

Nutrient deficiency in undisturbed, drained and rewetted peat soils tested with *Holcus lanatus*

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SUMMARY

Two fen peat soils, supporting a species-rich fen vegetation with a high nature value, and two accompanying drained fen peat soils, supporting vegetation types with a low nature value, were subjected to a study on nutrient deficiency. This study tested what effect rewetting of drained fen peat soils had on the nutrient deficiency. In each of the study areas, soil was collected from the wet site and from a neighbouring drained site. *Holcus lanatus* was used as a phytometer screening the wet soil under wet conditions and the drained soil when drained or rewetted. The soil taken from the wet site revealed a higher yield than the soil from the drained site in both study areas. Additional supply of K, in combination with N or P supply, further increased the biomass yield. K-deficiency was even stronger in the drained site of both study areas. Experimental rewetting did not entirely remove this deficiency and additionally enhanced N-deficiency. The results from this phytometer approach are discussed as related to results from field and laboratory experiments with vegetation as object of research.

Key-words: drained peat soils, *Holcus lanatus*, nutrient deficiencies, phytometer, rewetting.

INTRODUCTION

Drainage of peat soils causes several physical, chemical and biological changes. The peat structure changes and the water-holding capacity of the peat is affected negatively (Kayak & Okruszko 1990). An increase in mineralization often results in a higher soil fertility for the vegetation (Etherington 1975; Vermeer & Berendse 1983; Grootjans *et al.* 1985). The system changes into the direction of a vegetation adapted to drier conditions and a more nutrient-rich environment concerning N and P (Pastor *et al.* 1984; Vermeer 1986; Oomes 1990; Devito & Dillon 1993). There is also some evidence that the drainage of peaty and wet areas causes a decrease in potassium availability (Okruszko 1995; De Mars 1996; Van Duren *et al.* 1997, 1998).

The question is whether it is possible to reverse the effects of drainage and to restore or develop more species-rich wet vegetation types. Nature management practices aimed at restoring species-rich grasslands are often: lowering the soil fertility by nutrient export through hay cropping, grazing or even removal of the topsoil. Especially when dealing with wet vegetation types, restoring the hydrological site conditions has priority since hydrology is considered to be the determining factor for the type of vegetation to occur in wet grasslands (Klötzli 1987; Grootjans & Van Diggelen 1995; Okruszko 1995).

Besides creating a wet environment supporting vegetation adapted to anoxic soil conditions, the effects of rewetting are also related to the availability of nutrients. It has been shown that rewetting lowers the nitrogen availability (Patrick & Tusneem 1972; DeLaune *et al.* 1981; Grootjans *et al.* 1985; Bakker 1993). On the other hand phosphate availability might increase resulting from anaerobic or anoxic conditions and a low redox potential (Patrick & Khalid 1974; Caraco *et al.* 1989; Roelofs 1991). This causes a higher solubility of iron phosphates. The impact of rewetting on the K-availability is not yet well understood.

In order to be able to take the most efficient measures to influence nutrient availability it is necessary to have knowledge about which nutrients are the most deficient to the vegetation. In our research we assessed the nutrient deficiency for four different peat soils. First we tested soil from a relatively nutrient-rich and relatively high-productive wet site supporting a well-developed *Calthion palustris* vegetation and a neighbouring drained site with a degraded stand. Then we performed the same kind of experiment with soil from another but less productive study area with a wet site supporting a well-developed *Caricion curto-nigrae* and another drained site with a degraded stand. We focused on the following research questions: (1) In what way does the drained site differ from the wet site considering the type and/or extent of nutrient deficiency? (2) Does rewetting of drained peat soils change the type and/or extent of nutrient deficiency?

To answer these questions, we grew *Holcus lanatus* as test plant on soil taken from the two study areas to the greenhouse, each represented by an intact (wet) and a drained site. We applied a modified double pot set-up (cf. Pegtel 1987). Samples from the drained site were kept undrained or rewetted. In addition, part of the drained treatment was given additional calcium carbonate, to check if there would be a pH effect. We compared soil from each of the four sites under different combinations of NPK-fertilizers, in a full-factorial design, to identify deficiencies.

