Allelopathic effects of wireweed (*Polygonum aviculare*)

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Summary

The hypothesis that wireweed (*Polygonum aviculare*) was responsible for severely restricting the germination of annual medics was tested with a series of laboratory and field experiments. These showed that a water-soluble agent was present in the leaves and green stems and that this interfered with the germination rate of both medic and lettuce and with the ultimate percentage germination of lettuce. The agent causes morphological deformities in germinating medic seedlings by interfering with cell division and early growth of meristems. It is concluded that the combination of effects caused by the wireweed would explain the failure of medic pastures to establish succesfully, particularly where the opening rains are likely to be brief and spasmodic.

Introduction

About 1970, massive failures of germination in self-regenerating annual medic pastures were observed in various parts of South Australia, but particularly in the southern part of Eyre Peninsula. The pastures were based on *Medicago polymorpha*, *M. truncatula* and *M. littoralis*, and although medic seed appeared to be plentiful on the ground at the opening of the season subsequent establishment and development were poor. This failure occurred in paddocks dominated by wireweed (*Polygonum aviculare*).

Wireweed, a serious weed of cereals, competes with crops during their growth and, particularly in late-sown crops, interferes physically by blocking harvest machinery. Effective herbicidal techniques (Department of Agriculture, South Australia, 1981) are widely used in cereals but hitherto, because wireweed has been recognized as useful summer feed for over a century (Anon., 1859), it has been tolerated in pastures.

The association between wireweed and the germination problem was so striking that we felt that the wireweed was directly affecting the medic. Because of the wide variation in soil type, plant density and annual rainfall of the affected areas, it did not seem likely that competition was responsible for the problem. One possible explanation was that the wireweed was the source of an allelopathic agent which interfered with the germination and early growth of medic.

Allelopathy is the phenomenon in which phytotoxic secondary metabolites are released into the soil and inhibit growth of nearby plants (Rice, 1974; Swain, 1977). Some authors have been reluctant to acknowledge that the phenomenon exists (Mueller-Dombois and Ellenberg, 1974; Harper, 1977; Grime, 1979). The main objection is that although these substances do occur in plants and produce inhibitory effects in laboratory tests, reports do not show conclusively that the effects are significant in the field. Later work by C. H. Muller and associates in particular (Bell and Muller, 1973) and others has met these arguments.

periments designed to test the hypothesis of allelopathy were conducted and are reported here.

Materials and methods

Laboratory work

A preliminary test in which (i) the leaves and green stems, (ii) the woody stems, and (iii) the roots were extracted in distilled water showed that the leaves and green stems were richest in the chemical inhibitor, and that the woody stems were considerably less so. The root extract had no observable effect. As a result of this test, the extract from wireweed plants required for the experiments was prepared from the leaves and green stems only.

For the laboratory tests reported here, two lots of plant extract were prepared from green material collected at the Northfield Research Centre, Adelaide, on 2 February and 1 March 1976. Prior to 2 February there had been 27 mm of rainfall spread over 10 days, the highest reading for one day being 11 mm on 12 January, 21 days earlier. In contrast, in the five days prior to the 1 March collection, 45 mm of rain had fallen.

The plant extract was prepared as follows. Leaves and green stems were cut in each of six 10 × 10 cm quadrats in a thick patch of wireweed. The cut material was weighed and the average weight per quadrat calculated. Four of the samples, adjusted to the average weight of the six samples (16.2 g), were steeped in 250 mL of distilled water for 24 hours. The green material was not macerated or broken beyond what was necessary to push it into the container. The extract was decanted, filtered, bulked and stored in a stoppered glass bottle in a domestic-type refrigerator.

A soil extract was prepared as follows. From the six quadrats utilized previously, soil to 1 cm depth was collected. Four samples, adjusted to average air-dry weight (138 g), were prepared. These samples were then treated identically to the plant material.

The March extracts were prepared similarly. The average weights of plant material and soil were 15.9 g and 98 g respectively. These extracts were used in only one experiment, so unless mentioned otherwise, all tests were made with the extracts made from the samples collected in February.

