

The influence of season on the suppression by *Pteridium aquilinum* leaf extracts of root growth in *Avena fatua*: a possible influence on the distribution of *Philippia evansii*

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Philippia evansii has colonized south aspect sites extensively but has been less successful in the valley bottoms, despite the growth rate of valley bottom plants being significantly greater than that of south aspect plants.

Pteridium aquilinum is dominant in the valley bottoms and fronds are shown to contain water extractable phytotoxins which inhibit radicle extension in *Avena fatua* L. It is suggested that these toxins have contributed to the slow rate of colonization of valley bottom sites by *P. evansii*.

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Philippia evansii se koloniserings van suidelike glooiings vind op groot skaal plaas, maar is minder suksesvol in die bodems van die valleie ten spyte daarvan dat die groeitempo van valleibodemplante beduidend hoër is as dié van plante op suidelike glooiings.

Daar word getoon dat *Pteridium aquilinum* blare wateroplosbare fitotoksiene bevat wat kiemwortelverlenging in *Avena fatua* belemmer. Daar word voorgestel dat hierdie gifstowwe bygedra het tot die stadige koloniserings van die valleibodemgroeiplekke deur *P. evansii*.

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Introduction

Allelopathy is 'the inhibition of germination, growth or metabolism of one plant because of the release of chemicals by a different plant' (Stewart 1975). The release of toxic compounds from different parts of *Pteridium aquilinum* (L.) Kuhn, has been regarded as the primary agent allowing this fern to become dominant in parts of North America and Costa Rica (Gleissman 1976). In the Natal Drakensberg *P. aquilinum* occurs on moist deep soils where it may invade *Themeda triandra* grassland, eventually forming a closed canopy (Killick 1963). In these situations allelopathy may be a significant factor conferring competitive advantage on *P. aquilinum*.

In a study of succession following fire exclusion in the sub-alpine zone of the Drakensberg, Granger (1976) noted that *Philippia evansii* N.E. Br. spread from the moist valley bottom sites, where it had some protection from fire, up the south aspect slopes. This led Granger & Schulze (1977) to postulate that colonization of these sites was favoured by the cool moist conditions. Everson & Breen (1983) demonstrated, however, that *P. evansii* growing on the south aspect sites experienced significantly more water stress than those in the valley bottom. This led them to question why *P. evansii* had been so successful on the south-facing slopes where it was experiencing more water stress.

This research tested the hypothesis that *P. aquilinum*, which was dominant on the moist soils of the valley bottom, produced phytotoxins which retarded colonization of these sites by *P. evansii*.

Materials and Method

The study area has been described in detail in Everson & Breen (1983). The observations reported here were made in Catchment IX at Cathedral Peak State Forest (29°00'S; 29°15'E) during 1976 and 1977.

Growth

Shoot extension was used as an index of growth at three sites; a site (PA) where *P. evansii* was associated with *P. aquilinum* and two control sites (C_1 , C_2) on a south aspect slope where it was associated with grasses (Figure 1). Five *P. evansii* shrubs were randomly selected at each site. On the five largest branches of each shrub the four highest shoots were numbered 1–4, giving 100 shoots at each site. The shoots were characterized by having the distal end lighter in colour than the rest of the shoot, and a reference nylon thread was secured at this point. This represented the base point for estimation of shoot extension (Farnsworth 1955; Kozłowski 1964).

