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REVIEW

Restoration ecology of aquatic and terrestrial vegetation on non-calcareous sandy soils in The Netherlands*

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INTRODUCTION

Plant and animal diversity of the Dutch landscape is mostly restricted to (semi-)natural ecosystems in nature reserves. Many of these plant and animal species are at this moment seriously threatened by environmental stresses, such as air pollution, eutrophication, desiccation or lowering of the water table and habitat fragmentation (e.g. Westhoff 1979; Vos & Zonneveld 1993). The preservation of biodiversity in existing nature reserves and natural areas is one of the most important aims in European nature conservation, besides the creation of new habitats (e.g. Marrs 1993; Anderson 1995).

Many endangered plant and animal species, however, have been declining in the last decades in The Netherlands, although they are growing in managed nature reserves. One of the main threats to these species is the increase in airborne sulphur (SO_y) and nitrogen (NH_x and NO_y) deposition. S and N pollutants have been shown to acidify ecosystems, and may cause damage to vegetation especially by soil-mediated processes, such as decreases in buffer capacity, base saturation and increases in heavy metals (Al) (e.g. Van

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Nomenclature of plant species follows Van der Meijden (1990) and of syntaxa Schaminée *et al.* (1995, 1996).
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Breemen *et al.* 1992; Ulrich 1983). Changes in N species are also associated with these processes (Roelofs *et al.* 1985). Deposition of airborne N compounds may, furthermore, cause eutrophication, because nitrogen is limiting for plant growth in many of these (semi-)natural, nutrient-poor ecosystems (e.g. Bobbink & Roelofs 1995a). The effects of desiccation of wet ecosytems are added to the just-mentioned acidifying and eutrophying consequences of atmospheric deposition. The negative effects are especially observed in oligotrophic, weakly buffered ecosystems in the areas with sandy Pleistocene deposits in The Netherlands (e.g. De Vries 1994; Bobbink & Roelofs 1995b).

Ecological restoration has to play a vital role in reducing the negative effects and to reinstate the damaged plant communities and associated animal life (Anderson 1995). It is crucial to repair and maintain these affected environments before the last populations are lost, as a future (genetic) source of dispersal of endangered species to newly created nature reserves and restored habitats. The aim of this paper is to identify key factors and processes which control the maintenance of characteristic plant species, both common and endangered, of Dutch nature reserves located on sandy, non-calcareous soils. Knowledge of the ecological functioning of these species in the vegetation enables the development and testing of optimal management strategies so as to adequately restore the abiotic conditions and the characteristic species composition of seriously acidified and/or eutrophied ecosystems. The following semi-natural ecosystems of high nature conservation importance on the sandy Pleistocene areas of The Netherlands are treated in detail: species-rich dry heaths and matgrass swards, species-rich wet heaths and shallow soft-water lakes.

ACIDIFICATION AND EUTROPHICATION OF MATGRASS SWARDS AND DRY HEATHS

Heathlands have, for a long time, been a part of the West European landscape. Heaths contain plant communities where the dominant life-form is that of the small-leaved dwarf shrubs forming a canopy of 1 m or less above soil surface. Dwarf shrub heathlands are widespread in the Atlantic and sub-Atlantic parts of Europe. In these parts of the European continent natural heathland is limited to a narrow coastal zone. Inland lowland heathlands are certainly man-made (semi-natural), although they have existed for several centuries. Lowland heaths are widely dominated by some *Ericaceae*, especially *Calluna vulgaris* in the dry- and *Erica tetralix* in the wet heathlands (Gimingham *et al.* 1979; De Smidt 1979; Gimingham & De Smidt 1983).

In recent decades the vegetation of dry heaths and nutrient-poor grasslands in The Netherlands has been affected by soil acidification and eutrophication as a result of atmospheric deposition. In dry heaths, atmospheric input of nitrogenous compounds has led to a transition from dwarf shrub-dominated to grass-dominated communities (e.g. Heil & Diemont 1983; Roelofs 1986; Van der Eerden 1992; Aerts & Heil 1993; Bobbink & Roelofs 1995a). Besides this shift in dominance, a reduced species diversity has been observed in these ecosystems. Species of the acidic *Nardo-Galion saxatilis* grasslands, and the related species-rich dry heathlands (*Calluno-Genistion pilosae*), seem to be especially sensitive. Many of these herbaceous species (e.g. *Arnica montana*, *Antennaria dioica*, *Dactylorhiza maculata*, *Genista pilosa*, *Genista anglica*, *Polygala serpyllifolia, Succisa pratensis* and *Thymus serpyllum)* have declined in The Netherlands and their occurrence is, at present, restricted to small patches on a few sites. It has been suggested that atmospheric deposition of S and N has caused such drastic abiotic changes that these species are unable to survive (Van Dam *et al.* 1986). Dwarf shrubs, as well as grasses, are nowadays dominant in areas formerly occupied by these endangered herbaceous species.

Enhanced nitrogen fluxes (e.g Bobbink & Heil 1993) onto the nutrient-poor heath soils lead to an increased nitrogen availability in the soil. However, most of the deposited nitrogen in western Europe originates from ammonia/ammonium deposition and may also cause acidification as a result of nitrification. Whether or not it is eutrophication, acidification or a combination of both processes (which is important) depends on pH, buffer capacity and nitrification rates of the soil. Roelofs *et al.* (1985) found that in dwarf shrub-dominated heathland soils, nitrification has been strongly inhibited at pH 4·0–4·2, and that ammonium accumulated while nitrate decreased to almost zero at these or lower pH values (De Boer 1989). Furthermore, nitrification has been observed in the soils from the habitats of the endangered species, due to their somewhat higher pH and buffer capacity. In soils within the pH range of 4·5–6·0, the acidity produced is buffered by cation exchange processes (Ulrich 1983). The pH will drop when base saturation of the exchange complex is depleted and this decrease indirectly results in an increased leaching of base cations, increased aluminium mobilization and thus enhanced Al:Ca ratios in the soil (Van Breemen *et al.* 1982). Furthermore, the reduction of the soil pH may inhibit nitrification and results in ammonium accumulation and consequently increased NH_4:NO_3 ratios. In a recent field study, the characteristics of the soil from several sites of these threatened heathland species have been compared with the soils from sites with dominance of dwarf shrubs or grasses (Houdijk *et al.* 1993). They have found that the discrimination between soil types was primarily based on differences in acidity and in the Al:Ca ratio in the water extracts. Generally the endangered species (e.g. *Arnica montana*, *Polygala serpyllifolia*, *Thymus serpyllum*) grow on weak to moderately acid soils ($pH(H_2O)>4{\cdot}4$) with relatively high base cation concentrations and lower Al:Ca ratios. Soils where only dominant species were present, were more acidic and had higher Al:Ca ratios. At sites with dominance of grasses (*Deschampsia flexuosa* or *Molinia caerulea*), significantly higher concentrations of mineral N have been observed. Furthermore, ammonium concentrations and NH_4:NO_3 ratios were sometimes higher in the soils from dwarf shrub-dominated vegetation when compared with the ratios in the soil containing the endangered herbaceous species (Houdijk *et al.* 1993). In addition, Fennema (1992) has demonstrated that soils from locations where *Arnica montana* is still present had higher pH and lower Al:Ca ratios than soils of former *Arnica montana* stands. No differences were found in total soil nitrogen concentrations and in NH_4:NO_3 ratios.

In 1993–94 we have studied the chemical composition of the topsoils of well developed and poorly developed *Nardo-Galion* communities and *Calluna vulgaris*-dominated vegetation (*Genisto pilosae-Callunetum*) in The Netherlands (Fig. 1). As shown before, the soils of *Nardo-Galion* communities are characterized by slightly higher pHs, higher base cation concentrations and lower Al:Ca ratios, compared with the soils of *Calluna vulgaris* stands. In the poorly developed *Nardo-Galion* communities, soil ammonium concentrations are clearly higher ($P<0{\cdot}05$) than in the well-developed stands of this community. This indicates that despite Al:Ca ratios, increased NH_4^+ concentrations may be associated with the decline of these species. It is concluded that the decline of many herbaceous species in dry heath and grassland communities is mainly caused by soil acidification and related changes in the mineral balance of the soil.

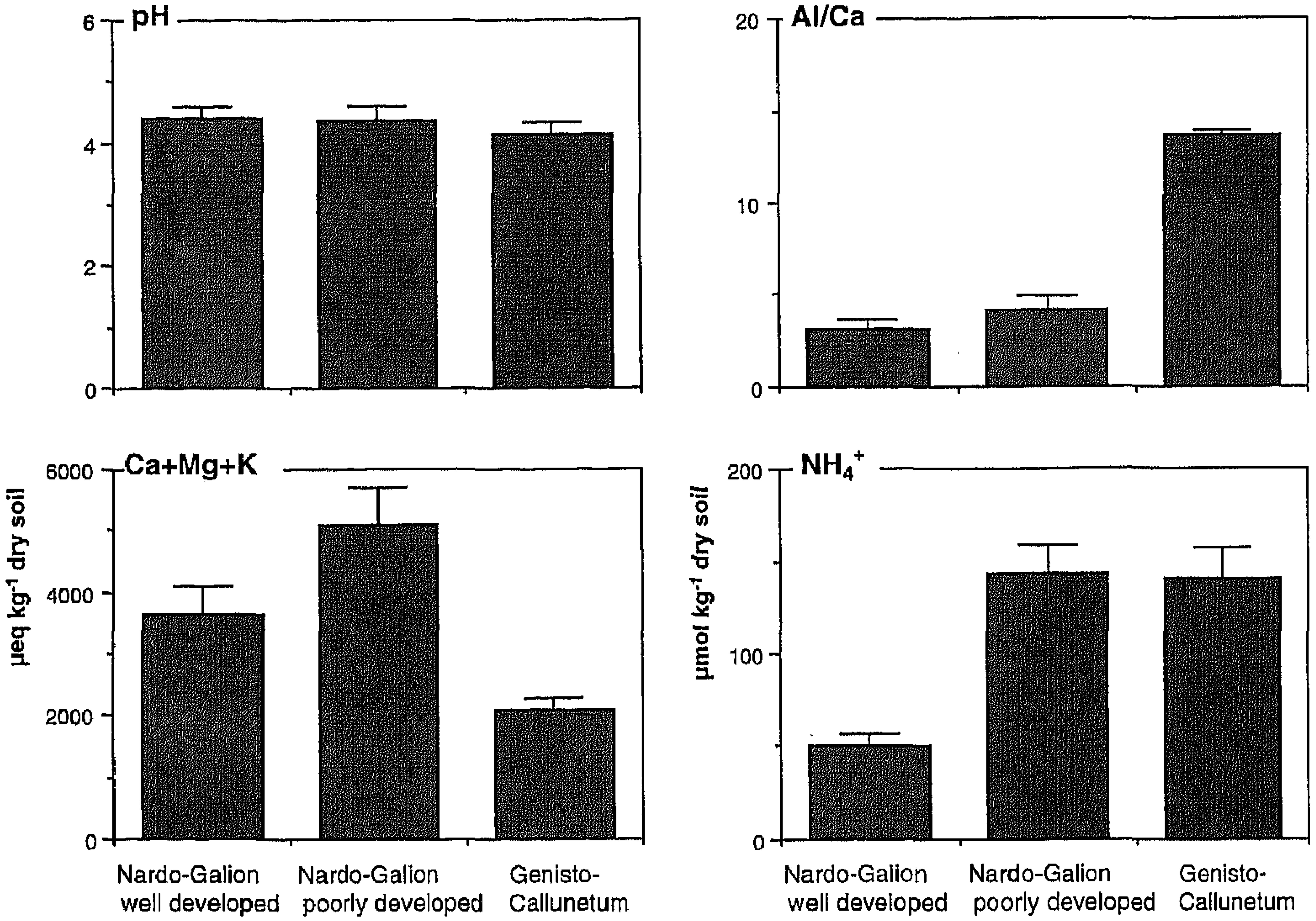

Fig. 1. Soil pH, Al:Ca ratios (in mol mol^{-1}), NH_4^+ concentrations (µmol kg^{-1} dry soil) and base cations concentration (µeq kg^{-1} dry soil) in well developed *Nardo-Galion communities* (n=8); poorly developed *Nardo-Galion* communities (n=13) and dry *Calluna vulgaris* dominated heaths (*Genisto-Callunetum*; n=48) as sampled in 1993 or 1994. pH, Al:Ca ratio and NH_4^+ have been measured from water extracts, whereas the base cation content is the sum of exchangeable Ca^{2+}, Mg^{2+} and K^+ concentrations (after Bobbink *et al.* 1996).

