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An experimental comparison of aluminium and manganese susceptibility in *Antennaria dioica, Arnica montana, Viola canina, Filago minima* and *Deschampsia flexuosa*

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SUMMARY

Antennaria dioica, Arnica montana, Viola canina and *Filago minima* are declining in The Netherlands and are even locally extinct. This process of decline has been associated with an increased rate of acidification of soils and an increased availability of aluminium and manganese to plants up to potentially phytotoxic levels. This paper examines whether, and to what extent, aluminium and manganese are important environmental variables in determining the decline in plant species. Susceptibility to ionic aluminium and manganese was studied in three experiments under controlled conditions. Young plants were grown on a complete nutrient solution containing variable concentrations of aluminium, manganese or aluminium plus manganese (pH 3·8). Responses (dry weights after 5 weeks of growth) were compared to those of *Deschampsia flexuosa*, known to be aluminium and manganese resistant.

Arnica montana was the most resistant, up to concentrations of 80 mg l^{-1} aluminium, *Antennaria dioica* and *Viola canina* somewhat less, and *Filago minima* was relatively sensitive. All the species were relatively manganese-resistant up to concentrations of 312·5 mg l^{-1} manganese, with the exception of the relatively sensitive *Filago minima*. *Arnica montana, Viola canina* and even *Deschampsia flexuosa*, were adversely affected by high concentrations of aluminium (80 mg l^{-1}) and manganese (300 mg l^{-1}), when supplied simultaneously. It was concluded from these results that increased amounts of aluminium and manganese available in the plants' rooting zone are unlikely to account for the decline in the investigated species of the alliance Violion caninae. The sensitivity to aluminium and manganese of *Filago minima* may, however, be responsible for its decline. The potential significance of other possible (interacting) environmental factors is discussed.

Key-words: Aluminium-resistance, *Antennaria dioica, Arnica montana, Deschampsia flexuosa, Filago minima*, manganese-resistance, seedling growth, *Viola canina.*

INTRODUCTION

There is now a decline in the distribution of some herbaceous plant species in The Netherlands. This includes *Antennaria dioica* (L.) Gaertner, *Arnica montana* L., *Viola canina* L. and *Filago minima* (Sm) Pers. (Van Dam *et al.* 1986). The first three species are character species of the alliance Violion caninae. This syntaxon classifies grasslands on moist, low nutrient, moderately acid to neutral humic (podzolic) soils (Westhoff & Den Held 1969). *F. minima*, character species of the alliance Thero-Airion, is found growing on dry, low nutrient, moderately acid to neutral sandy soils (Westhoff & Den Held 1969). *A. dioica*, *A. montana*, *V. canina* and *F. minima* in general show a preference for acid soils (Small 1946; Ellenberg 1979).

Various suggestions have been made concerning the causes of this decline; these are: (i) lowering of the groundwater table, (ii) eutrophication, (iii) changed management practices, (iv) land reclamation, and (v) urbanization and road construction. The decline has also been correlated with the effects of 'acid rain' (Van Dam *et al.* 1986), i.e. the deposition of 'acids' due to SO_2-, NO_x- and NH_3-emissions in the atmosphere. The effects of these depositions on plant vitality can be direct and/or indirect (Hutchinson & Havas 1980). Van Dam *et al.* (1986) suggested that soil acidification might be a possible mechanism leading to the decline in the four species.

Indirect effects of acid deposition on the vitality of plants are often considered to be more important than direct ones (Ulrich & Pankrath 1983). Indirect effects can be expected when some soil characteristics change. The input of NH_4^+, NO_3^-, H^+ and SO_4^{2-} is considered to be an important factor that influences the chemical and physical status of soils (Van Breemen *et al.* 1983). Much attention has been paid to the mobilization of metal ions, such as Al and Mn^{2+}. By acidification these metal ions may reach phytotoxic concentrations.

Aluminium (Al) is a non-essential element for plant growth. It is known to be toxic for various plant species at low levels. (Thornton *et al.* 1986). Depending on the physical and chemical conditions of soils, e.g. pH, aluminium can occur in different forms. At pH <4, Al^{3+} is the dominant ionic species (Dalal 1975), which is generally considered to be harmful to plant-growth (Foy *et al.* 1978). Aluminium toxicity may be reduced by calcium and magnesium (Rhue & Grogan 1977; Runge 1984) and the type of nitrogen supply (Rorison 1985). Unlike Al, manganese (Mn) is a micronutrient. Depending on the pH and redox potentials, Mn^{2+} and Mn^{4+} ae the most common ionic forms of this metal in soil solutions. The most common form at a low pH and at low redox potentials is Mn^{2+}, which is potentially the most phytotoxic.