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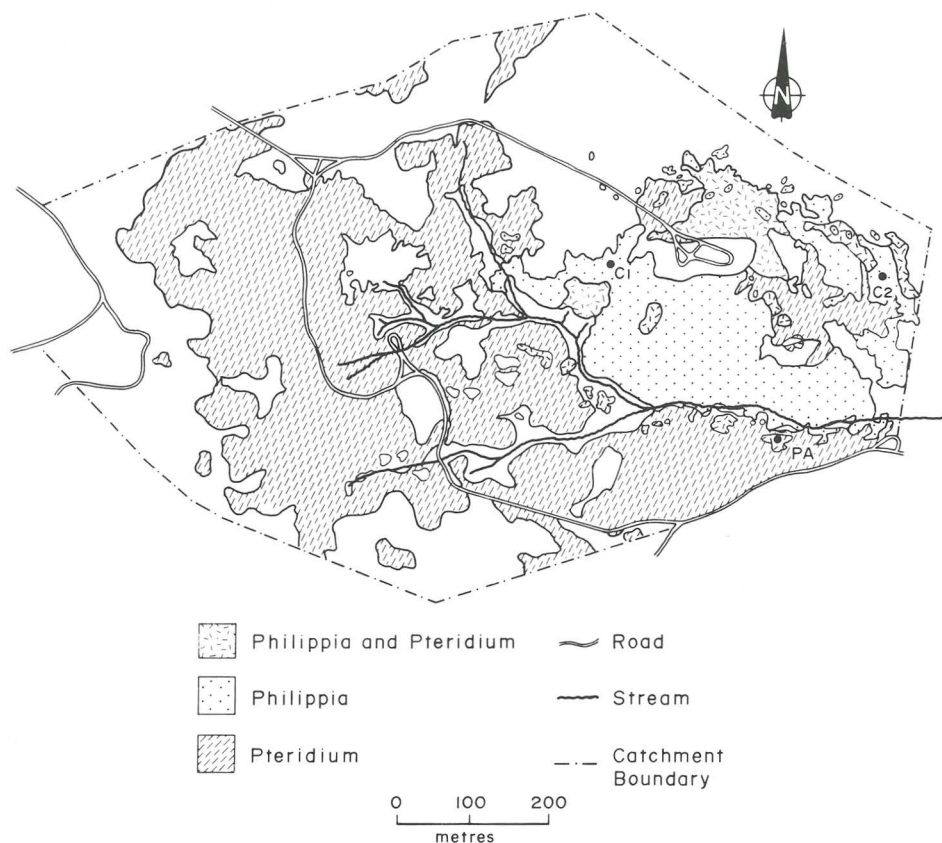


Figure 1 The distribution of *P. aquilinum* and *P. evansii* in Catchment IX (After Granger 1976). C₁ control site 1; C₂ control site 2; PA *Pteridium*-associated site.

Phytotoxin activity

Phytotoxin activity was assayed by a modification (Gleissman 1976) of the technique of McPherson & Muller (1969). Unfortunately, as all attempts to obtain reproducible laboratory germination with *P. evansii* seeds were unsuccessful, *Avena fatua* L. was used (Gleissman 1976). Caryopses were soaked in extracts of *P. aquilinum* or in distilled water (control) for two hours before planting.

Ten-gram samples of fronds collected in the field were extracted by shaking them for three hours with 100 cm³ of distilled water. The extract was filtered through Whatman No. 1 paper and concentrated under vacuum at 35 °C to 2,5; 5,0; 7,5 and 10 times the original strength. Solutions were frozen until required.

Five replicates of 10 caryopses for each extract concentration were placed in petri dishes (McPherson & Muller 1969) with 5 cm³ of extract. Petri dishes were wrapped in aluminium foil and incubated at 26 °C for 48 hours. Measurements of radicle extension were used as a measure of growth.

Results

Growth

The intervals between consecutive measurements (*ca* 1 month) were long and it was therefore not possible to infer precisely when growth ceased or restarted, or to derive instantaneous growth rates. Interpretation was further constrained by the emergence of unmarked lateral shoots which appeared to slow growth of the marked lead shoot. Within these constraints the measurement of shoot extension provided an index of growth rate at each site.

With the approach of winter, growth rate declined to 0,5 mm/week and remained at that level at all sites until the onset of more rapid growth in spring (Figure 2). The rate of increase

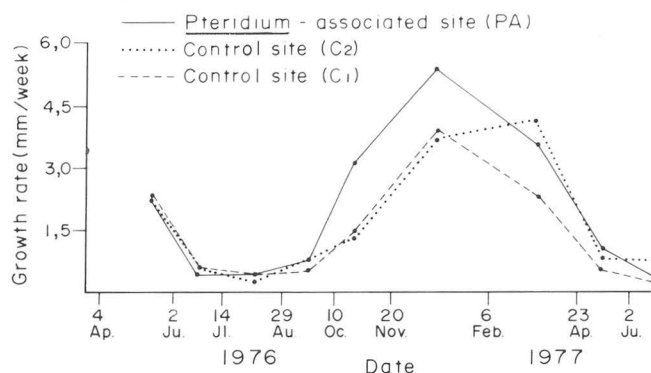


Figure 2 The seasonal changes in growth rates (mm/week) at the study sites. Growth is expressed as the mean rate between consecutive measurements.

of growth rate was much more rapid at the *Pteridium*-associated site than at the control sites, so that by 10 October the mean growth rates were 3 mm/week and 1,3 mm/week respectively. Maximum mean growth rates were 5,0 mm/week at the *Pteridium*-associated site and *ca* 3,5 mm/week at the control sites (C₁, C₂). High mean growth rate appeared to be prolonged at control site C₂, but by April 1977 rates had declined to low levels at all sites. These results demonstrate that established *P. evansii* plants, growing in association with *P. aquilinum*, were apparently under more favourable conditions than those growing on the recently colonized south aspect slopes.