RESTORATION OF DRY SPECIES-RICH HEATHS AND MATGRASS SWARDS

Because species-rich dry heaths and matgrass swards are mainly threatened by soil acidification, restoration should therefore focus primarily on counteracting these effects. Liming is a method widely used in agriculture and forestry in order to raise soil pH and to increase base saturation of the soil exchange complex and nitrification. It has also been used to counteract the negative effects of acidification in forests and lakes (e.g. Hüttl & Zöttl 1993; Henrikson *et al.* 1995). Therefore, field liming experiments have been set up in dry heath and *Nardo-Galion saxatilis* sites. The plots have also been sod cut to (i) to reduce the accumulation of nutrients in the systems (e.g. Berendse 1990; Aerts & Heil 1993) and (ii) initiate germination and establishment possibilities for endangered herbaceous species (Bakker 1989). An additional advantage of sod cutting is the reduced risk of enhanced mineralization rates. This often happens after liming of forest soils, when the organic topsoil is not removed (e.g. Meiwes 1995). It has been shown, furthermore, in the last decade that sod cutting of grass heath is an appropriate way to remove the accumulated nutrients and to restore development of dwarf shrubs (Werger *et al.* 1985; Diemont & Linthorst Homan 1989; Bruggink 1993).

We have studied the effects of liming in two Dutch heathland nature reserves; (i) Schoapedobbe (52°57′N; 6°16′E), where endangered species are still present and (ii) Borkeld (52°16′N; 6°29′E) where the last endangered *Nardo-Galion saxatilis* species disappeared in the early 1980s. The topsoil layer of the plots (*c.* 50 m^2), including above-ground biomass, was removed by sod cutting before the liming treatment started. The plots were treated twice with lime (99% $CaCO_3$) or with dolomite (80% $CaCO_3$, 20% $MgCO_3$) in the first 2 years of the experiment (300 kg ha^{-1} yr^{-1}). Topsoil chemistry, establishment of *Arnica montana* after experimental re-introduction (only at Schoapedobbe) and vegetation development have been quantified from 1990 to summer 1995.

Soil chemistry shows considerable variation in time, probably due to seasonal processes. However, addition of lime and dolomite has clearly caused an increase in pH and base cation concentrations in both sites, compared with control plots which had not been limed (Fig. 2). In addition, no significant differences in the soil chemistry of both sites have been measured after liming with lime or dolomite, compared with the control vegetation (Table 1). The effects of liming on soil chemistry are still apparent 5–6 years after the first application of the materials. These results clearly indicate that liming of sod-cut matgrass swards has led to weakly buffered, oligotrophic conditions more suitable for the development of endangered herbaceous species at both sites. Topsoil pH and Al:Ca ratios have clearly come into the range found typical for endangered dry heath species (Houdijk *et al.* 1993).

However, the development of the vegetation after liming differed strongly between the two sites during the study period. At Borkeld, the site where all endangered *Nardo-Galion saxatilis* species were not found since the early 1980s, a species-poor grass–heath community, co-dominated by *Calluna vulgaris* and *Nardus stricta* (total cover 65–75%), developed with or without liming. None of the endangered forb species, except for *Genista pilosa* of dry heath communities, established in the experimental plots. The development of *Genista pilosa* however, was not stimulated by the liming treatments, but found in all sod-cut plots (Table 2).

At the Schoapedobbe site, several endangered species such as *Arnica montana* and *Polygala serpyllifolia* are still present, although the populations have gradually declined. After sod cutting in early 1990, total cover of the vegetation gradually increased to 80–90% in 1995. In both the limed and the control vegetation, a grass–heath vegetation developed with many *Nardo-Galion saxatilis* species. Total species number was, however, higher in the vegetation treated with lime or dolomite, compared with the controls. Species characteristics of weakly buffered soils became especially more abundant in these limed plots (Table 2).

The effects of liming on *Arnica montana* were also studied in detail at Schoapedobbe; 4 × 25 seeds were sown in a grid under each treatment. These grids were examined annually for germination of the seeds and survival of the seedlings. Germination of the seeds of *Arnica montana* significantly increased to 70–80% in the vegetation treated with lime or dolomite, compared with 50–55% in the control situation. In addition, survival of the seedlings of *Arnica montana* was much higher ($P<0{\cdot}05$) in the plots treated with limestone or dolomite than in the control situation. This resulted in a large difference in number of plants still present in 1995: in the control vegetation only 4% of the plants are still alive, whereas in the plots treated with lime or dolomite, 40–45% are still present (Fig. 3).

It is concluded that liming after sod cutting is an adequate method to restore weakly buffered, oligotrophic soil conditions in acidified *Nardo-Galion saxatilis* grasslands or dry heaths. Recovery of the characteristic vegetation composition is, however, seriously limited when characteristic species have disappeared some years before the restoration measures begin. This is probably caused by the non-persistent seed bank (<5 years) of

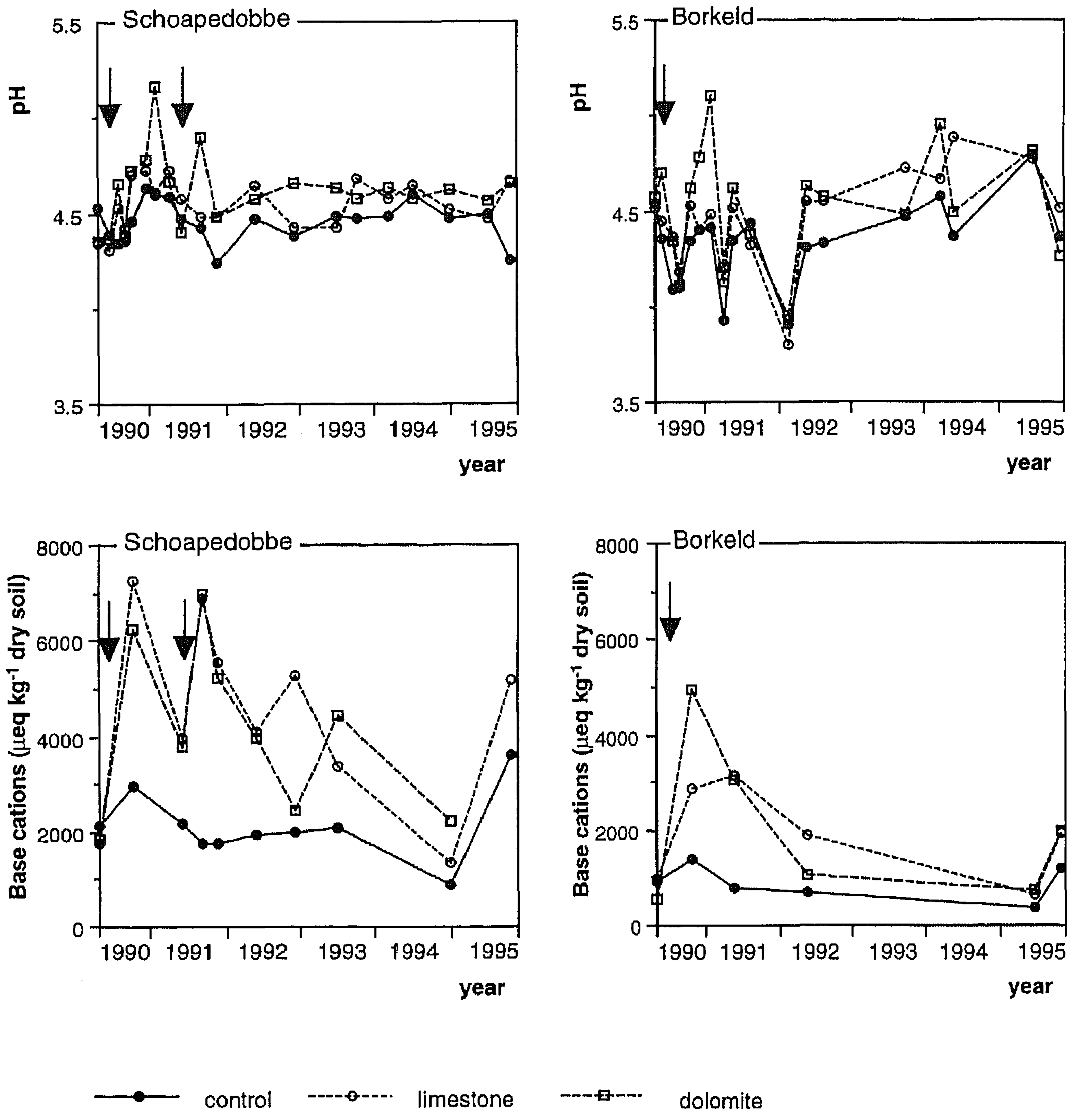

Fig. 2. Soil pH(H_2O) and base cation concentration (μeq kg^{-1} dry soil) in sod-cut matgrass swards at Schoapedobbe and Borkeld from 1990 to 1995 after the addition of lime or dolomite. Application indicated by arrows. Base cation concentration is the sum of exchangeable Ca^{2+}, Mg^{2+} and K^{+} concentrations. Closed circles: control treatment; open circles: addition of lime; open squares: addition of dolomite (after De Graaf *et al.* 1994 & Bobbink *et al.* 1996).

almost all endangered *Nardo-Galion saxatilis* species (Bakker *et al.*, this issue) and the restricted seed dispersal capacities of most perennial plant species (e.g. Verkaar *et al.* 1983; Grime *et al.* 1988).