In the laboratory tests, the seeds of the following species were used: lettuce (*Lactuca sativa* L. cv. Great Lakes), ryegrass (*Lolium perenne* L. cv. Victorian) and barrel medic (*Medicago truncatula* Gaertn. cv. Jemalong).

Experiment 1 Effect of plant and soil extracts on the germination of lettuce, ryegrass and medic.

For each species 100 seeds were plated out on filter paper in closed petri dishes. To each species, the following treatments were applied.

(i) watering with distilled water (control)
(ii) watering with plant extract (plant extract)
(iii) watering with soil extract (soil extract)

Each treatment was replicated three times. The dishes were housed in a germination cabinet set at 25°/15°C, alternating for 12 hours each in continuous light. Germination percentage and the times to reach median and maximum germination were recorded. Germination was considered to have occurred when the emerging radicle had attained a length of 2 mm.

Experiment 2 Temporary effects of the plant extract on medic germination.

Petri dishes containing 100 medic seeds, were subjected to the following treatments.

(i) watering with distilled water (control)

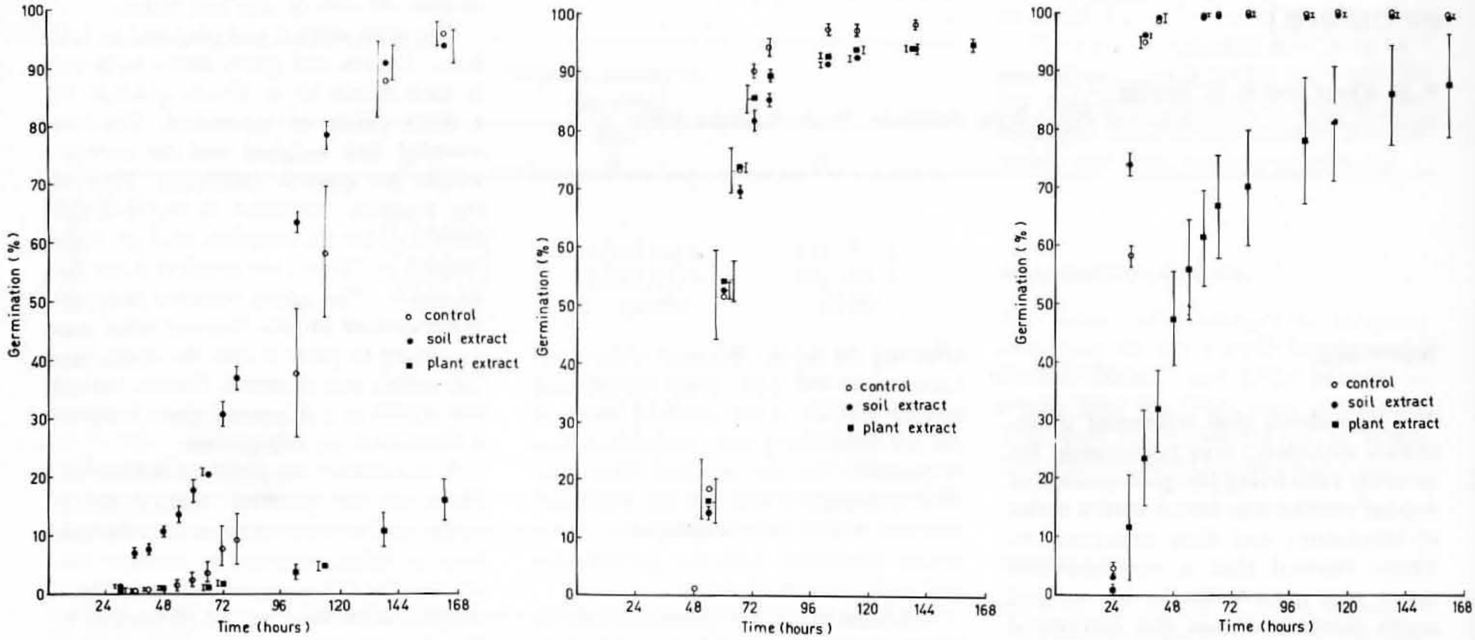

Figure 1a Lettuce

Figure 1b Ryegrass

Figure 1c Medic

Figure 1 The percentage germination of seed sown on three substrates watered respectively, with distilled water (control), the soil extract and the plant extract of wireweed. The vertical bar represents the standard error of each value.

