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Distribution and decline of endangered herbaceous heathland species in relation to the chemical composition of the soil

A.L.F.M. HOUDIJK, P.J.M. VERBEEK, H.F.G. VAN DIJK and J.G.M. ROELOFS
Department of Ecology, Section Environmental Ecology, Catholic University of Nijmegen, Toernooiveld, NL-6525 ED Nijmegen, The Netherlands

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Abstract

High atmospheric deposition of ammonium affects the physical and chemical status of the soil, increasing nitrogen availability, soil acidity and the mobilization of toxic metal ions. To investigate whether and how the decline of several herbaceous plant species in Dutch heathlands is associated with these processes, the chemical composition of the soil on which these species grow has been compared with the soil on which heathland species such as *Calluna vulgaris* (L.) Hull, *Erica tetralix* L. and *Molinea caerulea* (L.) Moench dominate.

The discrimination between both soil types was primarily based on differences in pH (H_2O), pH (NaCl) and the aluminium/calcium ratio in the waterextracts. Within the group of endangered herbaceous heathland species these soil parameters also varied. This led to a division into 4 groups of species:

- Dominating species growing on acid soils
- Herbaceous species growing together with dominating species on acid soils
- Herbaceous species growing together with dominating species on moderately acid soils
- Herbaceous species growing together with dominating species on weakly acid soils.

This study indicated that, unlike the decline of heather species, the decline of herbaceous species is not likely to be due to increased competition from grass species as a result of eutrophication. Soil acidification and the changed mineral balance in the soil are most likely to be responsible for the decline of all three groups of herbaceous plant species.

Introduction

Until the beginning of this century heathlands covered 800,000 ha of the pleistocene soils in the Netherlands. Since then the area of heathland decreased dramatically to 40,000 ha in 1980. The initial decline was mainly due to land reclamation for agricultural use. However, the decline during the last decades can be ascribed mainly to changes in management and atmospheric deposition. Since 1950 53% of all plant species in the Netherlands, and in heath and chalk-grasslands even 86%, showed some sort of decline (Centraal Bureau voor Statistiek, 1983) and dramatic shifts in species composition could be observed (Bobbink and Willems, 1987; Heil and Diemont, 1983).

In dry heathlands the originally dominant dwarfshrub *Calluna vulgaris* (L.) Hull has been largely replaced by the grasses *Molinia caerulea* (L.) Moench and *Deschampsia flexuosa* (L.) Trin. In wet heathlands *Molinia* nowadays dominates *Erica tetralix*. Generally, the raised nutrient availability in the soil, due to the extensified management practices and increased inputs of air-borne nutrients, is accepted to have caused this change (Aerts, 1989; Berendse and Aerts, 1987; Grime, 1979; Heil and Diemont, 1983; Hiel et al., 1988).

According to Van der Eerden et al. (1990) other heathland species, particularly those of the Violion caninae alliance, are probably even more sensitive to atmospheric deposition than heather species. However, unlike the latter the former seem to disappear already before grasses become dominant. At present many herbaceous plants have become rare and their occurrence is restricted nowadays to small patches on very few locations.

In the Netherlands primarily sulphuric and nitrogenous compounds, in particular ammonium, contribute to atmospheric deposition (Houdijk and Roelofs, 1991). Atmospheric deposition is known to affect the chemical and physical status of the soil, increasing nutrient availability, soil acidity and the mobilization of toxic metal ions (Houdijk et al., 1992; Van Breemen et al., 1982). However until now it is not known which of these soil processes are likely to attribute to the decline of the threatened herbaceous heathland species. For preservation of the species diversity in heathland ecosystems knowledge about these processes is essential. In the present study soil characteristics of the few remaining localities of several rare herbaceous species and those of *Molinia*, *Erica* and *Calluna* vegetations were used to establish whether direct and/or indirect effects of acidification and/or eutrophication resulting from atmospheric deposition may be responsible for this decline.