DECLINE OF SPECIES-RICH WET HEATHS AND RELATED GRASSLANDS

The West European lowland heaths of wet habitats are dominated by the dwarf shrub *Erica tetralix*. These wet-heath communities (*Ericion tetralicis*) are generally more species-rich than those of dry heaths (e.g. Gimingham *et al.* 1979; Ellenberg 1988).

Table 1. Soil Al:Ca ratio (mol mol^{-1}), NH_4^+, NO_3^- and PO_4^{3-} concentrations (μmol kg^{-1} dry soil) in sod-cut matgrass swards at Schoapedobbe and Borkeld after the addition of lime or dolomite and in the control vegetation (after de Graaf *et al.* 1994 & Bobbink *et al.* 1996). Mean and standard error over the experimental period (1990 to 1995; n=9–11) are given. All soil parameters have been measured from water extracts

	Al:Ca	NH_4^+	NO_3^-	PO_4^{3+}
Schaopedobbe				
Control	6.9 (1.57)	233 (89)	107 (34)	5.24 (1.70)
Limestone	3.6 (0.59)	211 (93)	70 (31)	5.32 (1.85)
Dolomite	2.7 (0.55)	216 (89)	118 (60)	7.01 (2.53)
Borkeld				
Control	17.8 (7.26)	67 (27)	40 (17)	2.70 (1.42)
Limestone	18.4 (10.4)	102 (38)	37 (20)	1.06 (1.06)
Dolomite	11.4 (4.97)	33 (16)	22 (11)	3.24 (1.87)

Characteristic plant species of species-rich wet heaths (*Ericetum tetralices orchietosum*) and related wet grasslands (*Junco-Molinion*) are: *Cirsium dissectum*, *Dactylorhiza maculata*, *Epipactis palustris*, *Gentiana pneumonanthe*, *Lycopodium inundatum*, *Narthecium ossifragum*, *Parnassia palustris*, *Pedicularis sylvatica*, *Rhynchospora fusca* and *Succisa pratensis*.

In recent decades, a drastic change in the species composition of Dutch wet heathlands has been observed. At present, many of these communities have been replaced by monospecific stands of the grass *Molinia caerulea*. It has been shown that this change in acid wet heaths has been due mainly to eutrophication as a consequence of atmospheric deposition (Berendse & Aerts 1984; Aerts & Berendse 1988) and dessication (Schaminée *et al.* 1995). Together with the decline of *Erica tetralix*, almost all of the rare plant species have disappeared from the system. The decrease in endangered wet-heathland species is partly caused by overshading from *Molinia caerulea*, but many species had already disappeared before the increase of *Molinia caerulea* began. It is hypothesized that species-rich wet heath vegetation is restricted to oligotrophic, but slightly or weakly buffered soil conditions. Therefore, we have recently quantified the vegetation composition and the abiotic conditions of a number of Dutch species-rich wet heath sites (19 sites; 200 plots), where some of the endangered species still occurred (Bobbink *et al.* 1996). All data have been collected at locations where *Erica tetralix* is still abundant and without dominance of grasses (c.f. *Molinia caerulea*). The differentiation between groups of species and chemical soil conditions is primarily based on differences in pH(H_2O), pH(NaCl) (not shown) and base cation contents (Table 3). This rationale leads to a division resulting in three groups of species. The first group consists of *Erica tetralix*, *Molinia caerulea*, *Drosera intermedia*, *Drosera rotundifolia*, *Gentiana pneumonanthe*, *Lycopodium inundatum*, *Rhynchospora alba*, *Rhynchospora fusca* and *Potentilla erecta*. Soil pH(H_2O) of these species is 4·5–5·0 with relatively low concentrations of base cations (mostly <6 meq kg^{-1} dry soil), and somewhat higher Al:Ca and ammonium:nitrate ratios. The second group consists of seven species: *Carex nigra*, *Carex panicea*, *Cirsium dissectum*, *Juncus conglomeratus*, *Narthecium ossifragum*, *Pedicularis sylvatica* and *Succisa pratensis*. These species are most common on soils with pH(H_2O) 5·0–5·5 and high base cation concentrations. Finally, a group of seven species

Table 2. Species composition (Braun-Blanquet scale) in summer 1995 of sod-cut plots (*c*. 50 m^2) at Schoapedobbe and Borkeld after treatment with lime or dolomite (see Fig. 2), and in the control vegetation (after Bobbink *et al.* 1996)

	Schoapedobbe				Borkeld			
vegetation cover (%)	75 Control	80 Lime	85 Dolom.	80 Control	65 Control	75 Lime	75 Dolom.	70 Control
Achillea millefolium	–	–	r	–	–	–	–	–
Arnica montana	–	+	r	r	–	–	–	–
Agrostis canina	2a	2b	2a	2b	r	+	1	1
Agrostis capillaris	+	+	+	+	–	–	–	–
Anthoxanthum odoratum	+	–	+	–	–	–	–	–
Calluna vulgaris	3	3	4	3	3	4	4	4
Carex pilulifera	2a	2a	2a	2a	+	1	+	+
Danthonia decumbens	2a	1	+	2a	+	r	r	r
Deschampsia flexuosa	–	–	–	–	–	+	–	+
Erica tetralix	–	–	–	–	1	1	2a	1
Festuca ovina	2m	2m	2a	2m	+	+	1	+
Galium saxatile	2m	2m	2m	2m	–	–	–	–
Genista anglica	2m	2m	2m	1	r	–	–	–
Genista pilosa	–	r	–	–	1	1	1	+
Hieracium laevigatum	–	+	+	1	–	–	–	–
Hieracium pilosella	1	2m	2m	–	–	–	–	–
Hieracium umbellatum	–	r	+	+	–	–	–	–
Holcus lanatus	–	–	–	–	–	–	r	–
Hypochaeris radicata	1	2m	2m	1	–	–	–	–
Juncus squarrosus	–	–	–	–	r	r	+	+
Leontodon autumnalis	–	+	–	–	–	–	–	–
Luzula multiflo s. conges	–	–	–	r	–	–	–	–
Molinia caerulea	1	1	1	2a	+	1	+	+
Nardus stricta	r	–	–	–	2a	2a	2a	2a
Plantago lanceolata	–	r	–	–	–	–	–	–
Polygala serpyllifolia	–	1	1	+	–	–	–	–
Potentilla erecta	1	2a	2m	1	–	–	–	–
Rumex acetosella	1	+	+	+	–	+	+	+
Taraxacum officinale s.s.	–	+	r	–	–	–	r	–
Tree seedlings:								
Amelanchier lamarckii	r	–	r	–	r	r	+	–
Betula pendula	–	–	–	–	–	r	+	r
Betula pubescens	–	–	–	–	r	r	r	–
Picea species	–	–	–	–	r	–	–	–
Pinus sylvestris	–	–	–	–	+	+	+	–
Prunus serotina	r	r	r	r	–	–	r	r
Rhamnus frangula	r	r	–	r	–	–	–	–
Sorbus aucuparia	r	r	–	–	–	–	–	–
Quercus robur	r	r	r	r	–	–	–	–
No. of species:	20	25	23	20	15	16	18	14

(*Anthoxanthum odoratum*, *Dactylorhiza maculata*, *Epipactis palustris*, *Juncus acutifloris*, *Parnassia palustris*, *Ranunculus flammula* and *Viola palustris*) has been distinguished; the species are characterized by highest soil pHs (5·5–6·0) and high base cation

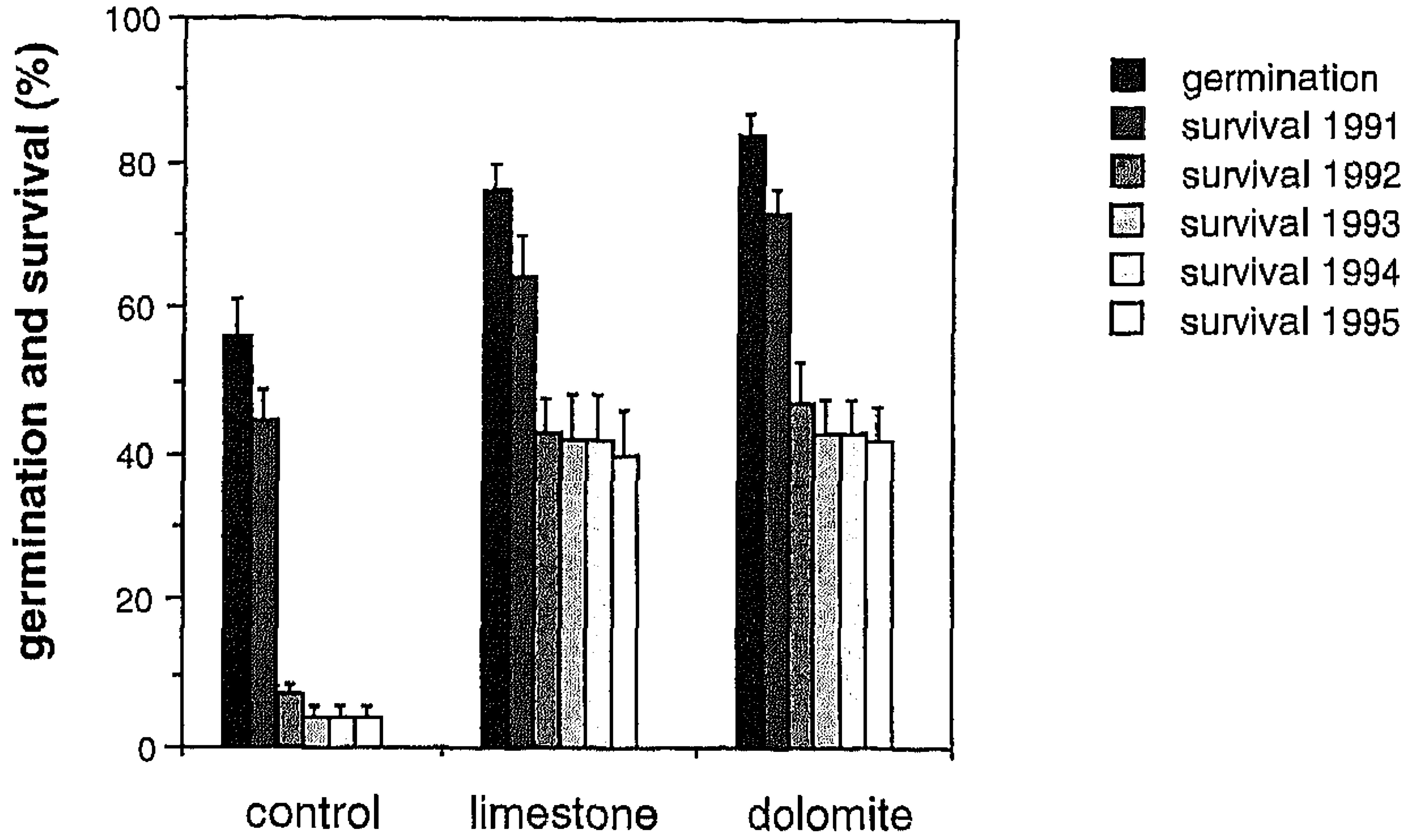

Fig. 3. Maximum germination of seeds ($n=25$; four plots) and survival of seedlings (% of germinated seeds+SE) of *A. montana* in sod-cut matgrass sward (Schoapedobbe) treated with lime or dolomite, and in the control vegetation, from 1991 to 1995; 98% of the applied seeds germinated in the greenhouse. After De Graaf *et al.* 1995; extended with data of 1995.

concentrations. All groups of species have been found on soils with low P concentrations (<9 μmol kg dry soil^{-1}) and Al:Ca ratios below 1; however, *Erica tetralix* and *Molinia caerulea* have been found on sites with relatively highest Al:Ca ratios (0·5–1). In wet heaths with dominance of grasses, topsoil pH is clearly lower, with high Al:Ca ratios and ammonium concentrations, as shown by Houdijk *et al.* (1993).