(ii) watering with distilled water for the first 24 hours, then flushing with plant extract which was used for watering thenceforth (water/extract)

(iii) watering with plant extract for the first 24 hours, then flushing with distilled water which was used for watering thenceforth (extract/water)

(iv) watering with plant extract (extract)

Each treatment was replicated three times and all other details were as in the previous experiment.

Experiment 3 Effect of plant and soil extracts (March) on medic and lettuce.
This experiment was identical to the first except that ryegrass was omitted and the extracts used were those made in March.

Experiment 4 Morphological and anatomical effects of the plant extract on germinating medic.
Medic seed was germinated for 72 hours in either distilled water (control) or plant extract. After that period the length of radicle and the length of root hair zone were measured on 30 seeds from each treatment.
The length of hypocotyl was measured in 10 plants from each treatment. Germinating radicles were sectioned, fixed and stained with sufranin and fast green, and examined microscopically.

Field work

Experiment 5 The effects of removing wireweed on medic establishment.
Quadrats 60 × 60 cm were set up at the Northfield Research Centre in an area infested with mature wireweed on 8 June 1976. The following treatments, each replicated three times, were imposed.

(i) 500 medic seeds were scattered evenly over the plot which was otherwise untouched (wireweed)

(ii) all wireweed top growth was removed and 500 medic seeds were scattered evenly over the plot (tops removed)

(iii) all wireweed top growth and the top 1 cm of soil was removed, then 500 medic seeds were scattered evenly over the plot (tops and soil removed)

(iv) 500 medic seeds were scattered evenly over a plot which was free of wireweed (no wireweed)

For the first two weeks germination counts were taken at convenient intervals, and beyond that period establishment counts were taken weekly. Between the opening rains on 16 May and the commencement of the experiment a total of only 13.3 mm of rain was recorded at the Northfield Meteorological Station adjacent to the site. During the first month of the experiment, another 10 mm was recorded. Because of the unusually dry winter, many plants died from about mid-July and the effects of the various treatments were obscured. The same criterion for germination was used as in the laboratory experiments. Establishment was taken as the plant being firmly rooted and producing new leaves.

Results

Experiment 1 The progressive germination of lettuce, ryegrass and medic seed as affected by the presence of plant and soil extracts are shown in Figure 1. The times taken to reach median and maximum germination are given in Table 1.

Experiment 2 In Figure 2, the cumulative germination of medic seed on the two constant substrates ('control' and 'extract') and on the two substrates changed about after 24 hours, is shown.

Experiment 3 The experiment carried out with the plant and soil extracts made in March showed no differences in the germination of medic or lettuce seed whether treated with extracts or not. The significance of this finding is discussed below.

Experiment 4 The data derived from the study of the morphological changes induced by the allelopathic factor are shown in Table 2. The action of the inhibitor early in the germination process was revealed by microscopic examination. The central cylinder of the root in the regions of vascular tissue differentiation was disorganized and individual cells were abnormally elongated. The central cylinder was replaced by a mass of rapidly-dividing, undifferentiated tissue.

Experiment 5 The germination of medic sown in field quadrats is shown in Figure 3. To provide a comparison more relevant to the field situation, establishment counts were made one month after sowing and are presented in Table 3. In all cases the percentage establishment is considerably below the germination figures as given in Figure 3. The greatest reduction was obtained for the fourth treatment as the soil, where these quadrats were sited, was more compacted than the adjacent wireweed infested area where the rest of the experiment was located.