Plant species of acidic, nutrient-poor soil conditions are likely to be adapted to low supplies of nitrogen and phosphorus, and be resistant to a high supply of ionic Al and Mn and apparently require high levels of iron (Fe) and Mn (De Neeling & Ernst 1986; Rorison 1986). *Deschampsia flexuosa* Trin., which is adapted to soils of high acidity, is known to be Al (Hacket 1962; Pegtel 1987) and Mn (Mahmoud & Grime 1977) resistant. Furthermore, its abundance and distribution has increased over the last decade, possibly due to airborne nitrogen and sulphur input, and to a lack of appropriate management practices. Therefore, this species was included in the study for comparison

In order to answer the question concerning whether and to what extent ionic Al and Mn are important soil factors that affect the distribution of *A. dioica*, *A. montana*, *F. minima* and *V. canina*, studies were carried out on the sensitivity of these species to Al and Mn in comparison with *D. flexuosa.*

MATERIALS AND METHODS

Seeds (achenes, caryopses) of *Antennaria dioica* (L.) Gaertner, *Arnica montana* L., *Deschampsia flexuosa* (L.) Trin., *Filago minima* (Sm.) Pers. and *Viola canina* L. were collected in the northern part of The Netherlands. *A. dioica* and *V. canina* were grown under controlled conditions before their seeds were used in the experiments. The seeds were stored dry, in paper bags, at 4°C, until they were needed (Pegtel 1988).

The seeds were germinated on an artificial potting soil (a mixture of coarse sand, beech litter, sphagnum peat and fertilized black peat). The conditions under which germination took place were 12 h light/25°C and 12 h dark/15°C. The seedlings were pre-grown on the same soil mixture in a climate room (16 h light/8 h dark; 23°C/15°C; 70%/90% relative humidity) for a maximum of 3 weeks. Light was provided by white fluorescent tubes that gave a radiation flux density of 50 W m^{-2} at plant height.

The method and equipment used in the solution culture experiments and the complete nutrient solution are described in Pegtel (1987). The phosphorus concentration was low (3·44 mg l^{-1}). Nitrogen was supplied as nitrate, because it has been shown (Gigon & Rorison 1972; Rorison 1985) that *D. flexuosa* grows equally well when nitrogen is supplied as NH_4^+-N or NH_3^--N at low pH. The pH of all the nutrient solutions was adjusted daily (with H_2SO_4) and maintained at 3·8. The nutrient solutions were renewed weekly. No precipitation was observed for either Al-salts or Mn-salts.

In the first experiment (March–May, 1986), Al was supplied as $Al_2(SO_4)_3.18H_2O$. Concentrations were 0, 5, 20 and 80 mg l^{-1} Al. In the second experiment (May–June, 1986) Mn was supplied as $MnSO_4.H_2O$. Concentrations were 0·3, 2·5, 62·5 and 312·5 mg l^{-1} Mn. In the third experiment (October–November, 1986), Al and Mn were supplied simultaneously to *D. flexuosa*, *A. montana* and *V. canina*. The concentrations were 80 mg l^{-1} Al and 300 mg l^{-1} Mn.

The treatments were repeated three times, randomized and involved five visually selected seedlings per tray. The five species were cultivated separately for 5 weeks. The phytomass yield (shoots and roots) per tray was measured on material dried at 70°C.

Results were analysed statistically with one-way ANOVA and Student's *t*-test was also applied ($P<0{\cdot}05$) when the differences that related to Al or Mn treatments were significant.

The nomenclature of taxa is according to Heukels & Van de Meijden (1983), that of the syntaxa follows Westhoff & Den Held (1969).

