PHENOLIC SUBSTANCES IN A HUMUSPODZOL PROFILE AND THEIR IMPACT ON SOME WOODLAND HERBS AT LOW NUTRIENT SUPPLY

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SUMMARY

Twelve years after clearance of a *Picea abies* stand, the spectrum of water-soluble phenolic acids in the soil still resembled that of an adjacent, undamaged stand. Ferulic and *p*-coumaric acid were the predominant phenolic compounds. Apparently, the spectrum of low molecular phenolics in the soil layers is affected by the original litter material over a long period. The concentrations of water-soluble acids was highest in the A_0-horizon. A comparison between the sites revealed that concentrations in the clearing were reduced with more than 50% compared to the undamaged stand.

The significance of the phenolic acids for plant growth was investigated for two herbaceous woodland (-clearing) species, *Senecio sylvaticus* and *Chamaenerion angustifolium*. Both species were tested for their sensitivity to phenolic acids in dependence of nutrient supply under greenhouse conditions. Severe growth reduction occurred at high phenolic acid concentrations (10^{-3} M). Plants that were restricted in growth by a low nutrient supply, were less affected by the intermediate phenolic acid concentrations of 10^{-5} and 10^{-4} M than plants grown at high nutrient supply. The results are discussed in view of vegetation succession on woodland clearings.

1. INTRODUCTION

Woodland clearings often occur as a result of human impact (clear-cutting) or natural events (storm damage, fire). Removal of the crown layer causes considerable changes in the water, light and temperature regime. The cycling of minerals and organic matter is then severely changed (BORMAN & LIKENS 1979; VAN ANDEL & ERNST 1985), thereby changing soil properties and growth conditions of plants in the herb layer. A typical woodland clearing vegetation becomes established, characterized on acid sandy soils by the association Epilobio-Senecionetum sylvatici (WESTHOFF & DEN HELD 1969). Initially, nutrient availability increases due to increased mineralization of soil organic matter (BORMAN & LIKENS 1979). During secondary succession to new woodland, however, nutrient conditions deteriorate by increased leaching.

Both *Chamaenerion angustifolium* (L.) Scop and *Senecio sylvaticus* L. often dominate the early phases of the clearing vegetation. They spread their roots in the organic humus layers. *Chamaenerion* is able to maintain itself during several tens of years, because of an efficient internal redistribution of accumulated nutrients between the perennial rhizomes and the annual shoots (VAN ANDEL & NELISSEN 1979). If vegetation does not become completely closed (at rather poor nutrient conditions), even the annual herb *Senecio sylvaticus* is able to

maintain itself for many decades. Populations of both species are thus confronted with decreasing nutrient availability in the course of time, which may have consequences for their sensitivity to organic compounds present in the soil solution. According to STOWE & OSBORN (1980) plants show an increased sensitivity to phenolic acids as nutrient conditions deteriorate.

Woodland(-clearing) soils are often rich in phenolic substances, including both monomeric phenolic acids as well as polymeric compounds like tannins (WHITEHEAD *et al.* 1982; KUITERS & DENNEMAN 1987). These compounds are released from living and dead plant material by leaching (ANDERSON 1973; KUITERS & SARINK 1986) and by the breakdown of lignin (FLAIG *et al.* 1975; ZIEGLER *et al.* 1986). Many plants show an altered growth when phenolic acids are present in their rooting milieu (FLAIG 1973; RICE 1984; EINHELLIG *et al.* 1982; BLUM *et al.* 1984; KUITERS & SARINK 1987). GLASS (1973) has argued that phenolic acids change membrane permeability, due to their lipid solubility, and cause leakage of ions like phosphate and potassium to the external milieu.

In this study we investigated the effects of phenolic acids on the growth of *Chamaenerion angustifolium* and *Senecio sylvaticus* under conditions of low nutrient supply. We also compared the chemical state of the soil between a homogeneous stand with *Picea abies* (L.) Karsten and an adjacent 12 year-old storm-felled clearing where both herbaceous species occurred. Especially the presence of phenolic acids in the different horizons was investigated, both qualitatively and quantitatively. The aim of this study was to gain more insight into the way in which chemical soil factors, both anorganic as well as organic, together influence plant growth.