Soil conditions have been studied in detail in altitudinal transects from dry via moist to wet situations in the eastern part of The Netherlands (Breklenkamp 52°26'N; 7°00'E). Highest altitudes of the study area are characterized by *Calluna vulgaris*, *Erica tetralix* and *Molinia caerulea* (E-F), lowest parts by vegetation dominated by sedges (*Caricion curto-nigrae*) (A-B), whereas the middle parts (C-D) are characterized by several endangered species (e.g. *Gentiana pneumonanthe*, *Pedicularis sylvatica*, *Succisa pratensis*). In this zone, soil pH(H_2O) is intermediate (5·0–6·0) with low Al:Ca ratios (<0·5) and high base cation concentrations (Fig. 4). This difference with the species-poor heath communities (E-F) is caused by seepage of buffered groundwater, as indicated by the numbers of days per year (*c.* 200) with groundwater in the rooting zone. The area with almost continuously high water tables possessed a vegetation dominated by sedges (Fig. 4). The results of both field studies clearly stress the importance of weakly buffered, nutrient-poor soil conditions, originating from seepage with buffered (local) groundwater in the rooting zone or loamy soil conditions, for the maintenance of endangered wet-heath/acidic grassland species in these ecosystems. Soil acidification, caused by both atmospheric deposition and lower groundwater influences (cf. Grootjans *et al.*, this issue), is thus a serious threat for the maintenance of species-rich situations.

RESTORATION OF DETERIORATED SPECIES-RICH WET HEATH ECOSYSTEMS

Experimental hydrological regimes have been tested in a nature reserve at Staverden in the central part of The Netherlands (52°16'N; 5°44'E). This former, species-rich wet

Table 3. Relation between characteristic wet-heathland species and soil pH, Al:Ca ratios (mol mol^{-1}), NH_4^+, NO_3^-, PO_4^{3-} concentrations (μmol kg^{-1} dry soil) and base cations concentrations (meq kg^{-1} dry soil), sampled in 1991–95. Median and coefficient of variation (V in %) are given. *n*=number of samples. All soil parameters (0–10 cm) have been measured from water extracts, except the base cation concentrations, which is the sum of exchangeable Ca^{2+}, Mg^{2+} and K^{2+} concentration (after Bobbink *et al.* 1996)

	n	pH	Base cations	Al:Ca	NH_4^+	NO_3^-	PO_4^{3-}
Erica tetralix	98	4.55 (13)	4.4 (191)	0.8 (141)	45 (119)	13 (178)	5 (103)
Molinia caerulea	167	4.71 (14)	5.0 (196)	0.4 (133)	69 (95)	20 (184)	4 (126)
Drosera intermedia	53	4.98 (12)	5.4 (88)	0.2 (162)	40 (101)	15 (101)	3 (110)
Drosera rotundifolia	31	4.71 (12)	3.6 (105)	0.6 (114)	34 (108)	13 (106)	5 (83)
Gentiana pneumonanthe	28	4.98 (12)	8.2 (130)	0.1 (168)	44 (70)	11 (122)	0.2 (131)
Lycopodium inundatum	16	4.81 (11)	1.8 (98)	0.7 (131)	34 (80)	19 (115)	1 (130)
Potentilla erecta	90	4.83 (14)	6.9 (139)	0.2 (162)	52 (95)	16 (189)	3 (121)
Rhynchospora alba	27	4.78 (14)	3.9 (95)	0.2 (173)	37 (99)	15 (97)	5 (83)
Rhynchospora fusca	18	4.66 (16)	7.4 (149)	0.2 (197)	30 (118)	12 (96)	1 (139)
Carex nigra	44	5.49 (15)	6.9 (144)	0.0 (186)	32 (119)	10 (128)	5 (119)
Carex panicea	77	5.48 (12)	13.6 (130)	0.0 (320)	41 (114)	17 (228)	0 (149)
Cirsium dissectum	42	5.39 (11)	40.9 (86)	0.0 (209)	66 (88)	18 (232)	0 (187)
Juncus conglomeratus	16	5.35 (11)	45.7 (110)	0.0 (171)	37 (108)	25 (173)	0 (142)
Narthecium ossifragum	31	5.32 (10)	6.4 (175)	0.0 (180)	46 (103)	21 (84)	3 (97)
Pedicularis sylvatica	24	5.21 (14)	6.8 (122)	0.1 (200)	46 (77)	12 (113)	0 (157)
Succisa pratensis	23	5.47 (11)	13.6 (105)	0.0 (214)	54 (103)	18 (101)	5 (104)
Anthoxanthum odoratum	48	5.62 (12)	6.8 (164)	0.0 (152)	46 (88)	17 (186)	9 (147)
Dactylorhiza maculatum	12	5.64 (14)	21.2 (72)	0.0 (208)	110 (63)	31 (54)	7 (70)
Epipactis palustris	6	6.16 (5)	8.7 (132)	0.0 (70)	40 (112)	14 (80)	5 (110)
Juncus acutiflorus	50	5.54 (14)	8.6 (124)	0.0 (261)	44 (99)	16 (99)	4 (116)
Parnassia palustris	14	5.52 (10)	7.7 (43)	0.0 (155)	40 (69)	13 (64)	1 (145)
Ranunculus flammula	48	5.69 (9)	7.4 (173)	0.0 (341)	32 (95)	15 (260)	0 (150)
Viola palustris	15	5.83 (8)	23.8 (104)	0.0 (97)	39 (117)	30 (203)	8 (77)

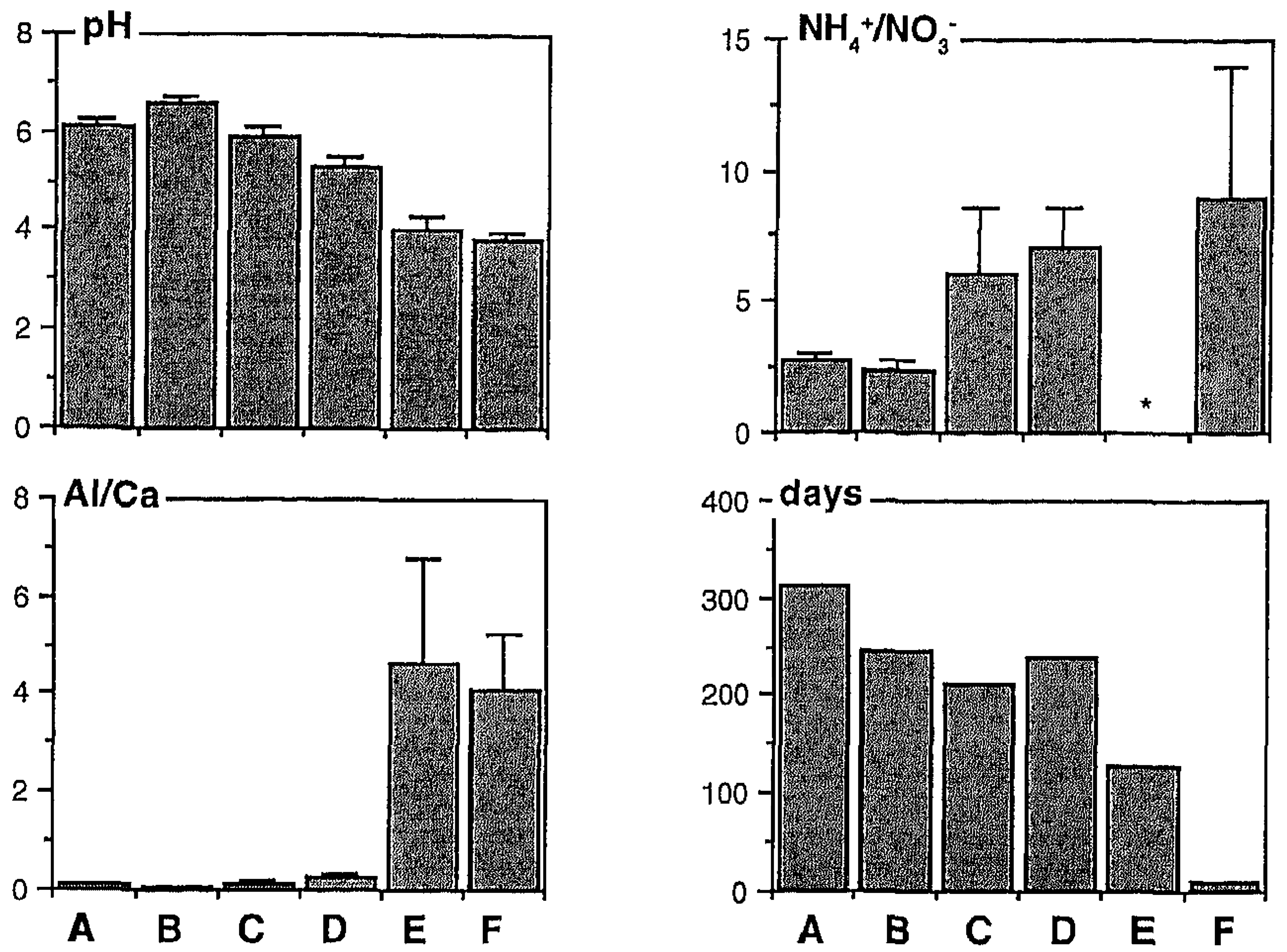

Fig. 4. Soil pH, Al:Ca ratios (in mol mol^{-1}), base cations concentration (μeq kg^{-1} dry soil) and the number of days with groundwater in the rooting zone in a transect from wet (A) to dry (F) conditions at Breklenkamp. Mean and standard error are given. pH and Al:Ca ratio have been measured from water extracts, whereas the base cation content is the sum of exchangeable Ca^{2+}, Mg^{2+} and K^{2+} concentrations. See text for characteristic species (adapted after de Graaf *et al.* 1994).

heathland is fed by a local hydrological system. A part of the site was planted with coniferous trees in the 1970s and, in addition, drained with small discharging ditches. This resulted in a groundwater table approximately 1 m below the soil surface. Consequently, the topsoil strongly acidified in the 1980s and the wet heath changed to a species-poor *Molinia caerulea* dominated sward. Only the main water stream and its banks are not acidified, because they still receive seepage of buffered groundwater (Cals *et al.* 1993). After removal of the vegetation and sod cutting in winter 1989/1990, drainage ditches have been closed and the water level in the groundwater-fed stream has been increased by adjustable damming to restore the original non-acidified, nutrient-poor conditions in the area. The abiotic conditions have been quantified with repeated topsoil sampling from 1989 to 1995. The establishment and development of the vegetation have been followed in 38 permanent quadrats (1·5 × 1·5 m) and a mapping of the vegetation of the whole area in 1992 and 1995.