Discussion

It would appear from Experiment 1 that a water-soluble substance can be leached from the plant which inhibits the germination of medic seeds. The lack of effect with the March extracts may be explained by the heavy rain which pre-

Table 1 The effects of wireweed plant and soil extracts on the time taken to reach median and maximum germination, and on the final germination percentage—mean of three replicates.

	Time (hours) to reach: median germination	maximum germination[1]	Maximum germination (%)
Lettuce			
control	108.0[b]	162	96.0[a]
soil extract	87.0[c]	162	94.0[a]
plant extract	129.7[a]	162	16.0[b]
significance	*	NS	***
Ryegrass			
control	59.9	134	98.3
soil extract	59.1	138	94.3
plant extract	58.8	162	94.7
significance	NS	NS	NS
Medic			
control	29.1[b]	56[b]	99.7
soil extract	27.9[b]	62[b]	99.7
plant extract	47.7[a]	162[a]	87.7
significance	**	***	NS

[1]The experiment was terminated at 162 hours.
*significant effect—$P < 0.05$
**significant effect—$P < 0.01$
***significant effect—$P < 0.001$
NS—not significant
Means followed by differing superscrips are significantly different within each column for each species.

Table 2 Effect of wireweed plant extract on the lengths of the hypocotyl, radicle and root-hair zones of germinating medic seed—mean of 30 measurements

	Control	Plant extract
length (mm) of hypocotyl[1]	4.3	2.2**
length (mm) of radicle	17.8	10.5***
length (mm) of root-hair zone	6.1	2.5***
length of root-hair zone as proportion of radicle length	0.33	0.20**

[1]Mean of 10 measurements only
**Treated differs from the control at $P < 0.01$
*** Treated differs from the control at $P < 0.001$

Table 3 Percentage establishment of medic, one month after sowing, influenced by various soil treatments (see text)—mean of three plots ± standard error

	Wireweed	Tops removed	Tops and soil removed	No wireweed
percentage establishment	6.6 ± 1.63	12.2 ± 2.20	28.1 ± 9.42	16.5 ± 4.33

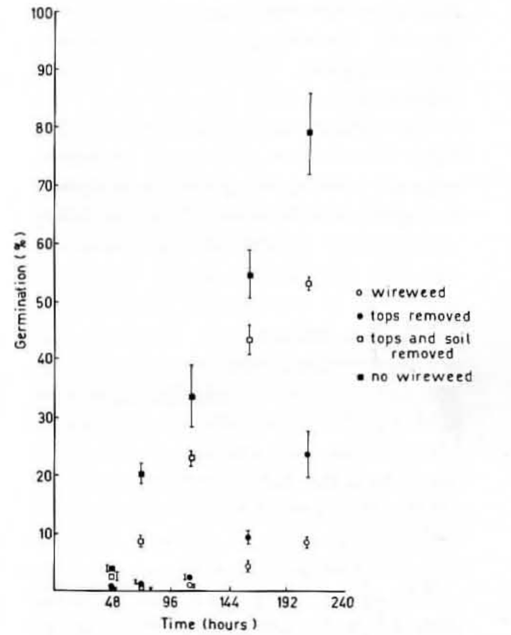

Figure 2 The percentage germination of medic seed subjected to four substrate treatments with wireweed plant extract. The vertical bar represents the standard error of each value.