The phytometric method has been proved to be useful as a bioassay in a number of cases (e.g. Rorison 1969; Dijkshoorn & Lampe 1980; Pegtel 1987; Pegtel *et al.* 1996; Wheeler *et al.* 1992). *Holcus lanatus* was, among other species, used as test plant by Pegtel (1987). This species has been shown to occur in the majority of plant communities related to the ones investigated in the present study. It is a very expressive phytometer because of its wide ecological range (see Weeda *et al.* 1994), its shoot biomass being an adequate parameter of soil fertility and/or deficiency (Pegtel 1987).

MATERIAL AND METHODS

Study areas

The first study area is located in the Drentse Aa nature reserve in The Netherlands (56°61'N, 6°60'E). This is a shallow valley consisting of several small streams and adjacent meadows and woodlands. Our study sites are located in the middle part of the Drentse Aa and are influenced by relatively calcium-rich ground water (1.5 mmol Ca/l) (Bakker & Grootjans 1991). The wet site, along the brook, represents a well-developed *Calthion palustris* stand dominated by *Caltha palustris*, *Scirpus sylvaticus*, *Filipendula ulmaria*, *Carex acutiformis* and *Ranunculus repens* and *R. acris*. Next to this field, separated by a ditch, was the drained site dominated by *Ranunculus repens*, *Holcus lanatus*, *Anthoxanthum odoratum* and *Plantago lanceolata*.

The second study area is located in the Zwarte Beek nature reserve near Koersel in Belgium (51°05'N, 5°18'E) and harbours a *Caricion cuto-nigrae* vegetation. The study sites are located in the middle part of the Zwarte Beek catchment. Parallel to the Zwarte Beek is the Oude Beek, hydrologically of main importance in draining the area adjacent to this stream. The vegetation in the drained site was mainly composed of *Agrostis canina* and *Juncus effusus*. The wet site was situated where the impact of the Oude Beek was much less. The vegetation in the wet site, influenced by relatively Ca-poor groundwater (C. Aggenbach *et al.*, internal report Plant Ecology, Groningen 1990), was dominated by *Carex rostrata*, *Carex nigra*, *Lotus corniculatus*, *Equisetum fluviatile*, *Potentilla palustris* and *Filipendula ulmaria*.

Pot experiment

Soil, taken from the wet and the drained site in the Drentse Aa nature reserve, was sieved (\varnothing 0.5 cm) and stored at 5°C until the start of the experiment. We applied four series in the experiment: (i) soil from the wet site which was treated wet; (ii) soil from the drained site in a drained treatment; and (iii) rewetting soil from the drained site. Additional to treatment (ii) we applied an extra series. Because rewetting of (weakly) acid soil causes a rise of the pH (Ponnamperuma 1972) we wanted to differentiate between the effect of a pH increase and the effect of anaerobic conditions. Therefore, soil from the drained site had a drained treatment with addition of CaCO₃ (1.30 g/pot to acquire 0.5 increase of the pH from 5.6 to 6.1).

In each series we replicated six times eight different nutrient treatments: none, N, P, K, NP, NK, PK and NPK, which resulted in a total of 192 pots. The nutrients were applied as 'Osmocote' slow-release fertilizers in the following amounts: N: 252 mg/pot, P: 176 mg/pot and K: 189 mg/pot. This was based on the response of *Caltha palustris* in a preliminary experiment, using the same set-up.

After mixing the fertilizers with 400 g soil per pot, the pots (\varnothing 12 cm) were filled and placed randomly in a climate chamber (8 h dark at 16°C and 16 h light at 23°C at an air moisture of 75%). One cloned tiller of *Holcus lanatus* (mean weight at the start: 0.015 \pm 0.001 g/plant) was planted per pot. After one week of acclimatization, the different treatments for the series were initiated by placing the 'wet' and the 'rewetted' treatment series in small plastic containers. They were filled with demi-water enriched with added NaHCO₃ and CaCl₂, to the amount of 60 mg Ca per litre (Ca-rich) for soil from the Drentse Aa, and 30 mg Ca per litre (Ca-poor) for soil from the Zwarte Beek, up to ground surface in the pots. The other pots in the drained treatment were watered daily with demi-water. The plants were harvested, dried (>24 h, 70°C) and weighed after 10 weeks. By then the roots had largely grown through the soil samples and penetrated the perforated plate into the culture solution.

Statistical analyses

The significance of the differences between the fertilizer applications within each treatment was tested using a one-way analysis of variance for each of both study areas. Contrasts were determined with a Tukey test.