Soil conditions are strongly influenced by the applied measures (Fig. 5, Table 4). Before restoration, pH(H_2O) of the topsoil was low (3·8–4·3), base cation concentrations were low and ammonium was the dominant N species. After the experimental measures in winter 1989/90, three hydrological zones developed; an infiltration zone, a seepage zone and an inundation zone. The soil conditons have been scarcely influenced by the restoration measures in the infiltration zone, compared with pretreatment values. In the moist infiltration zone, relatively high Al:Ca ratios (4–10) have been found. In the other zones, topsoil chemistry clearly improved, especially in the seepage zone; pH(H_2O) increased to values between 4·7–5·5, and base cation concentrations became markedly higher in the seepage and inundation zone after the restoration measures

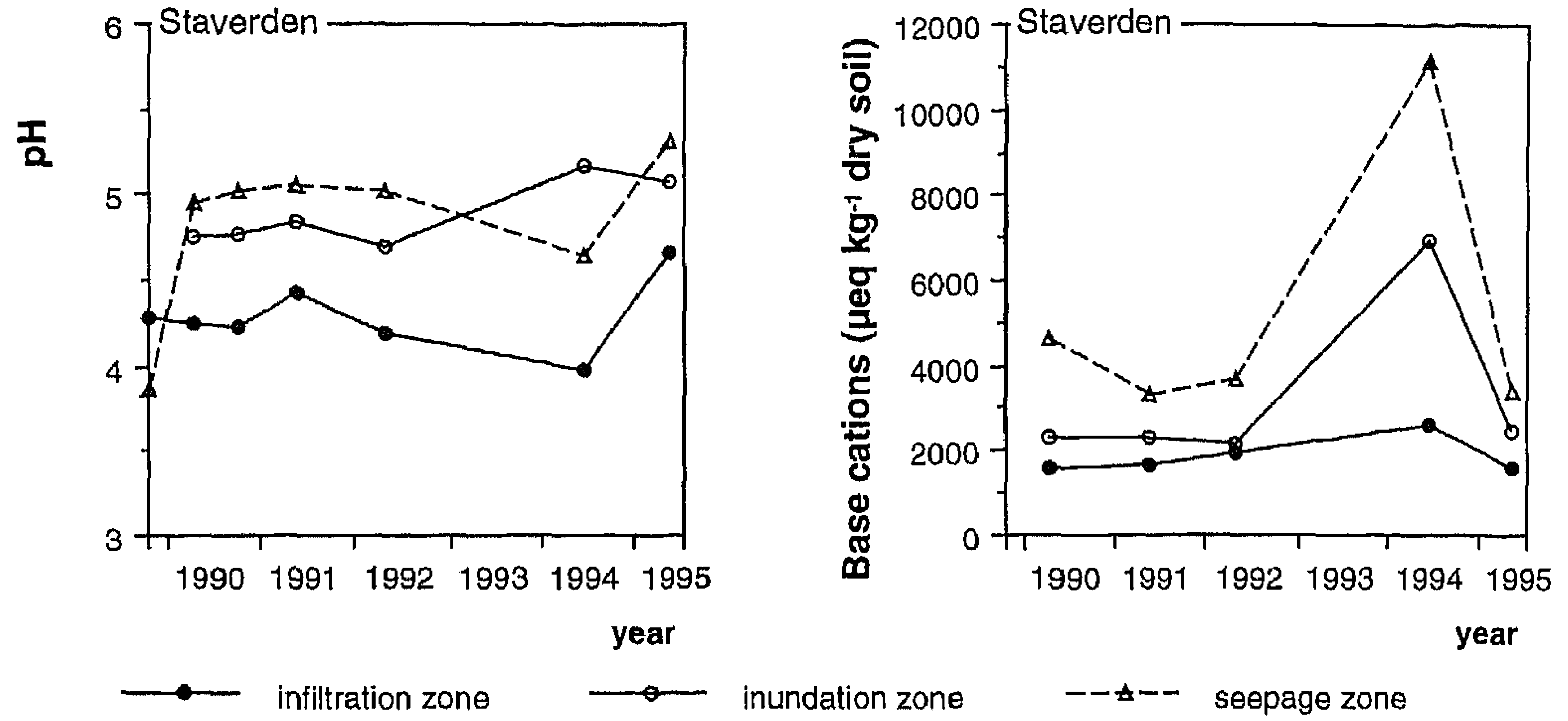

Fig. 5. Soil pH(H_2O) and base cations concentrations (µeq kg^{-1} dry soil) before restoration (no zones) and after restoration in three hydrological zones at Staverden. Closed circles: infiltration zone (n=19); open circles: inundation zone (n=10) and open triangles: seepage zone (n=9). Time of restoration: winter 1989/90 (after De Graaf *et al.* 1994 & Bobbink *et al.* 1996).

Table 4. Topsoil Al:Ca ratios (mol mol^{-1}), NH_4^+, NO_3^- and PO_4^{3-} concentrations (µmol kg^{-1} dry soil) before and after restoration in three hydrological zones (mean of 1990–92 measurements and minimum and maximum values) at Staverden (after De Graaf *et al.* 1994)

	Al:Ca	NH_4^+	NO_3^-	PO_4^{3-}
Before restoration	2.1 (0.5–7.0)	29 (4–61)	19 (4–168)	0.5 (0.0–10.6)
After restoration				
Infiltration zone	7.4 (4.5–8.8)	141(132–151)	15 (11–18)	1.9 (0.6–2.6)
Seepage zone	1.7 (0.7–2.7)	54 (35–72)	10 (8–12)	1.0 (0.0–3.0)
Inundation zone	2.7 (1.5–3.4)	70 (59–81)	4 (3–4)	2.0 (0.0–3.1)

(Fig. 5). Mineral N and P concentrations remained low and were hardly influenced by the restoration treatment (Table 4).

Before restoration, the former heath vegetation of Staverden was dominated by species-poor *Molinia caerulea* swards (>90% cover; 4–6 species per 1·5 × 1·5 m), with some *Erica tetralix* and *Calluna vulgaris* present. Only one plant species from the Dutch Red List has been observed before the restoration measures. The combination of sod cutting and hydrological measures has led to drastic changes in vegetation composition, compared with the pretreatment situation. In general, three main plant communities developed between 1990 and 1995. In the infiltration zone, a moist heath community characterized by *Ericion tetralicis* and *Calluno-Genistion pilosae* species has been found, with lowest species number per plot (8 ± 5) and very few plant species from weakly buffered soils. A species-rich wet heath community (*Ericetum tetralicis orchietosum*) has been found in the seepage zone in 1995, with a mean species number of 16 (±4), and high frequencies of endangered species (e.g. *Dactylorhiza maculata*, *Narthecium ossifragum*, *Succisa pratensis* and *Lycopodium inundatum*). In the permanent quadrats of the inundation zone, a *Caricion curto-nigrae* community (mean species number 12 ± 5) was found in 1995. This vegetation is characterized by several sedges (*Carex* spp.) and *Juncus acutiflorus*, with several (rare) species from *Parvocaricetea* communities. In 1995, a total of 19 plant species from the Dutch Red List were found in the area, compared with only one before the start of the restoration. For a more detailed description of the soil and vegetation development, see Bobbink *et al.* (1996) and Jansen *et al.* (1996).

It is obvious that sod cutting, in combination with suitable hydrological measures, restores acidified wet-heath soils by allowing seepage of buffered groundwater. Within a 5-year period, species-rich wet heath vegetation and related communites recovered in the area. It is likely that this relative quick response is related with the presence of many wet heath species in the soil seed bank (c.f. Bakker *et al.*, this issue) and seed sources in a nearby nature reserve (<500 m).

ACIDIFICATION AND EUTROPHICATION OF SHALLOW SOFTWATER LAKES

In oligotrophic softwater lakes and pools in western Europe, a vegetation type commonly occurs belonging to the *Littorelletea* (Schaminée *et al.* 1992, 1995). These *Littorelletea* communities are often characterized by the presence of isoetid plant species such as *Littorella uniflora, Lobelia dortmanna* and *Isoetes* spec. (Den Hartog & Segal 1964; Schoof-Van Pelt 1973; Wittig 1982). The fact that these plant species can often only survive in stagnant, extremely weakly buffered oligotrophic waters is related to the carbon budgets in those ecosystems. The carbon dioxide levels of the water layer in these systems are generally below 40 μmol l^{-1} and many species that depend on CO_2 uptake by the leaves are unable to take up enough CO_2 for net photosynthesis, as the diffusion rate of CO_2 in stagnant water is 10^4 lower compared to the diffusion in air (Madsen *et al.* 1993). In the sediment pore water of soft water bodies, however, the CO_2 level is 10–100 times higher compared to the water layer and can reach values up to 4000 μmol l^{-1} (Roelofs 1983). Isoetid plant species have several physiological and morphological adaptations to survive under those conditions:

- *Lobelia dortmanna* and *Littorella uniflora* are able to absorb free CO_2 by the roots (Wium-Andersen 1971; Søndergaard & Sand-Jensen 1979).
- *Lobelia dortmanna* and *Littorella uniflora*, plants with extensive lacunal systems, can recapture a considerable amount of the photorespired CO_2 which contributes to a more efficient assimilation (Søndergaard 1979).
- The underground biomass depends on the nutrient levels in the sediment (Sand-Jensen & Søndergaard 1979).
- *Littorella uniflora* and many species of the genus *Isoetes* have developed a diurnal acidification-deacidification cycle very similar to the Crassulacean Acid Metabolism (CAM) (Keeley 1982a,b).
- Isoetid plant species have a high oxygen release from the roots which stimulates mineralization and nitrification (Sand-Jensen *et al.* 1982; Roelofs *et al.* 1984; Roelofs *et al.* 1994).