RESULTS

Effects of aluminium

Visual symptoms. It appeared that Al affected roots more than shoots, except in the case of *D. flexuosa*. *A. dioica* showed thickened roots in response to aluminium. When Al concentrations exceeded 20 mg l^{-1}, the root tips turned black, the leaves became cupped and the roots clearly showed more reductions in growth than the shoots. At concentrations of 80 mg l^{-1} Al, *A. montana* had cupped leaves and stunted roots. *F. minima* was the most affected, in particular the roots, which were stubby at concentrations exceeding 20 mg l^{-1} Al. The shoots had many reflexed leaves of which the numbers were proportional to the Al concentrations. The roots of *V. canina* were stubby and extremely branched with all concentrations.

Table 1. Mean ($\pm$SD, $n=3$) shoot and root dry weights (grams per five plants) of young plants of *A. dioica*, *A. montana*, *F. minima*, *V. canina* and *D. flexuosa*, after 5 weeks of growth, in response to various concentrations of Al in complete nutrient solution of low phosphorus (3·4 mg l^{-1}) and low pH (3·8)

Al (mg l^{-1})	*Antennaria dioica*	*Arnica montana*	*Filago minima*	*Viola canina*	*Deschampsia flexuosa*
Shoot dry weight					
0	2·37±0·33	3·88±0·49	4·05±0·28	3·40±0·74	6·45±1·43
5	2·39 0·55	3·18 0·62	1·94* 0·11	3·75 0·34	6·00 0·32
20	1·09 0·11	3·71 1·17	1·82* 0·43	3·06 0·64	6·88 0·71
80	0·58* 0·08	2·26 0·28	0·71* 0·07	2·46* 0·82	4·90 0·64
Root dry weight					
0	0·51±0·11	1·72±0·04	1·01±0·17	1·07±0·13	2·77±0·19
5	0·38 0·02	1·48 0·21	0·66* 0·04	1·14 0·04	2·50 0·12
20	0·19* 0·04	1·25 0·46	0·51* 0·13	0·95* 0·06	2·54 0·36
80	0·05* 0·01	0·79 0·26	0·20* 0·02	0·72* 0·13	2·21 0·14

* Significant at $P<0·05$.

Yields. The dry weights of *A. montana* and *D. flexuosa* showed no variation, which is attributable to Al ($P<0·05$). The dry weights of *F. minima* did, however, show reductions to all aluminium concentrations ($P<0·05$), whereas those of *A. dioica* and *V. canina* only showed reductions at 20 mg l^{-1} (roots) or 80 mg l^{-1} (shoots) (Table 1).

Effects of manganese

Visible effects. No effects were seen on *D. flexuosa* at any of the Mn concentrations that were applied. Young leaves of *A. dioica* were chlorotic at 312·5 mg l^{-1} Mn and older leaves had black tops. Some roots were darker and uniformly coloured. *A. montana* almost always had chlorotic shoots at concentrations exceeding 12·5 mg l^{-1} Mn. At the highest concentration of Mn (312·5 mg l^{-1}), the young leaves were light-yellow with light-green nerves and had necrotic spots. The older leaves were dark-green with necrotic spots. *F. cinina* had chlorotic leaves and some leaves died at concentrations higher than 62·5 mg^{-1} Mn. At 312·5 mg l^{-1} Mn all the leaves were yellowish to brownish.

Yields. The dry weights of the shoots of all species were not significantly affected by manganese. The same was the case with the dry weights of the roots, except for those of *F. minima*, which were negatively affected by Mn at concentrations exceeding 62·5 mg l^{-1} Mn upwards (Table 2). Nevertheless, there was a trend to indicate that some stimulation in the growth of both shoots and roots could be established in response to concentrations up to 12·5 mg l^{-1} Mn; except in the case of *F. minima* (Table 2).

Combined effects of aluminium and manganese

Visible symptoms. D. flexuosa had young leaves the bases of which were yellow. The older leaves were dark-brown to reddish. Comparatively large numbers of leaves were desiccated or light-green to yellowish at the tops. The roots were somewhat stubby and more or less white. The leaves of *A. montana* were small and not fully developed. The older leaves often had brown spots, desiccated at the margins and the younger leaves were

Table 2. Mean ($\pm$SD, $n=3$) shoot and root dry weights (grams per five plants) of young plants of *A. dioica*, *A. montana*, *F. minima*, *V. canina* and *D. flexuosa*, after 5 weeks of growth, in response to various concentrations of Mn in complete nutrient solution of low phosphorus (3·4 mg l^{-1}) and low pH (3·8)