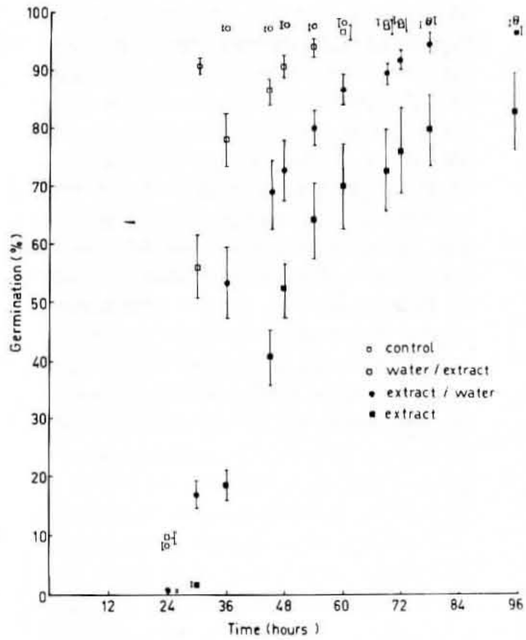

Figure 3 The field germination of medic subjected to four treatments — sowing in an area (i) infested with wireweed; (ii) from which the wireweed tops had been removed; (iii) as previous but the top 1 cm of soil was also removed and (iv) sowing in an adjacent area free of wireweed. The vertical bar represents the standard error of each value.

ceded the sampling, having leached the active agent from leaves and the surface layers of the soil. Similar results were obtained by McPherson and Muller (1969) in their studies of the allelopathic effects of *Adenostoma fasciculatum* in California.

It would appear that the top 1 cm of soil contains most of the agent, for the removal of this layer enhanced germination (Figure 3) and establishment (Table 3). Experience in the field has shown that cultivation enhances germination. The results of the field experiment reported here are consistent with the explanation that the uppermost layers of the soil, contaminated with the allelopathic agent, are diluted during cultivation.

The data presented in Figure 1 and Table 1 show that, of the species tested, ryegrass is the most tolerant. Lettuce was the most severely affected species, being significantly slower to germinate and finishing with a very highly significant reduction in percentage germination. Medic was intermediate, finishing with a non-significant reduction in percentage germination but a very highly significant slowing of the germination process. In lettuce, the soil extract significantly stimulated the early germination of the seeds, and there was also a significant difference in medic at 30 hours. The reasons for this are not clear.

The action of the allelopathic agent appears to be on cell division in the meristem and in the subsequent differentiation of the radicle. This is an early process taking place, in medic, within the first 24 hours of germination, as seen in Figure 2. It results in truncated, misshapen radicles bearing shortened root-hair zones; the hypocotyls are also significantly shorter (Table 2). These morphological disabilities reduce the likelihood of the successful establishment of the affected plants in a severe environment. It is even more important that the great reduction in the rate of germination, and subsequently in the rate of radicle growth, places germinating seed at a very great disadvantage. In the areas where the phenomenon has been observed in the field, opening rains may be spasmodic so, for successful establishment, the swift emergence of a radicle into the temporarily-wet top layer and its rapid elongation to follow the descending moisture as the soil dries out are essential. Cocks (1974) regards this as being a critical factor in the more successful establishment of barley grass (*Hordeum leporinum*) compared with ryegrass. Similarly, Piggin (1976) found that Salvation Jane/Paterson's curse (*Echium plantagineum*) established more successfully than did subterranean clover (*Trifolium subterraneum*), because the former had a radicle that grew more quickly than did that of the latter.

Although many plants have been shown to exert allelopathic effects (Rice, 1974; 1979), the family Polygonaceae has not been prominent. Recently, Datta and Chatterjee (1980a, b) have reported strong allelopathic effects in *Polygonum orientale*. They carried out leaching experiments and, as for *P. aviculare*, found a potent water-soluble allelopathic agent in the leaves. Using chromatographic techniques, they were able to conclude that the agent was a mixture of two glycosides. Their results, in general, were similar to ours and it is possible that the compounds involved in our species are identical or closely related. It is also likely that other species of *Polygonum* will be found to cause allelopathic effects.

The work reported here introduces allelopathy as another factor to be considered in the deterioration of medic pastures in South Australia which is causing concern to those trying to maintain the crop–pasture rotation. More recent survey work in South Australia (Kloot, unpubl. data) has shown that the association between wireweed infestations and the failure of medic regeneration is more widespread than originally thought. Unfortunately, further work in progress suggests that other volunteer species exert allelopathic effects on medics, a situation that Muller (1966) forecast on the basis that such a character conferred a very positive advantage on plants competing for limited resources in the mediterranean-type environment.

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