Besides carbon dioxide, the availability of other nutrients, such as phosphorus and nitrogen, is also often very low in these systems. As a result, a very stable ecosystem, with low productivity, can exist and be sustained for many years. Through pollen analyses of the sediments from a Danish lake, it is clear that there have been hardly any changes in the abundance of isoetid species between 6000 and 100 years ago. In the last

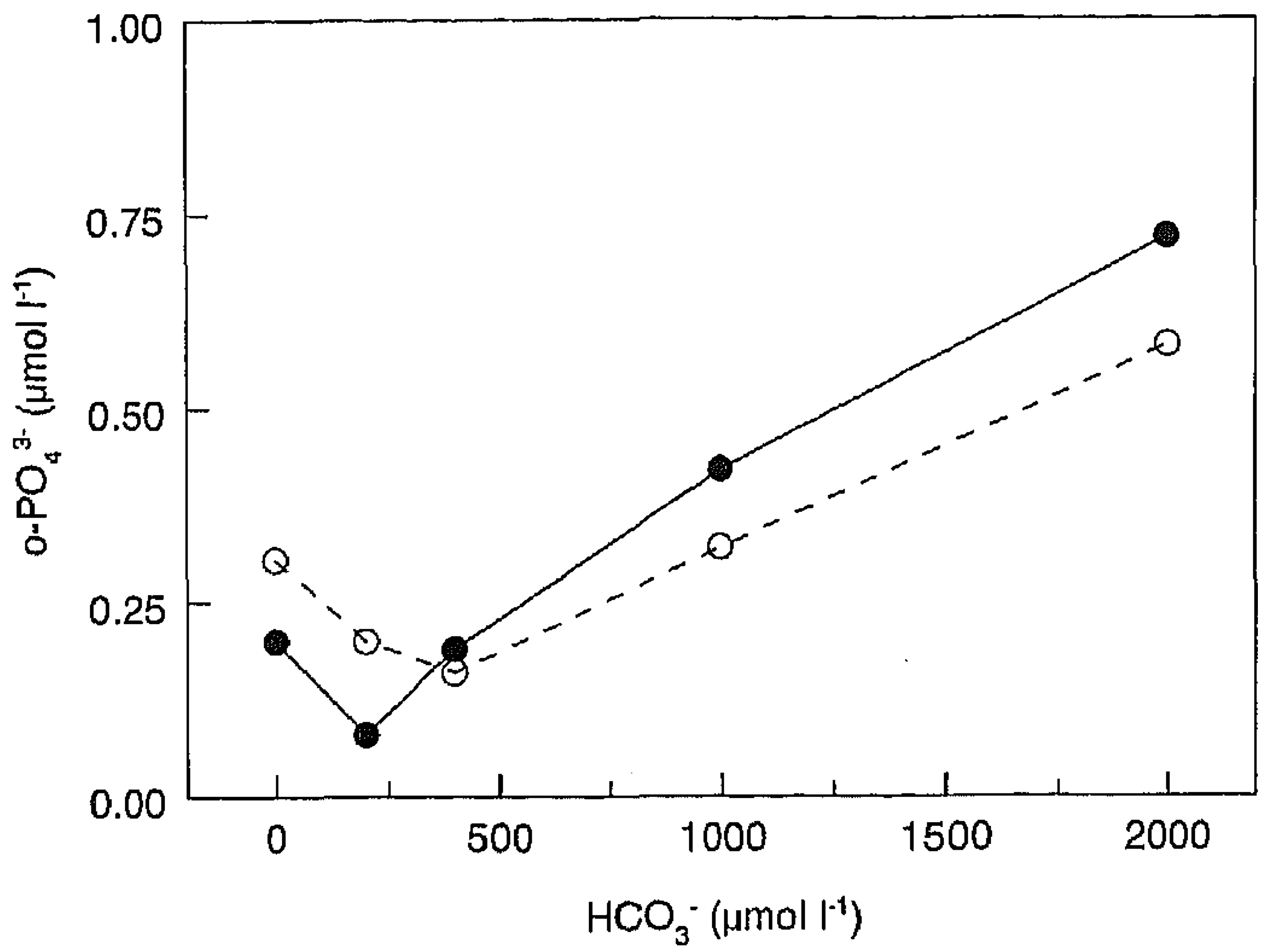

Fig. 6. o-Phosphate concentrations of the water layer (µmol l^{-1}) of mineral (open circles) and organic (closed circles) softwater sediments in glass columns after 20 weeks with different HCO_3^- concentrations of the water layer (after Bellemakers *et al.* 1990).

century, however, the isoetids decreased and the abundance of more eutrophic species increased (B. Van Geel, personal communication). In The Netherlands and Germany, there have also been many observations of eutrophication and the decline of isoetid species during the last century (Schoof-Van Pelt 1973; Westhoff 1979; Wittig 1982).

Roelofs (1983) found that in 12 of 53 waters from which isoetid species had disappeared since 1950, the water was now more or less turbid and covered by more eutrophic species such as *Lemna minor, Riccia fluitans, Myriophyllum alterniflorum* and *Ranunculus peltatus.* The alkalinity was higher compared to waters where isoetid species were still abundant. Also the nitrogen and phosphorus concentrations of the water layer and/or sediment pore water were much higher. Kok & Van de Laar (1990) found that increased alkalinity leads to increased mineralization rates in the sediments of softwater ecosystems. This can affect the phosphorus load to the water layer. Therefore, the effects of the alkaline water on both organic and mineral softwater sediments (Lake Beuven) were studied in glass columns. From the results of this experiment, it is clear that the phosphorus levels in the water layer are lowest at a very low alkalinity (Fig. 6). The phosphorus concentrations are much higher when the alkalinity of the water layer is high, which is in good agreement with the results of Kok & Van de Laar (1990). Also, at zero alkalinity (acidic conditions), the phosphorus load is clearly higher, so from these results it is likely that phosphorus limitation in the water layer can be best achieved by keeping the alkalinity low.

In 41 of 53 waters, where the isoetids had disappeared (Roelofs 1983), the water was, however, very clear and the vegetation dominated by *Juncus bulbosus* or submerged *Sphagnum cuspidatum.* These waters appeared to be very acid (mean pH=3·9). Luxurious growth of *Juncus bulbosus* and the concomitant suppression of isoetid species is often observed in acidified, shallow softwater bodies in western Europe (Van Dam & Kooiman-van Blokland 1978). Hultberg & Grahn (1975) and Grahn (1977) also observed an increased growth of *Sphagnum* spp. and *Juncus bulbosus* in acidified Swedish lakes but, in contrast to acidified West European waters, isoetids were still very abundant. Isoetid plants such as *Littorella uniflora* are known to be very acid resistant (Maessen *et al.* 1992), so it is not likely that the decline is a direct result of the low pH value. From field investigations mentioned earlier, it has become clear that acidification of soft waters in The Netherlands led to changes in the carbon and nitrogen budgets. The CO_2 levels of water and sediment pore water of the water bodies dominated by *Juncus bulbosus* or *Sphagnum cuspidatum* were much higher compared to non-acidified waters. Also, the ammonium levels were much higher and the nitrate levels lower in the acidified waters (Roelofs 1983).

From artificial rainwater treatments in mesocosms, it appeared that mass development of *Juncus bulbosus* only occurred when the acidifying precipitation contained ammonium (Schuurkes *et al.* 1987). This can explain why the acidified waters in Scandinavia are still dominated by isoetids. The waters are less shallow and the ammonium/ammonia deposition is much lower compared to central Europe.

For several years, however, there have also been observations of mass development of *Juncus bulbosus* or *Sphagnum* spp. in Swedish and south-west Norwegian lakes (Alenäs *et al.* 1991; Roelofs *et al.* 1994). All those lakes have been limed annually during the last decade. Alenäs *et al.* (1991) concluded that increased *Sphagnum* spp. growth could be attributed to reacidification after liming. Liming leads to precipitation of lime to the sediments. As a result, microbial activity increases, the sediments become anoxic on locations without dense stands of isoetids and the carbon dioxide, ammonium and phosphate levels in the sediment pore water increase (Roelofs *et al.* 1994). *Juncus bulbosus* can benefit from these higher nutrient levels in the sediments but needs relatively high CO_2 levels in the water layer. This is the situation which arises after reacidification of the water layer (Roelofs *et al.* 1995).

RESTORATION OF EUTROPHIED SHALLOW SOFTWATER LAKES

From previously mentioned investigations in Dutch eutrophied softwater ecosystems, it appears that *Littorelletea* species such as *Littorella uniflora* and *Lobelia dortmanna* decline or disappear as the water becomes more turbid and a shift to eutrophic macrophytes occurs. When the distribution of *Littorelletea* species is compared with the species from more eutrophic waters, it is clear that the latter only occur in waters with bicarbonate levels above 200 μeq l^{-1} and that *Littorelletea* species mainly occur in waters with bicarbonate levels below 200 μeq l^{-1} (DeLyon & Roelofs 1986). In many cases, the eutrophication and alkalinization is the result of input of eutrophic calcareous stream- or groundwater. The question arises whether it is possible to reduce the input of calcareous water to such a level that the lake becomes poorly buffered once more (<200 μmol $HCO_3 l^{-1}$). Under such conditions, only plant species which are adapted to carbon limitation in the water layer (*Littorelletea species*) can survive.

A case study was carried out to follow the restoration of Lake Beuven and Lake Banen, based upon the recovery of inorganic carbon and phosphorus limitation. Both formerly poorly buffered oligotrophic shallow waters had become eutrophied and alkalinised by the inlet of eutrophic, calcareous streamwater. In both cases, the mud layer and part of the dense *Phragmites australis* vegetation was removed. In the first case, Beuven, the inlet of streamwater was strongly reduced. In the second case, Lake Banen, the inlet of streamwater was stopped completely and here the alkalinity was regulated by inlet of calcareous groundwater.

Lake Beuven

Beuven is a late glacial shallow lake (70 ha; max. depth 1·5 m), situated east of Eindhoven in the south-eastern part of The Netherlands (51°24′N; 5°39′E). It belongs to a 2300 ha sandy heathland area. In the past, Lake Beuven was mainly fed by rainwater and some water from its small catchment. The water is hydrologically isolated from deeper groundwater by thin loam layers in the subsoil. Until the 1960s the water layer was dominated by submerged aquatic plants belonging to the *Littorelletea* (Schaminée *et al.* 1995), like *Littorella uniflora*, *Isoetes echinospora*, *Lobelia dortmanna*, *Elatine hexandra*, *Echinodorus repens* and *Luronium natans*. Since the late 1960s, the water has become very eutrophic, turbid and relatively alkaline as a result of the inlet of nutrient-rich, relatively calcareous streamwater (Peelrijt) which is, in fact, originally from the run-off of higher situated, heavily fertilized agricultural land. All submerged aquatic macrophytes disappeared within a few years. Only small populations in very shallow water in the littoral zone could survive. In 1986 most of the dense *Phragmites* vegetation and the complete mudlayer were removed. A small part of the lake was isolated from the rest by means of a dam. When necessary, water from the stream can be allowed into the small part of the lake where the nitrogen and phosphorus load of the water decreases by 80–90% within 2 weeks. This relatively calcareous, nutrient-poor water can be let into the large part of the lake so as to prevent acidification as a result of atmospheric deposition and to maintain the inorganic carbon at low levels in the water layer. In this way a water layer with a bicarbonate alkalinity of about 100 μeq l^{-1}, which results in a pH of *c.* 6·0, and a CO_2 level of about 50 μmol l^{-1}, is created. Thus, no submerged water plants which depend on CO_2 uptake by the leaves, such as *Juncus bulbosus* or *Spaghnum* spp., can reach high biomass and outcompete other species.