Table 1. The investigated heathland species, the alliances they belong to (Vc: Violion caninae, Gc: Calluno Genistion pilosae, E: Ericion tetralix, TA: Thero-Airion), their division into groups and the number of sites sampled

Species	Alliance	Number of localities
Calluna vulgaris (L.) Hull	Gc	10
Erica tetralix L.	E	9
Molinia caerulea (L.) Moench		10
Lycopodium clavatum L.	E	13
Rhynchospora fusca (L.) Ait.f.	E	12
Arnica montana L.	Vc	9
Genista pilosa L.	Gc	9
Gentiana pneumonanthe L.	Vc	11
Lycopodium inundatum L.	E	12
Narthecium ossifragum (L.) Huds.	E	10
Dactylorhiza maculata (L.) Soo	Vc	10
Genista tinctoria L.	Gc	10
Pedicularis sylvatica L.	Vc	13
Polygala serpyllifolia Hose	Vc	10
Thymus serpyllum L.	TA	10

Materials and methods

Site selection

All investigated species were found in heathlands on the loam-free, mineral soils in the Southern, Central and Eastern parts of the Netherlands as well as in the dunes in the Western parts. The selection of the endangered herbaceous heathland species (from now on referred to as herbaceous species) was primarily based on the availability of sufficient localities (ca. 10 per species). Furthermore, the abundance and the distribution of the selected species should have declined recently (Mennema et al., 1985; Van De Meijden et al., 1983). *Molinia* (referred to as grass species), *Calluna* and *Erica* (referred to as heather species) locations were selected on the absence of herbaceous species. These sites were dominated by either of the plant species, covering at least 60%. Table 1 shows which plant species were studied and the number of sites sampled.

Sampling

Sampling took place in May, June and July in random order. At each site, between or close to the roots of the selected species soil samples were taken, consisting of four subsamples of mineral sandy soil, taken just below the litter layer to a depth of 10 cm, using a brass tube (length 10 cm, ø 3 cm). The subsamples were put together in a polyethylene bag and mixed. 70 g of fresh soil were put into a 500 mL polyethylene bottle together with 200 mL bidistilled water or a 0.2 *M* NaCl solution and shaken for 1 h, after which pH was measured. After centrifugation for 15 min at 275,000 g, the supernatant was stored at −28°C until analysis. Dry soil was combusted for 4 h at 550°C in order to estimate the organic matter content.

Ca, Mg, Al, Mn, Zn, Fe, S and P were measured with an Inductively Coupled Plasma spectrophotometer (ICP), type IL Plasma 200. K and Na were assessed using a Technicon Flame photometer IV. Colorimetrical determination with a Technicon AAII system according to Technicon Methodology (Technicon corporation, 1969) and Kempers and Zweers (1986) was used for NO_3 and NH_4 respectively, and a Technicon AAI-system according to Technicon Methodology (Technicon corporation, 1969) and O'Brien (1962) for Cl.

Statistics

Scheffé's multiple comparison procedure (performed with the General Linear Models (GLM) procedure) was used as a test of significance for differences between means (SAS Institute Inc., 1985). This statistical operation was performed on log-transformed data, since these fitted better to the conditions of normality (Sokal and Rohlf, 1981). For presentation, the data were back-transformed. Consequently, the mean values given are geometrical means, which are the maximum likelihood estimators of the population medians.

Results

GLM analysis of individual soils variables of groups of species are presented in Table 2. Highest values of pH (H_2O), pH (NaCl) and water-extractable calcium concentrations and lowest Al/Ca ratios were measured in the soils of herbaceous species. Soils of *Molinia* vegetations showed the highest levels of waterextractable nitrate, ammonium and phosphorus and salt-extractable ammonium. Water extractable potassium levels and the ammonium/nitrate ratios in the soils of herbaceous species were of intermediate value.