2. MATERIAL AND METHODS

2.1 Sampling soils

On the Veluwe near Grolloo (The Netherlands) thousands of acres of coniferous woodlands have been damaged by storm in 1972/1973. These clearings have not always been reforested and at some locations a herbaceous vegetation has developed with (at later stages) woody species such as *Sambucus nigra* L., *Sorbus aucuparia* L. and *Betula pendula* Roth. Soil samples were taken from three sites. Site A was an undamaged stand with 80 year-old trees of *Picea abies*. *Senecio sylvaticus* occurred here as the only understory herb. Adjacent to this stand was a clearing (site B), with various plant species typical for the association Epilobio-Senecionetum sylvatici (WESTHOFF & DEN HELD 1969), with *Senecio* and *Chamaenerion* as the dominant herb species. At one location on this clearing (site C), 4–6 year-old saplings of *Betula* occurred indicating a spontaneous development to new woodland. In September 1984, five soil cores (upto 30 cm depth; ∅ 10 cm) were taken at each site. In the laboratory the samples were divided into the visible horizons, sieved (2 mm) and stored at –20 °C until analysis.

2.2 Soil analyses

The pH of the soil samples was determined in a soil suspension (5 g fresh soil

in 50 ml water), after shaking for 1 h. Concentrations of water-soluble and exchangeable minerals were determined by extracting with water and ammonium acetic acid respectively for two hours. Concentrations of total extractable minerals were determined by wet-ashing with a mixture of concentrated HNO_3 and $HClO_4$ (1:1). Lanthan nitrate was added for determination of Ca and Mg. All minerals were determined by atomic absorption spectrophotometry, except phosphorus which was determined colorimetrically, following the method of CHEN et al. (1956).

Phenolic acid analyses were carried out by shaking soil samples of 15 g in 100 ml distilled water (75 r.p.m.) during 20 h at room temperature. The solutions were filtered through Whatman paper no. 1 and concentrated to 10 ml in a rotating vacuum evaporator at 30°C. After acidification to pH 2.0 with 1 N HNO_3 three extractions with ethyl acetate followed. The water fractions were discarded and the organic fractions were combined and concentrated to 5 ml. A subsample of 100 μl was totally evaporated and dissolved in 100 μl pyridine. After trisilylilation with 100 μl BSTFA (N,N-Bis-trimethylSilyl-TriFluorAcetamide) the samples were analyzed by gaschromatography following the method described earlier (KUITERS & SARINK 1986). A standard mixture was used with 12 monomeric phenolic compounds. Hydrochinon was used as internal standard. All the cinnamic acids (in the standard solution) were of the trans isomers.

2.3 Greenhouse experiments

Seeds from *Senecio* were germinated in a commercial peat soil (Calceolaria) mixed with sand (1:1; v/v). After four weeks the seedlings were transplanted into plastic containers filled with 5 l nutrient solution. This solution contained nutrients in the following concentrations (mmol l^{-1}): 0.5 NH_4NO_3; 1 $CaCl_2$; 1 $MgSO_4$; 0.005 or 0.5 KH_2PO_4; 0.25 K_2SO_4; 0.1 NaCl; 0.05 H_3BO_4; 0.02 $MnSO_4$; 0.0001 $(NH_4)_6Mo_7SO_4$; 0.025 $ZnSO_4$; 0.002 $CuSO_4$; 0.1 $FeSO_4$ + 0.1 Na_2EDTA. The treatment began after two weeks of acclimatization. An equimolar mixture of seven commonly occurring phenolics was added, containing p-hydroxybenzoic, vanillic, syringic, salicylic, caffeic, p-coumaric, and ferulic acid. Total concentrations used were 10^{-5}, 10^{-4} and 10^{-3} M. Each concentration was combined with two levels of phosphate (0.005 and 0.5 mM). Eight seedlings were planted in each container and each treatment was replicated twice. The pH was adjusted with 1 N NaOH or 1N HCl to 4.5. The containers were placed randomly in a greenhouse with controlled climatic conditions (light/dark: 16/8 h; light intensity 50 W m^{-2}; temperature 22°C $\pm$ 5; 70% relative humidity). Every three days the solution was refreshed, as phenolic acids quickly disappear from solutions that are aerated. Plants were harvested after a growing period of 3 weeks, and biomass production was determined on material dried for 48 h at 60°C.