To study the difference between the study areas and effect of the different treatments and of the nutrients N, P and K on the aboveground biomass of *Holcus lanatus*, we applied an ANOVA with five factors: study area, treatment (rewetting, etc.), N, P and K. In this way we compared the wet with the drained treatment, the drained-CaCO₃ with drained+CaCO₃, the drained-CaCO₃ with the rewetted, and the wet with the rewetted

treatment within each study area. The last comparison was made to study whether the rewetted treatment resembled the wet treatment. The main effects of N, P and K were suppressed as well as the interaction of more than three factors. Homogeneity of variances was checked by means of Cochran's *C*-test.

RESULTS

The aboveground biomass produced in response to fertilization is presented in Fig. 1. The soil taken from the wet site (wet treatment) supports a higher yield than the soil taken from the drained site. This holds for both study areas. The wet site in the Drentse Aa area was more productive than the wet site in the Zwarte Beek area. Fertilization of this soil stimulated growth of *Holcus lanatus* more than the soil from the wet site of the Zwarte Beek. The biomass yield on the soil from the wet site in the Drentse Aa increased after K fertilization and especially in combination with P. The biomass yield in the wet site of the Zwarte Beek only increased significantly after NK and NPK fertilization.

In the drained treatment, K fertilization increased the biomass yield on the soil from both drained study sites. The increase was larger in the Drentse Aa. Statistical analysis of all treatments revealed, additionally, that P-supply increased the biomass yield in the drained soil from the Zwarte Beek.

The liming treatment did not differ from the drained treatment in the Drentse Aa experiment. In combination with addition of K, liming stimulated growth in soil from the drained site in the Zwarte Beek.

Rewetting the drained soil from the Drentse Aa increased the biomass yield in the control treatment ($P < 0.05$). When rewetted, potassium increased the biomass yield as it did in the drained treatment, but significantly less. The biomass yield of the control after rewetting the drained soil from the Zwarte Beek was similar to the yield of the control in the drained treatment. Rewetting after fertilization decreased the biomass yield compared to the same fertilization under drained conditions. PK fertilization increased the biomass yield considerably in the drained treatment, whereas it did not after rewetting.

The overall ANOVA (Table 1) describes per two treatments the significance of the factors: study area, treatment and of the interactions of these factors with N, P and K. For the present purpose, it was not considered useful to test the overall NPK effects. In all comparisons of two treatments, there is a significant difference between the study areas. The overall effect of the factor treatment is obvious in comparison 1, 2 and 4. Only liming did not give a significant effect. Concerning the wet and the drained treatment, the study areas showed no difference in the effect of N and P. The effect of K was stronger in the Drentse Aa, which is demonstrated by the significant interaction between study area and K. There was also a strong interaction between the treatment and K and an interaction between the treatment and N. When rewetting the drained peat soil, we detected a significant interaction between the study area and the treatment. Furthermore, all nutrients interacted with the factor study area and N and K interacted with the factor treatment. Comparing the drained treatment with the drained + CaCO₃ treatment, liming did not result in relevant significant differences. Comparison 4 shows the resemblance and differences between the rewetted and the wet treatment. The study areas differ in the effect of the treatment, N and K but we observed no significant interactions between the treatment and any of the nutrients.