However, individual soil variables of herbaceous species showed large variations (Table 3). Based on the most discriminating soil variables derived from Table 2 (pH, NH_4, NO_3, Ca, Al/Ca and to a lesser extent NH_4/NO_3) and considering the individual values of these soil variables the twelve herbaceous species are divided into three groups of species and compared with the

Table 2. Geometrical means of organic matter (% DW), water and salt-extractable variables (μmol. kg^{-1} DW) and ratios (mol.mol^{-1}) of herbaceous, grass and heather species. Different letters within a row indicate statistical differences between the soil variables of the three groups of heathland species at the 5% level according to Scheffé's multiple comparison analysis

Org. matter	Herbaceous species	Grass species	Heather species
	5.3 b	10.6 a	7.0 ab
Water-extractable variables			
NO_3	18 b	71 a	17 b
P	7 b	28 a	13 b
pH	4.6 a	3.9 b	4.2 b
NH_4	74 b	152 a	89 b
K	108 ab	175 a	61 a
Mg	22 a	17 a	10 a
Ca	84 a	13 b	7 c
Al	220 a	228 a	158 a
Al/Ca	2.6 b	17.4 a	23.5 a
NH_4/NO_3	4.1 ab	2.2 b	5.1 a
Salt-extractable variables			
pH	3.8 a	2.9 b	3.0 b
NH_4	97 b	367 a	194 b
K	240 b	453 a	272 ab
Mg	276 a	342 a	312 a
Ca	1432 a	1251 a	912 a
Al	903 a	2238 a	1725 a

Table 3. Geometrical means of organic matter (% DW), several water and salt-extractable soil variables (in μmol kg^{-1} DW) and ratios (in mol.mol^{-1}) of heathland species. N/N = NH_4/NO_3

Group	Species	Water-extractable variables										Salt-extractable variables					
		pH	NH_4	NO_3	P	K	Mg	Ca	Al	Al/Ca	N/N	pH	NH_4	K	Mg	Ca	Al
1	*C. vulgaris*	4.1	78	17	12	53	8	6	137	25.2	4.6	3.0	241	282	300	1071	1779
1	*E. tetralix*	4.2	98	12	14	68	12	10	174	17.8	8.0	3.0	147	281	359	925	1733
1	*M. caerulea*	3.9	152	71	28	119	17	13	228	17.4	2.2	2.9	367	453	342	1251	2238
2	*L. clavatum*	4.1	39	20	5	54	7	30	176	5.9	2.0	3.3	59	93	149	454	2485
2	*R. fusca*	4.2	112	22	8	175	11	48	259	5.4	5.0	3.5	118	292	126	542	2648
3	*A. montana*	4.5	86	13	6	114	12	55	246	4.5	6.4	3.6	104	273	241	963	2703
3	*G. pilosa*	4.5	84	12	3	118	11	37	136	3.7	7.1	3.7	112	184	113	377	983
3	*G. pneumonanthe*	4.4	140	34	15	166	31	109	392	3.6	4.2	3.5	123	397	337	1917	2123
3	*L. inundatum*	4.7	47	10	3	98	15	58	128	2.2	4.8	4.0	60	153	52	290	856
3	*N. ossifragum*	4.4	147	26	9	318	56	87	222	2.5	5.6	3.6	150	487	451	994	1247
4	*D. maculata*	4.8	107	35	12	74	51	242	348	1.4	3.1	3.8	110	194	1043	7023	394
4	*G. tinctoria*	5.4	37	14	11	86	43	126	134	1.1	2.6	4.3	58	294	345	4519	133
4	*P. sylvatica*	4.9	61	15	6	104	33	151	285	1.9	4.0	4.0	117	220	497	3870	510
4	*P. serpyllifolia*	4.6	81	17	7	90	25	134	246	1.8	4.8	3.7	105	297	397	1239	942
4	*T. serpyllum*	5.2	53	15	13	72	40	154	209	1.4	3.5	4.3	111	320	860	5179	217

group of dominant heathland species (*Molinia*, *Erica* and *Calluna*) (Table 4).