After replenishment of the water layer with rainwater in 1986, there was a rapid acidification of the water layer down to pH 4·5 after 6 months. From that time on small quantities of calcareous water from the isolated part of the lake were allowed to create optimal conditions, as described earlier. The water quality developed as expected. Before the restoration, the bicarbonate alkalinity was high and fluctuated in line with high or low precipitation rates. The phosphorus concentration in the water layer clearly correlated with its alkalinity. After the restoration measures, the alkalinity and phosphorus level of the water layer were always very low and the water was very clear, except for 1992 when, by accident, too much calcareous water was let into the main lake (Fig. 7; Table 6).

The development of the aquatic vegetation after the restoration was spectacular. Within 1 year the whole lake was colonized by *Littorelletea* species. Most abundant was *Littorella uniflora*, but many other species such as *Echinodorus repens*, *Luronium natans*, *Lobelia dortmanna*, *Hypericum elodes* and *Eleocharis acicularis* developed well (Table 5). Even *Isoetes echinospora,* a species which was last recorded in The Netherlands in 1972, established, obviously from spores in the sediment. Such a quick recovery of the vegetation is only possible when there are many living seeds or spores present in the sediments, so it is likely that in sediments of eutrophied softwater lakes, seeds or spores of *Littorelletea* species can survive at least some decades. Seed-bank experiments of Arts & Van der Heijden (1990) revealed that *Littorelletea* species developed from sediments of lakes where those species had disappeared more than 30 years ago. Now, 10 years after the restoration measures, the water quality is still very good and the aquatic vegetation is also in good condition. Above the waterline, however, as could be

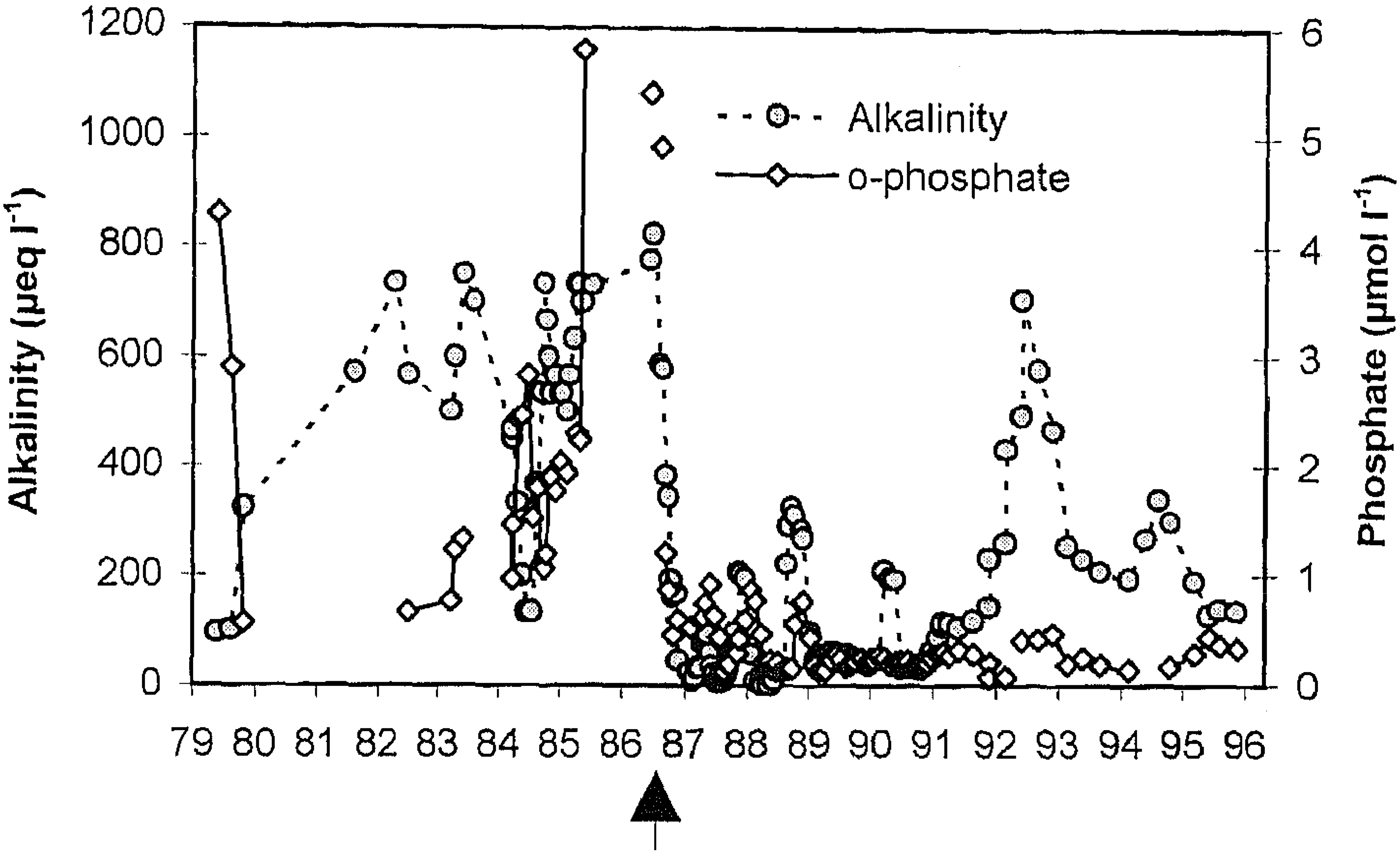

Fig. 7. Alkalinity (µeq l^{-1}; closed circles) and o-Phosphate concentrations (µmol l^{-1}; open symbols) in the water layer of Beuven before and after restoration measures. Arrow indicates restoration (after Bellemakers *et al.* 1993 & Brouwer *et al.* 1996).

expected, there is too robust a development of grasses. These grasses are mainly *Agrostis canina* on the windy, mineral north-eastern shores and *Phragmites australis* on the more sheltered, slightly organic sediments along the south-western shores and most shallow parts of the lake. The growth of these emergent or terrestrial plants is not restricted by low CO_2 levels in the water layer. The atmospheric deposition of nitrogen is high in this region (20–40 kg N ha^{-1} yr^{-1}) and it is known from several studies that nitrogen stimulates the growth of (semi-)aquatic grass species in those soft water lakes and their surroundings (e.g. Schuurkes *et al.* 1987; Aerts & Berendse 1988).

Lake Banen

Lake Banen, located in the south-western part of The Netherlands (51°16′N; 5°48′E), is a shallow, late glacial softwater lake with an area of about 20 ha. (max. depth 1·5 m). During the holocene, the lake gradually changed to a peat bog but, as a result of peat cutting in the nineteenth century, was converted back to an open water body. The sediments are mainly organic (peat remnants) and sandy along the north-eastern shores. In the first part of this century, the lake was fed by rainwater and water from its small catchment. The lake water was poorly buffered and the vegetation was dominated by *Littorelletea* species as *Isoetes echinospora, Littorella uniflora, Echinodorus repens, Scirpus fluitans* and *Pilularia globulifera.* After 1950 the water became eutrophied by inlet of eutrophic streamwater (Rietbeek), originating from heavily fertilized agricultural land and water from the river Meuse. Between 1980 and 1990, no *Littorelletea* species were recorded in the lake (Table 5). There was only a small pool, isolated from the lake, where a number of *Littorelletea* species were found.

At the end of 1988 the ditch allowing eutrophic streamwater into the lake was filled up. Since then the alkalinity has gradually decreased (Table 6). In early 1991, alkalinity reached values typical for softwater lakes. Within a few months almost the entire lake was again colonized by many *Littorelletea* species (Table 5). In winter 1992/93, the mud

Table 5. Aquatic macrophyte vegetation of Beuven (main lake) and Banen before and after the restoration measures. The abundance of the species is indicated with: 1, rare; 2, scarce; 3, frequent; 4, locally dominant; 5, dominant (dominating large parts of the lake). (after Bellemakers *et al.* 1993 & Brouwer *et al.* 1996)

	Beuven		Banen	
Species	Before (1976–85)	After (1986–95)	Before (1980–88)	After (1991–95)
Isoetids				
Littorella uniflora	2	5	—	2
Lobelia dortmanna	1	3	—	—
Isoetes echinospora	—	2	—	1
Echinodorus repens	1	3	—	3
Luronium natans	1	3	1	1
Others				
Apium inundatum	—	2	—	1
Callitriche hamulata	2	2	—	3
Callitriche platycarpa	—	—	1	1
Chara globularis	—	—	—	1
Deschampsia setacea	—	1	—	—
Elatine hexandra	2	4	—	1
Eleocharis acicularis	2	4	—	4
Eleocharis multicaulis	2	2	—	—
Eleocharis palustris	—	—	—	1
Fontinalis antipyretica	—	—	4	1
Hypericum elodes	1	4	—	1
Juncus bulbosus	4	2	—	4
Lemna minor	3	2	2	2
Lemna trisulca	—	2	—	—
Lythrum portula	1	3	—	2
Mentha aquatica	—	—	—	2
Myriophyllum alterniflorum	—	—	2	3
Nitella flexilis	—	—	—	3
Nitella translucens	—	—	—	3
Nymphaea alba	—	—	2	1
Nymphoides peltata	—	—	—	1
Pilularia globulifera	—	2	—	1
Polygonum amphibium	2	2	—	—
Potamogeton gramineus	—	3	2	3
Potamogeton natans	2	2	—	—
Potamogeton obtusifolius	—	1	—	—
Potamogeton pusillus	1	1	2	—
Ranunculus peltatus	—	—	2	—
Riccia fluitans	2	2	—	—
Scirpus fluitans	—	—	—	2
Sparganium natans	—	—	1	2
Sparganium minimum	2	2	—	—
Utricularia australis	2	2	—	3
Utricularia vulgaris	—	—	3	—
No. of species	18	25	11	27

Table 6. Water chemistry of the water layer of Lake Beuven and Lake Banen before and after restoration (see text). Mean and standard error (between parentheses) of HCO_3^-, pH, NH_4^+, NO_3^- and o-PO_4^{3-} (μmol l^{-1}) are given (after Bellemakers *et al.* 1993 & Brouwer *et al.* 1996)

	Beuven		Banen	
	Before (n=32)	After (n=97)	Before (n=11)	After (n=18)
HCO_3^-	503 (44)	155 (21)	1155 (28)	113 (8)
pH	7.4 (0.2)	5.9 (0.1)	7.4 (0.1)	5.6 (0.1)
NH_4^+	25 (4)	13 (1)	23 (4)	19 (5)
NO_3^-	38 (12)	27 (6)	9 (2)	19 (5)
o-PO_4^{3-}	1.88 (0.31)	0.38 (0.04)	0.27 (0.04)	0.27 (0.03)

layer and part of the *Phragmites australis* vegetation, which occupied more than 50% of the former lake area, was removed. From that time on, alkalinity has been maintained at a level of approximately 100 μeq l^{-1} by the controlled inlet of nutrient-poor, calcareous groundwater. Since that time the water has been clear and the aquatic, submerged vegetation is well developed and stable with many *Littorelletea* species (Table 5).