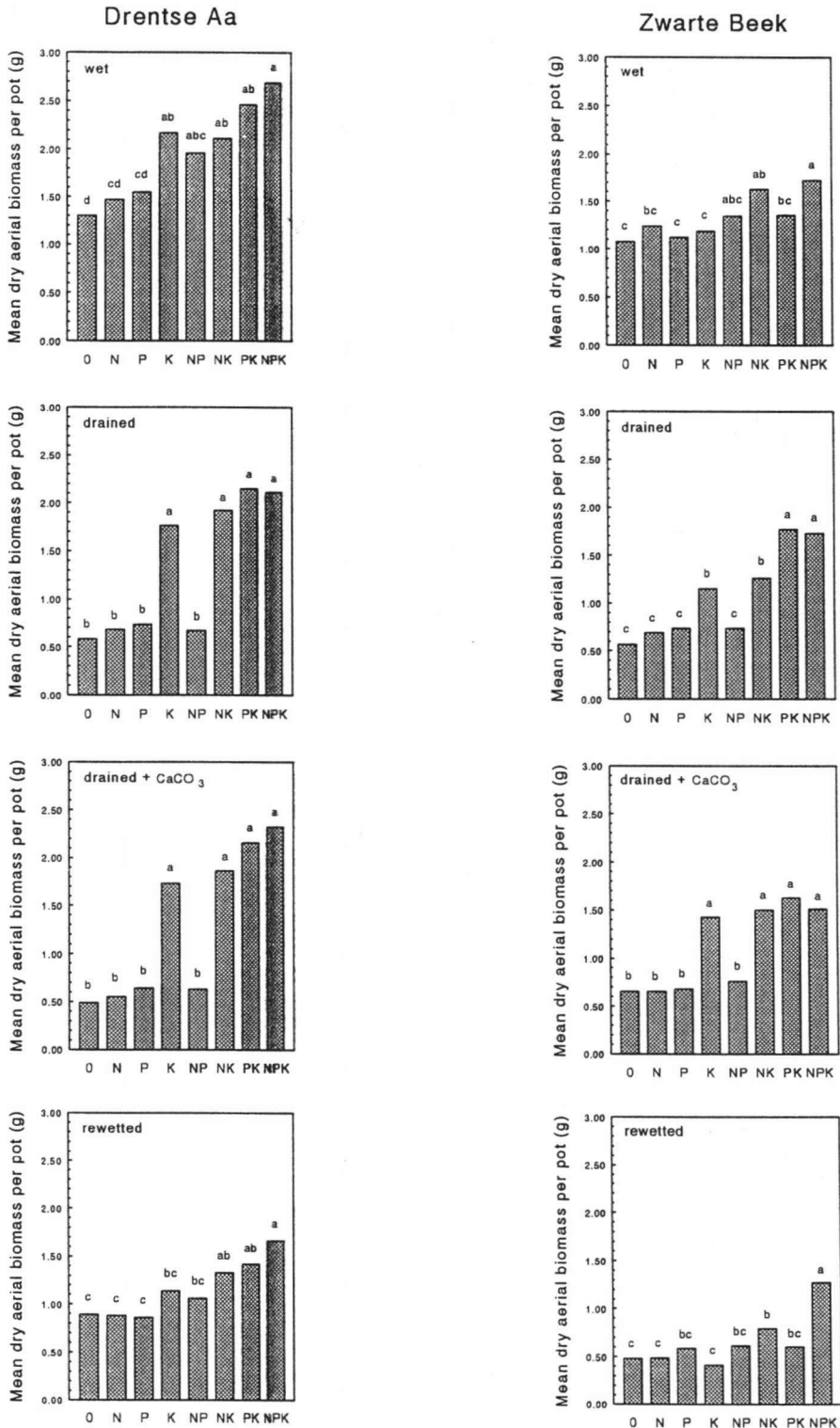


Fig. 1. Mean dry shoot biomass of *Holcus lanatus* after full-factorial fertilization with N, P and K. Significance of differences was tested using a one-way ANOVA with Tukey contrasts ($n=6$).

Table 1. Analysis of variance with the following five factors: SA=study area, T=treatment, N=nitrogen, P=phosphorus, K=potassium. Each of the four columns represents a comparison of two treatments: 1=wet and drained, 2=drained and rewetted, 3=drained and drained+CaCO₃, 4=wet and rewetted. The main effects of N, P and K were suppressed as well as the interaction of more than three factors

	1	2	3	4
SA	***	***	***	***
T	***	***	NS	***
SA × T	***	***	NS	***
SA × N	NS	*	NS	**
SA × P	NS	**	NS	NS
SA × K	***	***	***	**
T × N	*	***	NS	NS
T × P	NS	NS	NS	NS
T × K	***	***	NS	NS
SA × T × N	NS	NS	NS	NS
SA × T × P	**	NS	*	**
SA × T × K	NS	NS	NS	NS

DISCUSSION

Effect of past drainage on nutrient deficiency

In both study sites, past drainage in the field apparently has caused a K-deficiency of the peat soil. Mowing and leaching may deplete the K-pool (Kayak & Okruszko 1990; Koerselman *et al.* 1990). In situations where no flooding with surface water occurs and where the soil substrate is rather poor in K, the proportion of potassium remaining adsorbed to soil particles may be not sufficient to meet the demands from several plant species. The effect of a stepwise nutrient addition is presented in Fig. 2. Each line indicates a significant increase in the aboveground biomass yield. The steepness of the lines may be seen as a measure of nutrient deficiency. In this type of presentation, the relative importance of the different nutrients shows immediately. K-deficiency was a constraint in the wet site of the Drentse Aa and appears even stronger in soil from the drained site. Although we have no measures from the period before drainage, we derive from our results (cf. also Van Duren *et al.* 1997, 1998) that past drainage caused a shift from mainly N-deficiency to mainly K-deficiency in the Zwarte Beek area.