The data of root, shoot and root/shoot ratio were averaged over the eight plants per container and these means tested for homogeneity with the Bartlett test. The log-transformed data were analyzed by two-way analysis of variance (SOKAL & ROHLF 1981).

In a second experiment plants of *Chamaenerion* were tested for their sensitivity

to phenolic acids. Besides a low P supply, these plants were also subjected to a low N or K supply and a combined low NPK supply. Seeds from *Chamaenerion* were germinated on a commercial peat soil (Calceolaria) mixed with sand (1:1 v/v). After six weeks the seedlings were transplanted into pots filled with 600 ml nutrient solution, the same as used in the experiment with *Senecio*. After one week of acclimatization the treatments were started. A mixture of 7 phenolic acids, the same as mentioned before, was added in concentrations of 10^{-4} M and 10^{-3} M. Each of the phenolic acid concentrations was combined with five different nutrient conditions (see *table 1*).

Two seedlings were transplanted into each pot and each treatment was replicated five times. Growth conditions were the same as described earlier. After a growth period of 6 weeks, plants were harvested. Biomass production was determined on material dried for 48 h at 60 °C. Data were analyzed in the same way as described for *Senecio*.

3. RESULTS

3.1 Field situation

All soils had a pH between 2.9 and 3.3, which is typical for humuspodzol profiles. The mineral content of the soils at the three sites, i.e. the *Picea* stand (A), the 12 year-old stormfelled site (B) and the part of this clearing where saplings of *Betula* were established (C), are presented in *table 2*. At all sites the A_0 horizon had the highest amount of nutrients. The largest differences between the sites occurred in the A_1 horizon. Especially the elements K, Na, Mg, P and Mn were much lower at sites B and C. No distinct differences occurred between the latter two sites.

The type and amount of water soluble monomeric phenolic compounds identified in the soil horizons at the three sites are presented in *table 3*. Of the 12 phenolic compounds present in the standard sample, 7 to 9 compounds could be identified in the aqueous soil extracts. The spectra of phenolic compounds were similar at the three sites: ferulic acid and *p*-coumaric acid were the dominant phenolic compounds at all sites in all horizons. Syringic, caffeic, benzoic nor cinnamic acid were detected in any of the soil samples. The phenolic content was highest in the A_0 horizons and decreased with increasing depth. Differences

Table 1. Concentrations (mM) of the macronutrients N, P and K applied in the experiment with *Chamaenerion angustifolium*.

treatment	N	P	K
low N supply	0.2	0.5	1.0
low P supply	2.0	0.025	1.0
low K supply	2.0	0.5	0.05
low NPK supply	0.2	0.025	0.05
control	2.0	0.5	1.0

Table 2. pH and mineral content of the soil horizons of a humus podzol profile at site A (homo-geneous stand with *Picea abies*), site B (12 year-old clearing) and site C (clearing with 4–6 year-old saplings of *Betula pendula*).
T = total, E = exchangeable and W = water-soluble content. ND is below the detection level: <0.1 mmol kg^{-1} dw for P, K, Na, Ca and Mg, Fe and Mn and <0.01 mmol kg^{-1} dw for Zn.