Phytotoxin activity

Water soluble extracts of *P. aquilinum* collected on 28 April, when the fronds were beginning to senesce, were effective in significantly retarding radicle extension of *A. fatua* only when

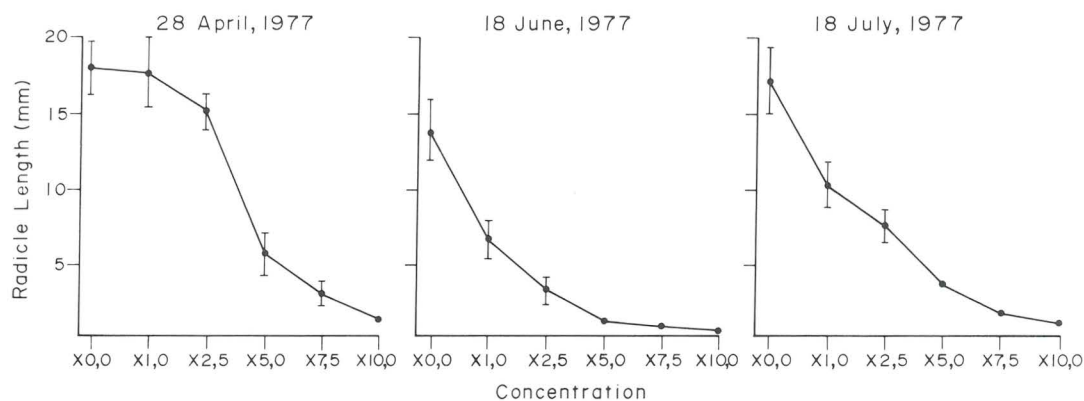


Figure 3 Inhibition of radicle extension in *A. fatua* by a range of concentrations of *P. aquilinum* leaf extract at different times of the year. Vertical bars represent the 95% confidence intervals.

the extract had been concentrated five times or more (Figure 3). When dead fronds were used to prepare the extract in June and July the extract, without any concentration, reduced radicle growth significantly, and at high concentration growth was completely inhibited. It has been suggested that the osmotic potential of concentrated medium may contribute to the inhibition of radicle extension. Del Moral & Cates (1971) have, however, demonstrated similar growth inhibition after correction for differences in osmotic potential. In addition, after the same degree of concentration, inhibition increased between April and June (Figure 3). Inhibition therefore results more from the presence of toxins than from osmotic potential.

Discussion

There is conclusive evidence that once established, *P. evansii* colonizing the moist valley bottom sites, grows much more rapidly than those plants which have colonized the south aspect slopes since fire exclusion. The observation that *P. evansii* has been relatively unsuccessful in advancing over the valley bottom implies that there is some constraint acting on the early stages of establishment. It would appear, however, that seed supply is not constraining colonization since *P. evansii* originally spread from the valley bottom (Granger & Schulze 1977) where personal observation has shown that there was abundant seed production. Seedling establishment appears to be the stage of development most affected.

Phytotoxins accumulating in the fronds of dense stands of *P. aquilinum* during the winter months could be leached in sufficiently high concentrations to inhibit seed germination in spring when the first rains are expected to occur.

Although the experiments reported here were conducted on *A. fatua*, other workers have demonstrated similar effects on the establishment and growth of woody plants (Del Moral & Cates 1971; Stewart 1975). Stewart (1975) has also suggested that the accumulation of dead fronds in dense bracken may be several inches thick, a situation which does arise in Catchment IX, thereby presenting a significant additional barrier to seedling emergence.

These are undoubtedly not the only factors controlling successful establishment of *P. evansii* in this area. For instance, growth ring analysis at the three sites indicated that the age of these shrubs (10–14 years) corresponded very closely with the interval since the last fire, which occurred in 1964. This, together with the fact that there has been no recent germination of seeds (i.e. absence of young plants) suggests that there was a flush of germination immediately after the last fire but not since (Everson 1979). This enhancement of germination

by fire has been reported for other species (Quick 1935; Sampson 1944; Stone & Juhren 1951 and others).

From results demonstrating the inhibitory effects of *P. aquilinum* on *A. fatua*, and other cited evidence in this connection (Rice & Parenti 1967; Hanes 1971; Neill & Rice 1971), it is inferred that *P. evansii* is subjected to similar constraints in its colonization of moist areas of Catchment IX. Thus, the rapid expansion of *P. aquilinum* together with its production of phytotoxins would have restricted the colonization of these sites by *P. evansii*, which would be better able to compete on the cooler and drier south aspect where *P. aquilinum* is less abundant.

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