The first group of species consists of the heather species and *Molinia*. pH in the soils of this group was low (3.9–4.1) and the lowest waterextractable calcium levels and the highest Al/Ca ratios were measured. NH_4/NO_3 ratios in these soils were of moderate value. *Lycopodium clavatum* L. and *Rhynchospora fusca* (L.) Ait. f. form the second group of species growing on soils with similar pH values as those in the soil of the dominant species. However, the Al/Ca ratio

Table 4. Geometrical means of organic matter (% DW), water and salt-extractable variables (μmol kg^{-1} DW) and ratios (mol mol^{-1}) of group 1, 2, 3 and 4. Different letters within a row indicate statistical differences between these four groups of species at the 5% level according to scheffé's multiple comparison analysis. For explanation of group division see Table 3

Org. matter	Group 1 8.1 a	Group 2 5.8 ab	Group 3 5.5 ab	Group 4 4.8 b
Water-extractable variables				
NO_3	30 a	21 a	17 a	18 a
PO_4	18 a	6 b	6 b	9 b
pH	4.1 c	4.1 c	4.5 b	5.0 a
NH_4	118 a	64 a	93 a	63 a
K	83 a	95 a	148 a	85 a
Mg	13 bc	9 c	21 ab	37 a
Ca	10 c	37 b	66 b	157 a
Al	189 a	222 a	208 a	235 a
Al/Ca	19.7 a	5.7 b	3.2 b	1.5 c
NH_4/NO_3	3.9 ab	3.1 b	5.4 a	3.5 ab
Salt-extractable variables				
pH	3.0 c	3.4 b	3.7 a	4.0 a
NH_4	269 b	821 a	1040 a	982 a
K	347 a	157 b	273 ab	259 ab
Mg	342 ab	137 c	183 bc	567 a
Ca	1074 b	494 c	731 bc	4461 a
Al	1923 a	2562 a	1421 a	360 b

in the soil of group 2 was lower. The remaining herbaceous species all grow on soils with higher pH values. The third group consists of five species: *Arnica montana* L., *Genista pilosa* L., *Gentiana pneumonanthe* L., *Lycopodium inundatum* L. and *Narthecium ossifragum* (L.) Huds. The pH and the NH_4/NO_3 ratio in the soil of this group were higher than and the Al/Ca ratio and water extractable calcium levels were comparable to those of group 2. Group 4 was formed by *Dactylorhiza maculata* (L.) Soo, *Genista tinctoria* L. *Pedicularis sylvatica* L., *Polygala serpyllifolia* Hose and *Thymus serpyllum* L. In the soils of this group highest pH values, water and salt extractable calcium levels and lowest salt extractable aluminium levels and Al/Ca ratios were measured.

Discussion

Soil composition

At present Dutch heathlands are dominated by grass species like *Molinia* and *Deschampsia* and the dwarfshrub species *Calluna* and *Erica*. This study confirms the findings of Roelofs et al. (1985) and De Boer (1990) that both heather and grass species prefer acid soils whereas the soil composition merely differs in nutrient, particularly nitrogen, content: soils of heather species have low and those of grass species have high nitrogen contents. The enhanced nutrient availability, primarily resulting from the high ammonium deposition and the reduced nutrient removal due to extensified management, was found to account for the observed changeover from dwarfshrub to grass dominated heathlands (Aerts, 1989; Heil and Diemont, 1983; Roelofs, 1986).

The comparison on basis of individual soil variables emphasized the importance of the ratios of aluminium to calcium, besides pH and calcium (Table 3). Generally, nutrient levels (nitrogen and phosphorus) in the soils of the herbaceous species were much lower than in the soil of *Molinia* and comparable with those in the soils of dwarfshrub species. These findings, together with the fact that herbaceous species are not specifically replaced by grass species but that they are also replaced by heather species, indicate that acidification probably forms the greatest threat for their existence. Van Dam et al. (1986) also correlated the decline of herbaceous species with the effects of acid rain due to the deposition of acid and acidifying substances as ammonium, sulphate and nitrate and Fennema (1990) attributed the decline of *Arnica montana* to the acidifying effect of the enhanced ammonium deposition rather then to its eutrophicating effect.