Effect of rewetting on nutrient deficiency

K-deficiency seems less severe after rewetting. This is not necessarily the case. The growth of *Holcus lanatus* is less stimulated by K-fertilization after rewetting than it was in the drained treatment. It might also be that K-availability is enough to support growth while the presence of large amounts of NH₄⁺ hamper the uptake of K⁺ (Marschner 1995). Indeed, field measurements showed that in the Zwarte Beek study area N is mainly present as NH₄⁺ (Boeye *et al.* 1997). Chemical analyses of plant tissue may provide additional information to check this possibility. However, it is evident that rewetting of a K-deficient soil does not remove the problem of K-constraint for plant growth.

Rewetting may result in additional N-deficiency. This might be valuable in nature management because many management practices are often aimed at reducing

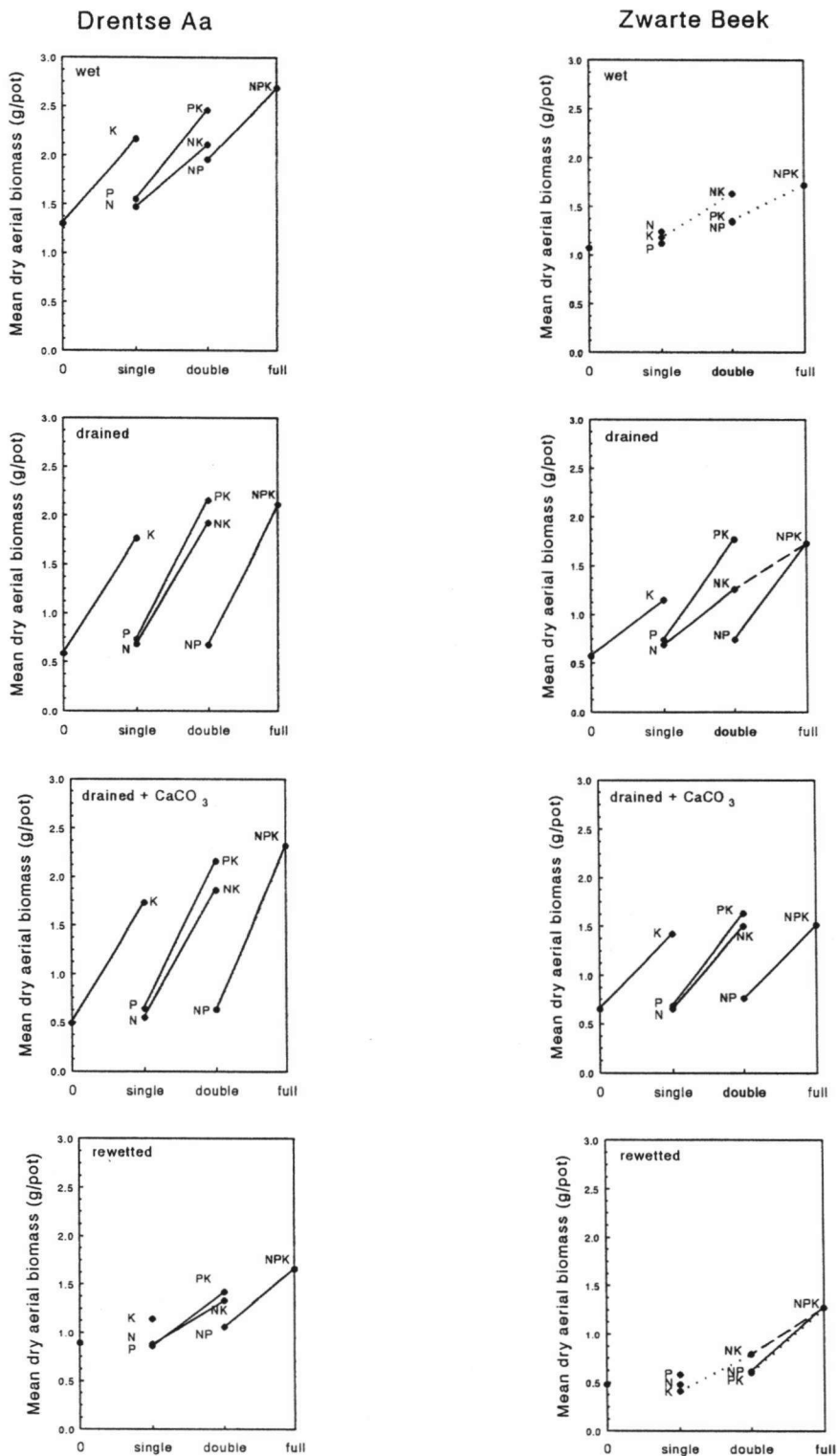


Fig. 2. Mean dry shoot biomass of *Holcus lanatus* after full-factorial fertilization with N, P and K. Significance of differences was tested using a one-way ANOVA with Tukey contrasts ($n=6$). Lines represent a significant increase in biomass after application of a specific nutrient.

N-availability. Also, colimitation is seen as a factor promoting species diversity (Tilman 1982). Our results support the idea of a limited availability of nitrogen as a result of changes in N-mineralization and denitrification.

Comparison of study areas

The soil taken from the wet sites in both study areas revealed a higher yield of the test plant compared to the drained sites. This remarkable effect cannot be an indirect effect of a change in pH (see the results from the drained site with added calcium carbonate). It more probably results from the relatively strong K-deficiency in the drained soil, which might have a higher impact than N-deficiency in the wet soil.

The Drentse Aa study area had a higher productivity and a higher increase of biomass after fertilization, compared to the Zwarte Beek sites. This was expected since it supports a vegetation type indicating a nutrient-richer soil environment with a relatively higher yield. The more pronounced K-deficiency, also in the wet site, is thought to be due to slight drainage of the wet site.