Mn (mg l^{-1})	*Antennaria dioica*	*Arnica montana*	*Filago minima*	*Viola canina*	*Deschampsia flexuosa*
Shoot dry weight					
0·3	6·44±2·07	4·51±1·11	7·61±1·49	4·53±0·93	4·11±0·55
2·5	7·04 2·90	6·42 1·44	7·33 0·40	3·45 1·45	4·67 0·74
12·5	8·12 1·98	5·26 1·25	7·10 0·60	6·15 2·08	5·17 0·94
62·5	2·83 1·92	5·70 1·31	5·76 0·55	3·56 0·44	4·90 0·64
312·5	4·17 1·05	2·82 0·90	2·97 0·35	1·93 0·99	3·70 1·26
Root dry weight					
0·3	0·69±0·19	2·68±0·35	1·59±0·26	1·35±0·26	1·51±0·14
2·5	0·84 0·29	2·83 0·51	1·50 0·14	1·46 0·46	1·52 0·07
12·5	0·85 0·20	3·28 0·83	1·34 0·08	1·74 0·63	1·86 0·48
62·5	0·44 0·20	2·90 0·65	1·12* 0·10	1·52 0·12	1·63 0·35
312·5	0·39 0·06	0·93 0·15	0·42* 0·07	1·14 0·52	1·48 0·16

* Significant at $P<0·05$.

Table 3. Mean ($\pm$SD, $n=3$) shoot and root dry weights (grams per five plants) of young plants of *A. montana*, *V. canina* and *D. flexuosa*, after 5 weeks of growth, in response to high concentrations of Al (80 mg l^{-1}) and Mn (300 mg l^{-1}) in complete nutrient solution of low phosphorus (3·4 mg l^{-1}) and low pH (3·8)

Al (mg l^{-1})	Mn (mg l^{-1})	*Arnica montana*	*Viola canina*	*Deschampsia flexuosa*
Shoot dry weight				
0	1·1	9·17±0·71	10·01±0·45	8·93±0·47
80	300	1·27* 0·06	1·70* 0·11	5·09* 0·98
Root dry weight				
0	1·1	4·06±0·36	1·72±0·12	2·37±0·22
80	300	0·41* 0·05	0·80* 0·11	1·27* 0·28

*Significant at $P<0·05$.

light-yellow, with green nerves and green bases. Only the first strongly branched (lateral) roots were greyish, had black tops and were slightly elongated. The older leaves of *V. canina* were scorched and exhibited a purple to greyish colour whereas the younger leaves were grey to yellowish. Cotyledons were still present and they were also discoloured. The roots were somewhat stubby and ochreous, with white tops.

Yields. When exposed to high concentrations of both Al (80 mg l^{-1}) and Mn (300 mg l^{-1}) the dry weights of the shoots and roots of *A. montana*, *V. canina* and *D. flexuosa* were significantly reduced compared to those of the control plants (Table 3).

DISCUSSION

Effects of aluminium

It can be concluded from the results that *A. dioica*, *A. montana*, *F. minima* and *V. canina* responded differently to ionic Al. *D. flexuosa* and *A. montana* can be classified as relatively resistant to Al. *A. dioica* and *V. canina* somewhat less resistant and *F. minima* relatively sensitive.

The roots of *A. dioica* and *V. canina* were more affected than the shoots. This is in agreement with the known effects of Al. Roots are, in general, more susceptible to ionic Al than shoots (Foy *et al.* 1978). However, important reductions in growth were not observed in these species in response to rather high concentrations of ionic Al. Growth stimulation by Al of *D. flexuosa* (Hackett 1962; Pegtel 1987) and *A. montana* (Pegtel 1987) was not detected in this study. This may possibly be due to different growth conditions: in the first series of experiments (Pegtel 1987) a heated greenhouse was used.

In contrast to the species of the Violion canina, *F. minima* can be classified as a susceptible species to Al, because even low concentrations of Al had a negative effect on growth.