Site	soil horizon	pH (H$_2$O)		minerals (mmol kg^{-1} dw)							
				P	K	Na	Ca	Mg	Fe	Mn	Zn
A	A$_0$	3.3	T	16.7	12.9	3.6	71.7	12.5	18.8	1.2	0.10
			E	2.4	6.2	3.3	46.7	7.5	0.1	0.5	0.08
			W	2.4	6.1	3.3	4.2	2.1	0.1	0.1	0.02
	A$_1$	2.8	T	10.0	8.9	8.7	19.8	9.8	13.3	0.9	0.12
			E	0.1	3.2	4.2	19.7	4.2	0.2	0.4	0.07
			W	0.1	2.8	4.2	2.1	1.1	0.3	ND	0.03
	A$_2$	2.9	T	2.6	3.9	2.6	6.6	4.4	10.2	0.1	0.10
			E	ND	0.4	2.6	6.6	4.4	0.1	ND	0.01
			W	ND	0.3	2.1	0.8	0.6	0.1	ND	0.01
B	A$_0$	3.1	T	17.0	11.8	6.9	74.0	12.3	19.5	1.0	0.13
			E	3.2	5.4	3.8	34.5	6.9	0.1	0.3	0.13
			W	3.2	4.7	4.0	4.0	2.1	0.1	0.1	0.06
	A$_1$	3.0	T	4.9	3.8	3.2	23.7	3.8	10.8	0.4	0.15
			E	ND	0.8	2.7	23.0	2.7	0.1	0.1	0.14
			W	ND	0.8	2.7	1.7	0.8	0.1	ND	0.03
	A$_2$	3.3	T	2.3	2.7	2.7	11.1	2.4	7.2	0.1	0.10
			E	ND	0.1	2.7	11.1	2.4	0.1	ND	0.10
			W	ND	ND	1.4	0.2	0.4	0.1	ND	0.01
C	A$_0$	2.9	T	16.2	11.4	7.6	57.2	14.1	21.5	1.0	0.10
			E	2.2	4.7	4.4	28.1	5.6	0.1	0.3	0.09
			W	2.2	3.9	4.3	3.2	1.5	0.1	0.1	0.05
	A$_1$	2.9	T	2.2	2.7	3.3	17.5	2.4	9.4	0.4	0.10
			E	ND	0.7	3.0	17.5	2.4	0.1	0.1	0.03
			W	ND	0.1	2.0	0.8	0.6	0.1	ND	0.01
	A$_2$	3.0	T	2.0	2.1	2.2	10.9	2.0	8.7	0.6	0.10
			E	ND	0.2	2.1	10.9	2.0	0.1	ND	0.02
			W	ND	ND	1.7	0.5	0.5	0.1	ND	0.01

between the three sites occurred mainly in the A$_1$ horizon, with lowest concentra-tions in the clearing. The phenolic content in the A$_0$ and the A$_1$ horizon under the birch saplings was higher compared to the rest of the clearing.

3.2 Greenhouse experiments

Biomass production of *Senecio* plants grown on nutrient cultures with sufficient or low phosphate supply in combination with different concentrations of phen-olic acids are presented in *fig. 1*. In the absence of phenolic acids, total biomass production was reduced to 54% at low phosphate supply, indicating that plants

Table 3. Water-soluble phenolic acids in the soil horizons of the three different sites. fer = ferulic, pco = p-coumaric, phb = p-hydroxybenzoic, mco = m-coumaric, oco = o-coumaric, van = vanillic, sal = salicylic, gen = gentisic acid. ND is below detection level of 1 μg g^{-1} dw.

| Site | horizon | phenolic acids (μg g^{-1} dw) | | | | | | | | |
		fer	pco	phb	mco	oco	van	sal	gen	total
A	A_0	8	9	6	3	2	3	5	5	41
	A_1	15	6	1	2	1	1	1	ND	27
	A_2	2	1	ND	ND	ND	ND	ND	ND	3
	B_{2h}	2	1	ND	ND	ND	ND	ND	ND	3
	B_{22}	ND	ND	ND	ND	ND	ND	ND	ND	ND
B	A_0	13	5	1	3	ND	1	ND	ND	22
	A_1	6	1	1	1	ND	ND	ND	ND	9
	A_2	4	2	1	1	ND	ND	ND	ND	8
	B_{2h}	3	1	1	ND	ND	ND	ND	ND	5
	B_{22}	ND	ND	ND	ND	ND	ND	ND	ND	ND
C	A_0	9	5	1	2	2	3	3	3	28
	A_1	9	2	1	1	1	ND	1	ND	15
	A_2	1	1	1	1	ND	ND	1	ND	5
	B_{2h}	2	1	ND	1	ND	ND	ND	ND	4
	B_{22}	2	1	1	1	ND	ND	ND	ND	5

