. However, the close relationship between ψ and shoot weight in all unwatered but not in well-watered populations provides strong evidence for the central role of water as the limiting factor under these conditions. Furthermore, we consider that the exceptionally negative value of ψ in suppressed, rusted individuals provides some evidence that the slow growth of these plants was a result of their being at particular disadvantage in competition for water. Rust consistently increased the inequality of the distribution of ψ as well as changing its mean value. This was especially pronounced in mixtures in which ψ was negatively skewed in controls but positively skewed in rusted components. Thus, in a substantial proportion of control plants from stressed mixtures, the remission of water stress was pronounced. Conversely, many rusted individuals in mixture were substantially more severely water-stressed than in monocultures, and these were of low status in the shoot dry weight hierarchy. Indeed, ψ in these plants was lower than expected from the relationship between shoot weight and ψ in other stressed populations.

The low competitive ability of suppressed plants in mixtures, whether based on competition for water or other resources, was evident in the high value of K_{cr} for the sub-class of lowest status in the hierarchy. An inverse relationship between K_{cr} and plant status was apparent in both wet and dry treatments. As we reported before (Paul & Ayres, 1986a), the behaviour of highly suppressed, rusted individuals was central in determining the overall impact of infection on competitive ability. Under drought, rusted plants were consistently at a competitive disadvantage, the lowest value of K_{cr} being 1.34; declining status simply exaggerated this disadvantage. The significance of plant status was greater under well-watered conditions where plants of high status in the hierarchy were at no competitive disadvantage ($K_{cr} = 0.99$ and 1.03 in the two classes of highest

status) but those of lowest rank suffered greatly in mixture ($K_{cr} = 3.32$). The mechanism of differential interference in the absence of water stress is uncertain but may have resulted from the severe shading of suppressed plants. We found previously that such a shading effect was highly dependent upon planting density (Paul & Ayres, 1986a) and it seems probable that interactions between rust and water stress on competition in the field may also show substantial density dependence.

The impact of rust, whether in natural infections of mixed vegetation or artificially induced epidemics aimed at biocontrol of weeds, may thus be expected to be greatest when water is limiting, which may frequently be the case, even in the relatively moist climate of the UK. The frequent and heavy irrigation of the well-watered plots in this experiment may have resulted in a freedom from water deficit atypical of natural summer conditions in the field. Water availability may also be limited in winter when the soil is at low temperature and especially when it is frozen. We have shown that rusted groundsel plants suffer severe damage when the soil is frozen (Paul & Ayres, 1986b), in part because of their inability to control water loss (Paul & Ayres, 1985). The small magnitude of rusted plants' disadvantage in competition with control groundsel in well-watered plots is likely to have underestimated the effect under field conditions throughout the year.

K_{cr} determined here under field conditions was substantially lower than the value of 1.59 obtained at the same planting density using well-watered, pot-grown populations in the glasshouse (Paul & Ayres, 1986a). The effects of rusts on interference in pot-grown populations of other species as determined by K_{cr} have tended to be rather greater than recorded here (Groves & Williams, 1975; Burdon *et al.* 1981, 1984). In previous investigations, the impact of root competition will have been exaggerated by the small root volume of the container. Even with frequent watering, it is likely that some soil water deficit will have arisen in containers in warm glasshouse environments. Measures of interference between rusted and uninfected plants obtained in pot-based studies may thus be subject to some overestimation due to the presence of mild water deficits. Our understanding of the impact of rusts on the competitive ability of their hosts in nature remains limited and awaits further investigation under realistic field conditions.

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