All species, but *D. flexuosa* in particular, were capable of raising the pH of the nutrient solutions which was adjusted daily. This may be the result of the type of nitrogen nutrition (Rorison 1985). Nitrate as the nitrogen source generally leads to an increase in pH due to the release of HCO_3^--ions (Haynes & Goh 1978). An increase in the rhizosphere pH has been interpreted to be a mechanism of Al resistance (Foy *et al.* 1978). Other mechanisms might be the formation by complexes of Al (inside or outside plants), precipitation with, for example, phosphate (inside and/or outside plants), or storage in vacuoles, etc. (Wright 1943).

Effects of manganese

The species reacted differently to Mn. Although not statistically established, there are indications that, like *D. flexuosa*, the species *A. dioica*, *A. montana* and *V. canina* can be classified as being relatively resistant and *F. minima* relatively sensitive to Mn as compared to Al. Nevertheless, the differences between species were less clear than in their responses to Al.

D. flexuosa is known to be very Mn tolerant (Mahmoud & Grime 1977; Pigott 1970). The three species of the Violion caninae responded in a similar way to Mn. Though no significant differences could be established, there are indications that these species, like *D. flexuosa*, reach an optimal phytomass production at 12·5 mg l^{-1} Mn. It seemed, therefore, that these species require relatively large amounts of Mn. *F. minima*, on the contrary, does not show a Mn requirement higher than 0·3 mg l^{-1}. These results may confirm that plant species from acid soils have a relatively high Mn requirement (Ernst & Nelissen 1979).

Except in the case of *D. flexuosa*, the species exhibited symptoms of Mn toxicity. The effects of Mn were particularly observed on shoots. Phytotoxic levels of Mn supply are most commonly observed in visible symptoms (iron chlorosis), rather than in the reduction of vegetative growth. This is the opposite in the case of Al (Foy *et al.* 1978). Iron chlorosis may be the result of a decrease in Fe^{3+} transport from roots to the shoot due to $FePO_4$ precipitation following oxidation of Fe^{2+} to Fe^{3+} by Mn^{4+} in the roots (Kuo & Mikkelsen 1981). A possible mechanism of tolerance is a high oxidizing capacity of roots, which results in the transformation of Mn^{2+} to Mn^{4+} (Foy *et al.* 1978).

Effects of aluminium and manganese

The combined effects of high concentrations of Al and Mn were detrimental to *A. montana*, *D. flexuosa* and *V. canina*. As the growth of *D. flexuosa* was also adversely affected, there are no indications to assume that similar high concentrations occur under field conditions. Combined Al and Mn resulted in more marked reductions in growth than when these elements were supplied separately. A high concentration of Al (80 mg l^{-1}) did not reduce Mn toxicity and vice versa. Manganese toxicity might, however, be reduced by other Al/Mn ratios (Foy *et al.* 1978).

Ecological aspects. Seedlings were grown for a limited period. The results, however, may have important consequences because it is commonly observed that the seedling stage is the most susceptible to adverse conditions. *A. dioica*, *A. montana* and *V. canina* were shown to be not, or only weakly, sensitive to relatively high concentrations of Al or Mn. Increased levels of ionic Al and Mn in solutions are, therefore, not likely to be important soil factors in the regulation of the distribution of these species. Resistance to Al and Mn is considered to be an adaptation to acid soils (Rorison 1986).

F. minima, on the contrary, appeared to be sensitive to both Al and Mn. If concentrations of these ions in soil solutions increase, the growth and development of *F. minima* is probably affected negatively.

The decline in the species of the Violion caninae must be due to factors other than Al and/or Mn toxicity.

It has been established that Mn tolerance of *D. flexuosa* (Pigott 1970; Mahmoud & Grime 1977) may play an important role in the regulation of its competitive ability. Because *D. flexuosa*, *A. dioica*, *A. montana* and *V. canina* did not show differences in sensitivity to Mn, competitive abilities do not seem to be (dramatically) affected by the Mn available in the soil.

Competitive abilities could be affected by other factors. Current levels of atmospheric nitrogen depositions, the influence of the vegetation (structure) in intercepting and modifying their input (Mayer & Ulrich 1980) and the lack of appropriate management, resulting in the accumulation of organic matter, increases the fertility of the top soil. This most probably benefits *D. flexuosa* (Heil 1984) more than the others. Furthermore, accumulated litter of *D. flexuosa* may have a negative effect on seed germination and seedling establishment of other species (Jarvis 1964).

Finally, it also seems worthwhile to study the direct effects of air pollutants, and the interactions between direct and indirect effects.

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