The drained site in the Zwarte Beek showed P-deficiency when K-deficiency is compensated by fertilization. The Zwarte Beek is very Ca-poor (Boeye *et al.* 1997). Liming+K-addition increased the yield. This is probably due to an increased pH and base saturation.

Comparison of the phytometer approach with vegetation experiments

The total amounts of N, P and K in peat give no indication of the availability of these nutrients to plants (Verhoeven 1986). A straight way to determine which nutrient(s) limit(s) the biomass production is to use a factorial fertilization experiment, preferably full-factorial to be able to determine possible interactions between nutrients. This is a time-consuming and expensive procedure and not always possible when studying threatened vegetation types. Application of fertilizers is not always allowed in nature reserves and disturbing rare plant communities may be questionable. Furthermore, in both study areas the vegetation in the drained site is different from that in the wet site. Therefore the field fertilization experiments describe the nutrient deficiency for a particular vegetation present in that site. Then, comparison of the type and extent of nutrient deficiency between the wet and the drained site in the field is not fully satisfactory. This experimental approach enabled us to obtain a more objective determination of the differences in nutrient supplying capacity of the peat soils, and we were able to test this under different conditions.

Nevertheless, we performed experiments with the entire vegetation in both study areas for comparison (Van Duren *et al.* 1997, 1998). The Drentse Aa as well as the Zwarte Beek study area have been subjected to full-factorial fertilization experiments in the field. These experiments revealed K-deficiency in the drained sites, N-deficiency in the wet site of the Zwarte Beek and N-deficiency with to a lesser extent K-deficiency in the wet site of the Drentse Aa. A double-pot experiment using vegetation samples from the research sites revealed similar results. However, we also observed some differences. No P-deficiency was detected in these vegetation experiments, in contrast to our experiments with *Holcus lanatus* in which we found P-deficiency, especially in the drained site of the Zwarte Beek. It is probable that *Holcus lanatus* has a relatively high P-demand. Such species specific effects can easily remain hidden when conducting experiments with a whole vegetation in which species have different nutrient demands.