Soil acidification

The acidifying effect of atmospheric deposition can either be direct or indirect. Although all the investigated herbaceous species show a preference for acid soils (Ellenberg, 1979; Westhoff and Den Held, 1969), the pH (H_2O) of these soils is generally somewhat higher than in the soil of the dominating species. Indirectly, soil acidification might lead to the loss of exchangeable base cations and the mobilization of toxic metal ions like aluminium (Ulrich, 1983). In the present study however, aluminium content in soils of dominating and herbaceous species did not differ significantly. Kroeze et al. (1989), who tested aluminium susceptibility of several species of the Violion caninae alliance, concluded that the decline was not likely to be due to an increased aluminium availability. Generally, organically complexed aluminium is assumed to be less toxic than inorganic aluminium forms. However, Mulder (1988) found that in the mineral layer of Dutch heathland soils 95% of aluminium is available in as aquous Al^{3+}. Aluminum toxicity may also be reduced by calcium and magnesium and several investigators (Boxman et al., 1991; Ulrich, 1983) found that the concentration of calcium relative to aluminium formed a better measure to estimate aluminium toxicity. This Al/Ca ratio appeared to be much higher in the soil of the dominating species (Table 3). Further acidification of the soil of herbaceous species may lead to higher Al/Ca ratios which may in turn cause the decline of these species.

Generally, it is assumed that nitrification is limited in acid heathland soils. In heathland soils covered with a healthy dwarfshrub vegetation nitrification rates seem to be inhibited in soils with a pH of 4.0–4.2 (Roelofs et al., 1985). However, in grass dominated heathland soils with similar pH, nitrate production is relatively high (De Boer, 1990). In the present study nitrification in the soil of the grass species is reflected by the low NH_4/NO_3 ratios but even more clearly by the high nitrate contents of these soils. Nitrate contents, in both, dwarfshrub dominated heathland soil sand in the soils of the herbaceous species, were lower. According to Kinzel (1982) Ericacae show very low nitrate reductase activity which may indicate that these species hardly use nitrate to meet their N-demand. In contrast, some current experiments with several herbaceous species showed that they generally seem to prefer nitrate when both nitrogen-forms are offered and that cation uptake benefits from nitrate-nutrition (per. com. De Graaf). When this is the case it can explain the relatively high NH_4/NO_3 ratios in the soils of herbaceous species. Further acidification might slow down nitrate production and may prevent nitrate nutrition which accounts for the decline of the investigated herbaceous species.

Discrimination of groups of species

Processes that may cause the decline of herbaceous heathland species are discussed by comparing the chemical soil composition of three groups of herbaceous species with that of the dominating heathland species (*Molinia*, *Calluna* and *Erica*) growing on acid soils with high Al/Ca ratios.

Soils of species of group 2 (*Rhynchospora fusca* and *Lycopodium clavatum*) have similar pH values but lower Al/Ca ratios. Therefore, the species belonging to group 2 may decline as a result of an indirect effect of acidification, i.e. raised Al/Ca ratios.

The relatively high pH (4.5–4.8) values in the soil of group 4 (*Dactylorhyza maculata*, *Polygala serpyllifolia*, *Pedicularis sylvatica*, *Thymus serpyllum* and *Genista tinctoira*) together with the high base cation contents indicate that this group of species occurs on weakly buffered soils in the cation exchange buffer range (pH 4.2–5.0) (Ulrich, 1983).

Group 3 (*Lycopodium inundatum*, *Gentiana pneumonanthe*, *Arnica montana*, *Narthecium ossifragum* and *Genista pilosa*) forms an intermediate group. These species grow on soils with higher pH values than in the soil of group 1 and 2 but pH values are lower than those in soils of group 4. Calcium levels and Al/Ca ratios are similar to those of group 2 but lower and higher than in group 4 respectively. Soil acidification probably forms the greatest threat for both groups of species (group 3 and 4). Eventually, however, also increased Al/Ca ratios and decreased NH_4/NO_3 ratios in the soil as a consequence of soil acidification may also cause the decline.

Conclusions

Generally the soils of the threatened herbaceous heathland species range from acid to weakly acid and are nutrient-poor. Largest discrimination between these soils and those of the dominant heathland species (*Calluna*, *Erica* and *Mollinia*) was related to pH, the Al/Ca ratio and to a lesser extent to the NH_4/NO_3 ratio. On account of the soil composition the heathland species can be divided into four groups. This study suggests that the direct and indirect effects of acidification, due to enhanced atmospheric deposition, may be responsible for the decline of all three groups of herbaceous species.

In order to provide causal relationships ecophysiological and culture experiments were carried out with some of the species involved. The results of these experiments will be discussed in a next paper.

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