RESTORATION OF ACIDIFIED SHALLOW SOFTWATER LAKES

As already mentioned, most of the formerly weakly buffered softwater ecosystems in the Netherlands are now acidified as a result of atmospheric deposition (e.g. Roelofs 1983; Arts 1990; Van Dam & Buskens 1993; Bobbink & Roelofs 1995b). In almost all these waters, the typical softwater macrophytes (most *Littoreletea* species) have disappeared and have been replaced by *Juncus bulbosus* or submerged *Sphagnum cuspidatum*. Mass development of *Juncus bulbosus* is only possible when the CO_2 levels in the water layer are relatively high and the ammonium levels in the water or sediment are high (Schuurkens et al. 1987). Liming of waters to counteract acidification is not a good option as liming leads to increased mineralization in the sediments, resulting in very high levels of carbon dioxide, ammonium and phosphate levels in the sediment pore water (Roelofs *et al.* 1994). Another problem is that the waters acidify again, often within a few months. This results in very high CO_2 levels in the water layer because of the high diffusion rate of CO_2 from the supersaturated sediment pore water to the overlying water. In buffered water, most CO_2 is converted into HCO_3^-, but in acid water all inorganic carbon occurs as CO_2. This combination of effects leads to mass development of *Juncus bulbosus* (Brandrud *et al.* 1995, Roelofs *et al.* 1995). A possibly better option is to compensate acidification by the inlet of calcareous groundwater. This creates the possibility to keep the water poorly buffered without the detrimental effects of lime in the sediment.

Bergvennen is a collective of nine shallow moorland pools, varying in size between 0·5 and 5 ha, in non-calcareous Pleistocene sandy deposits and situated in a heathland area in the eastern part of The Netherlands (52°25′N; 7°00′E). All pools are strongly acidified by atmospheric deposition. In the first half of this century, the vegetation of these moorland pools was dominated by *Littorellion* species (Schaminée *et al.* 1995) such as *Littorella uniflora, Lobelia dortmanna* and *Isoetes lacustris.* Four moorland pools were

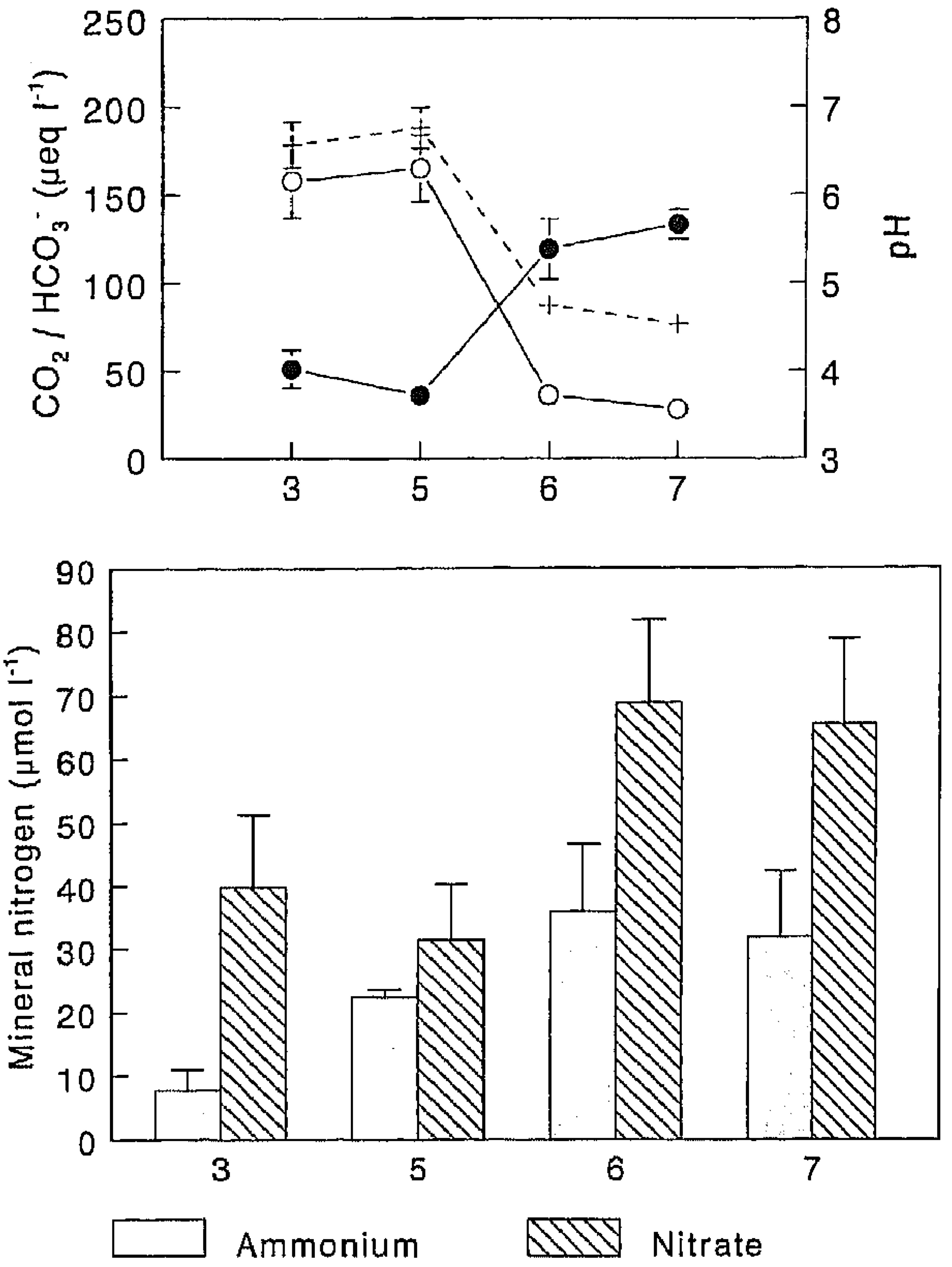

Fig. 8. A. Water chemistry of the water layer (summer values June–September 1994) of Bergvennen pools 3 (n=5), 5 (n=2), 6 (n=5) and 7 (n=5) after restoration and inlet of groundwater in pool 3 (see text). Mean and standard error of pH (crosses), HCO_3^- (open circles) and CO_2 (closed circles) (μmol l^{-1}) are given (after Brouwer *et al.* 1996). **B.** Ammonium and nitrate concentrations (μmol l^{-1}) of the water layer (summer values June–September 1994) of Bergvennen pools 3 (n=5), 5 (n=2), 6 (n=5) and 7 (n=5) after restoration and inlet of groundwater in pool 3 (see text). Mean and standard error are given (after Brouwer *et al.* 1996).

selected for the experimental input of calcareous groundwater, pools 3, 5, 6 and 7. Before restoration, the vegetation in all these pools was dominated by *Juncus bulbosus* and submerged *Sphagnum cuspidatum.* No isoetid plant species occurred, except for a few spots with *Littorella uniflora* plants in pool 3 and pool 6. There is an altitudinal gradient between the pools; pool 3 is the most elevated, followed by 5, 6, and 7, respectively. In the winter of 1993/94, all vegetation and the complete mud layer was removed from those pools. The pools are connected with each other by ditches. Since spring 1994 calcareous groundwater from a well near pool 3 has been introduced into that pool. The inlet of water stops when the alkalinity of pool 6 reaches a level of 200 μeq.l^{-1}. This results in an alkalinity gradient from pool 3 (highest) to pool 7 (lowest) (Fig. 8). In all pools nitrate has become an important nitrogen source and ammonium levels dropped to low levels as a result of nitrification. There is also a gradient in CO_2 which is lowest in pool 3 and highest in pool 7. In pools 3–5 the CO_2 levels are clearly below 100 μmol CO_2.l^{-1}, a value which is too low for mass development of *Juncus bulbosus.* Within a few weeks all *Juncus bulbosus* plants turned a brown colour and began to decay in the pools with the lowest CO_2 levels. In 1995, flowering plants of the isoetids *Lobelia dortmanna* and *Littorella uniflora* were observed in pools 3, 4 and 5. Thus, inlet of calcareous groundwater seems a promising alternative to counteract the negative effects of acidification in shallow soft waters.

CONCLUDING REMARKS

In this paper key factors which control the maintenance of characteristic, endangered plant species of Dutch nature reserves located on sandy, non-calcareous soils have been identified. This knowledge of the ecological functioning of these species enables the development of optimal management strategies, which have been tested in the field so as to adequately restore the abiotic conditions and characteristic diversity. Several semi-natural ecosystems of high nature conservation importance on the sandy Pleistocene areas of The Netherlands have been treated in detail, in view of the relative importance of acidification and/or eutrophication as cause of the decline of many endangered species. It is, of course, obvious that for long-term preservation of the restored ecosystems, the inputs of atmospheric pollutants should decrease below the set critical loads (e.g. Bobbink & Roelofs 1995b).

It is shown that application of relatively low amounts of lime to increase pH and base saturation has been, after sod cutting, an adequate measure to restore weakly buffered, oligotrophic soil conditions in acidified and eutrophied *Nardo-Galion* grasslands and formerly species-rich dry heath. The recovery of the characteristic vegetation composition is, however, seriously limited when the characteristic species disappeared from the surroundings some years before the restoration measures started. This is probably caused by the non-persistent seed bank of many of these plant species (Bakker *et al.*, this issue). Experimental re-introduction of the plant species involved should be considered under these conditions to restore these typical plant communities. It has become obvious that the studied restoration strategies are most successful, when some individuals of these plant species are still present before restoration starts.

It has been demonstrated that weakly buffered soil conditions are a prerequisite for the maintenance of many endangered wet heath species. Acidification, caused by atmospheric deposition and desiccation, is thus a serious threat for these ecosystems, together with the enhanced N deposition. Restoration of the former hydrological conditions in species-rich wet heath and related grasslands, after sod cutting, has been an adequate measure against soil acidification and eutrophication. It became clear that many characteristic plant species, which disappeared already several years before restoration, developed well after an increased influence of groundwater seepage. It is likely that many seeds persist for a relatively long time under these more or less wet eutrophic conditions. A serious constraint for the restoration of these wet heaths is when the seepage water is also acidified; additional research is needed to solve this problem.

The vegetation of shallow softwater lakes is significantly restricted by inorganic carbon and phosphorus in the water layer. Restoration of eutrophied softwater lakes by stopping the inlet of eutrophied water and removal of the sediments leads to a quick recovery of the former species-rich *Littorelletea* community, because of the re-establisment of carbon and phosphorus limited water conditions. From the fast re-colonization of typical macrophyte species, it can be concluded that many seeds or spores persist for at least decades in anaerobic organic sediments.

Restoration of acidified aquatic ecosystems, after removal of the organic sapropelium layer and controlled inlet of weakly buffered groundwater to prevent reacidification by atmospheric deposition, leads to appropriate water conditions (limitation by inorganic carbon) and a quick recovery of acid resistant species such as *Lobelia dortmanna* and *Littorella uniflora.* Non-acid tolerant endangered plant species do not appear in the first years after restoration. The seeds of these species probably do not persist during acid conditions, and the re-establisment of these plant species may be a serious constraint for restoration in future.

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