Some authors (Koerselman & Verhoeven 1993; Wassen *et al.* 1995; Koerselman & Meuleman 1996; De Mars 1996) are convinced that nutrient ratios of plant material give insight in limiting nutrients. The validity of this last-mentioned method was discussed by Pegtel *et al.* (1996). In addition to a fertilization experiment it provides a check as to whether plants were able to take up the nutrients added and the results are much more convincing when nutrient ratios point in the same direction as the fertilization experiment. In the present bioassay, plant yield was not sufficient to determine its mineral contents, but we analysed samples from our vegetation experiments, from which we derived that the N:K ratios of the vegetation pointed at K-deficiency in the drained sites of both study areas (Van Duren *et al.* 1997, 1998). From data reviewed by Pegtel (1987) and Pegtel *et al.* (1996) we draw the conclusion that the response of *Holcus lanatus* in terms of the shoot biomass is sufficiently indicative of soil fertility, probably even more than its mineral contents, because the latter may be more species specific than the biomass response.

CONCLUSIONS

The phytometer approach reveals that drainage, especially when accompanied by mowing, may cause a decrease in K-availability in this type of soil. After rewetting, the nutrient deficiency of the drained peat soil resembles more that of the undrained peat soil compared to soil without rewetting. It also shows that rewetting does not entirely remove the K-deficiency and enhances N-deficiency. The P-deficiency, detected by *Holcus lanatus* in the drained site of the Zwarte Beek area, was not found in related field experiments.

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REFERENCES

- Bakker, J.P. (1993): *Nature management in Dutch grasslands*. Occasional Symposium No. 28, British Grassland Society, pp. 115–124. *Proceedings of a joint meeting between the British Grassland Society and the British Ecological Society held at Leeds University, 27–29 September 1993*.
- Bakker, J.P. & Grootjans, A.P. (1991): Potential for regeneration in the middle course of the Drentsche A brook valley (The Netherlands). *Verh. Ges. Okol.* **20**: 249–263.
- Boeye, D., Verhagen, B., Van Hasebroeck, V. & Verheyen, R.F. (1997): Nutrient limitation in species-rich lowland fens. *J. Veg. Sci.* **8**: 415–424.
- Caraco, N.F., Cole, J.J. & Likens, G.E. (1989): Evidence for sulphate-controlled phosphorus release from sediments of aquatic systems. *Nature* **341**: 316–318.
- DeLaune, R.D., Reddy, C.N. & Patrick, W.H.J. (1981): Organic matter decomposition in soil as influenced by pH and redox conditions. *Soil Biol. Biochem.* **13**: 533–534.
- De Mars, H., Wassen, M.J. & Peeters, W.H.M. (1996): The effect of drainage and management on peat chemistry and nutrient deficiency in the former Jegrznia-floodplain (NE Poland). *Vegetatio* **126**: 59–72.