suffered from P deficiency. Under high P supply, 10^{-5} M phenolic acids diminished growth, whereas at low P supply no growth reduction occurred compared to the control. Growth was severely affected at 10^{-3} M phenolic acids and this was independent of the nutrient condition. Shoot biomass was more influenced than root biomass (*fig. 1*). The root/shoot ratio was negatively correlated (r = −0.53) with plant weight, resulting in a higher root/shoot ratio at 10^{-3} M phenolic acids ($P < 0.05$), whereas the low phosphate supply significantly increased this ratio ($P < 0.01$).

Biomass production of *Chamaenerion* grown on nutrient solutions with phenolic acids and different forms of low supply of various nutrients are presented in *fig. 1*. Low supplies of N, P or K reduced biomass production in the absence of phenolic acids to 49, 66 and 47% respectively, compared to the control. Low N supply and to a smaller extent low P supply, reduced biomass of the shoot more than that of the roots, resulting in a significant higher root/shoot ratio ($P < 0.001$). The effects of the phenolic acids were most pronounced under adequate nutrient conditions. Biomass production was independent of the nutrient situation at 10^{-4} and 10^{-3} M phenolic acids, indicating that growth reduction was relatively larger at the good growth conditions. Phenolic acids had no significant effect on the root/shoot ratio (*table 4*). No synergistic effects could be established under the combined stress of N, P and K.
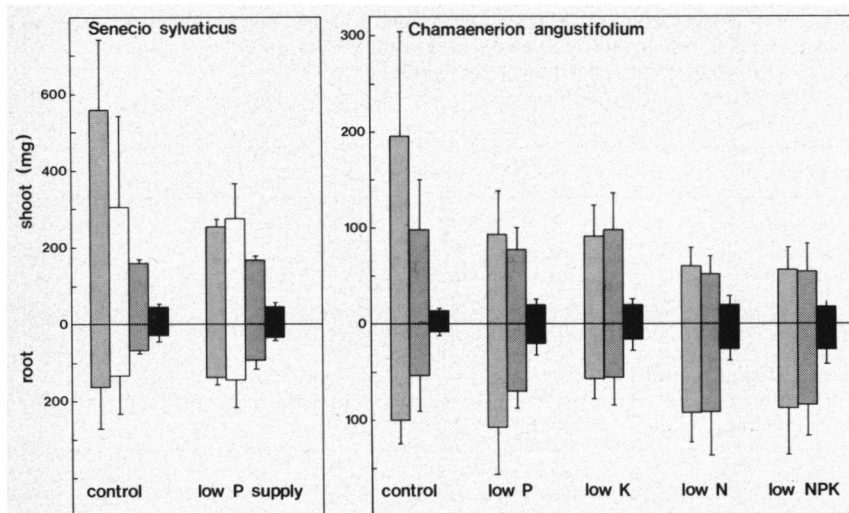
4. DISCUSSION

4.1 Field conditions

Figure 1. Effects of phenolic acids on shoot and root biomass of *Senecio sylvaticus* and *Chamaenerion angustifolium* under different conditions of low nutrient supply.
☐ control, ☐ 10^{-5} M, ▨ 10^{-4} M, ■ 10^{-3} M phenolic acids.

Twelve years after clearance of the *Picea abies* stand, the spectrum of phenolic acids in the soil still resembled that of the adjacent undamaged stand. Apparently, the presence of humus material in the soil from spruce trees determines the types of phenolic acids that are released over a long period. Presumably this is the result of lignin breakdown (SWIFT *et al.* 1979; ZIEGLER *et al.* 1986), a process that occurs slowly (FLAIG *et al.* 1975). JALAL & READ (1983), investigating *Calluna* vegetations, also demonstrated that the composition of organic acids in a soil had not changed 18 years after the *Calluna* vegetation had been replaced.

Although the composition of the phenolic acids in the soil at the clearing that we investigated had not changed, the concentrations in the organic soil layers were reduced with more than 50%, related to an increase in leaching rate and absence of any further deposition of fresh needle litter. An increase in leaching rate in the clearing was also reflected in the mineral content of the soil. The mineral status of the soil beneath the *Picea* trees was rather poor, but the availability of nutrients was further reduced in the clearing. Removal of the crown layer disturbs nutrient cycling processes (BORMANN & LIKENS 1979; VAN ANDEL & ERNST 1985) and increased mineralization of organic matter, followed by increased leaching of water-soluble compounds, occurs. Part of the available nutrients also become steadily accumulated in perennial herbs (VAN ANDEL & NELISSEN 1979), thereby reducing nutrient availability for seedlings of other plants (VAN ANDEL & ERNST 1985). The presence of 6 year-old *Betula* saplings at one location had no significant effect on the chemical soil properties.

The distribution of the phenolic acids over the podzol profile was mainly confined to the organic A-horizons, conform the results of LODHI (1975) and MA-

Table 4. Levels of significance of the effects of phenolic acids and nutrient supply on shoot and root biomass and root/shoot ratio of *Senecio sylvaticus* and *Chamaenerion angustifolium.*
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns = not significant.

Senecio sylvaticus

source of variation	df	root	shoot	r/s
phenolic acids	3	**	***	*
nutrient supply	1	ns	ns	**
interaction	3	ns	ns	ns
error	8			

Chamaenerion angustifolium

source of variation	df	root	shoot	r/s
phenolic acids	2	***	***	ns
nutrient supply	4	***	**	***
interaction	8	*	***	ns
error	75			

CIAK & HARMS (1986). Highest concentrations were found in the A_0 horizon. Among the phenolic acids, ferulic and *p*-coumaric acid were the dominant compounds.

4.2 Greenhouse experiments

The ecological significance of the presence of phenolic acids in the soil solution was investigated in greenhouse experiments with *Chamaenerion angustifolium* and *Senecio sylvaticus*, which both occurred in the 12 year old clearing. We tested their sensitivity for phenolic acids at different nutrient conditions. STOWE & OS-BORN (1980) suggested that under low nutrient supply, plants are more sensitive to phenolic acids. This is consistent with the findings of GLASS (1973) and HARPER & BALKE (1981), who found that phenolic acids can change membrane permeability, resulting in reduced uptake or increased leakage of ions to the external milieu. Our results did not confirm this hypothesis. The plants that were restricted in growth by a low supply of N, P or K, were not more inhibited by phenolic acids than plants growing under better nutrient conditions. On the contrary, at low concentrations of 10^{-5} and 10^{-4} M phenolic acids, plants of both species showed relatively more growth reduction when grown on a high nutrient supply compared to the plants grown under low nutrient supply. This indicates that phenolic acids assert their influence rather by interfering directly with other growth restricting processes than by reduction of ion uptake. Phenolic acids can affect IAA and gibberellin synthesis (ZENK & MULLER 1963), energy metabolism (DEMOS *et al.* 1975) and photosynthesis and respiration (PATTERSON 1981). Direct effects on ion uptake are more likely to occur when the root membrane is damaged, which occurs only at high phenolic acid concentrations.

4.3 Vegetation succession

The phenolic acids released by the humic material present in the soil can, as demonstrated in the greenhouse experiments, inhibit the performance of herbaceous plants. This can have serious consequences for vegetation development at woodland clearings. Selection of certain species may occur as herbs do not show the same reaction to phytotoxic properties of litter. Especially in the early growth stages, grass species are less sensitive to allelochemicals than dicotyledonous species (KUITERS et al. 1986). Indirectly, the growth of herbs may also be affected by reduced infection and activity of mycorhizzal fungi. OLSEN et al. (1971) and LINDEBERG (1985) have demonstrated that mycorhizzal fungi are relatively sensitive to phenolic substances, compared to typical litter decomposers and ROSE et al. (1983) found that litter leachates seriously influenced the growth of mycorrhizal fungi. Besides herbs the successful establishment of woody species may be inhibited in this way as well. In forestry problems by the regeneration or the reforestation of clearings are often ascribed to the presence of phenolic substances in the soil (DEBELL 1970, FISHER 1980).

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