- Devito, K.J. & Dillon, P.J. (1993): The influence of hydrologic conditions and peat oxia on the phosphorus and nitrogen dynamics of a conifer swamp. *Water Resources Res.* **29**: 2675–2685.
- Dijkshoorn, W. & Lampe, E.J.M. (1980): A plant test for sufficiency of phosphorus based on the phosphorus-nitrogen interaction in sunflower nutrition. *Neth. J. Agric. Sci.* **28**: 135–146.
- Etherington, J.R. (1975): *Environment and Plant Ecology*. John Wiley, New York.
- Grootjans, A.P., Schipper, P.C. & Van der Windt, H.J. (1985): Influence of drainage on N-mineralization and vegetation response in wet meadows I. *Calthion palustris* stands. *Acta Oecol. Oecol. Plant.* **6**: 403–417.
- Grootjans, A.P. & Van Diggelen, R. (1995): Assessing the restoration prospects of degraded fens. In: Wheeler, B.D., Shaw, S.C., Fojt, W.J. & Robertson, R.A. (eds.): *Restoration of Temperate Wetlands*, pp. 73–90. John Wiley, Chichester.
- Kayak, A. & Okruszko, H. (1990): Grasslands on drained peats in Poland. In: Breymeyer, A.I. (ed.): *Ecosystems of the World 17A: Managed Grasslands*, pp. 213–253. Elsevier Scientific Publishers, Amsterdam.
- Klötzli, F. (1987): Disturbance in transplanted grasslands and wetlands. In: Van Andel, J., Bakker, J.P. & Snaydon, R.W. (eds.): *Disturbance in Grasslands*, pp. 79–96. Junk, Dordrecht.
- Koerselman, W. & Verhoeven, J.T.A. (1993): Eutrofiëring van laagvenen, interne of externe oorzaken? *Landschap* **10**: 31–44.
- Koerselman, W. & Meuleman, A.F.M. (1996): The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. *J. Appl. Ecol.* **33**: 1441–1450.
- Koerselman, W., Bakker, S.A. & Blom, M. (1990): Nitrogen, phosphorus and potassium budgets for two small fens surrounded by heavily fertilized pastures. *J. Ecol.* **78**: 428–442.
- Okruszko, H. (1995): Influence of hydrological differentiation of fens on their transformation after dehydration and on possibilities for restoration. In: Wheeler, B.D., Shaw, S., Fojt, W. & Robertson, R.A. (eds.): *Restoration of Temperate Wetlands*, pp. 113–120. John Wiley, Chichester.
- Oomes, M.J.M. (1990): Changes in dry matter yields during the restoration of species-rich grasslands. *J. Veg. Sci.* **1**: 333–338.
- Pastor, J., Aber, J.D., McLaugherty, C.A. & Melillo, J.M. (1984): Aboveground production and N and P cycling along a mineralization gradient on Blackhawk Island, Wisconsin. *Ecology* **65**: 256–268.
- Patrick, W.H. Jr & Tusneem, M.E. (1972): Nitrogen loss from flooded soils. *Ecology* **53**: 735–737.
- Patrick, W.H. Jr & Khalid, R.A. (1974): Phosphate release and sorption by soils and sediments: effect of aerobic and anaerobic conditions. *Science* **186**: 53–55.
- Pegtel, D.M. (1987): Soil fertility and the composition of natural grassland. In: Van Andel, J., Bakker, J.P. & Snaydon, R.W. (eds.): *Disturbance in Grasslands*: 51–66. Junk, Dordrecht.
- Pegtel, D.M., Bakker, J.P., Verweij, G.L. & Fresco, L.F.M. (1996): N, K and P deficiency in chronosequential cut summer-dry grasslands on gley podzol after cessation of fertilizer application. *Plant Soil* **178**: 121–131.
- Ponnamperuma, F.N. (1972): The chemistry of submerged soils. *Adv. Agron.* **24**: 29–96.
- Roelofs, J.G.M. (1991): *Vegetation under chemical stress: effects of acidification, eutrophication and alkalisation*. PhD Thesis, University of Nijmegen.
- Rorison, I.H. (1969): Ecological interferences from laboratory experiments on mineral nutrition. In: I.H. Rorison (ed.): *Ecological Aspects of Mineral Nutrition*, pp. 155–175. Blackwell, Oxford.
- Tilman, D. (1982): *Resource Competition and Community Structure*. Princeton University Press, Princeton.
- Van Duren, I.C., Boeye, D. & Grootjans, A.P. (1997): Rewetting of a degraded poor fen vegetation; effects on biomass, nutrient deficiency and the restoration prospects. *Plant Ecology* (in press).
- Van Duren, I.C., Pegtel, D.M., Aerts, R.A. & Inberg, J.A. (1998): Nutrient supply in undrained and drained *Calthion* meadow. *J. Veg. Sci.* (in press).
- Verhoeven, J.T.A. (1986): Nutrient dynamics in minerotrophic peat mires. *Aquat. Bot.* **25**: 117–137.
- Vermeer, J.G. (1986): The effect of nutrients on shoot biomass and species composition of wetland and hayfield communities. *Acta Oecol. Oecol. Plant.* **7**: 31–41.
- Vermeer, J.G. & Berendse, F. (1983): The relationship between nutrient availability, shoot biomass and species richness in grassland and wetland communities. *Vegetatio* **53**: 121–126.
- Wassen, M.J., Olde Venterink, H.G.M. & De Swart, E.O.A.M. (1995): Nutrient concentrations in mire vegetation as a measure of nutrient limitation in mire ecosystems. *J. Veg. Sci.* **6**: 5–16.
- Weeda, E.J., Westra, R., Westra, Ch. & Westra, T. (1994): *Nederlandse Oecologische Flora (5)*. VARA, VEWIN, Amsterdam.
- Wheeler, B.D., Shaw, S.C. & Cook, R.E.D. (1992): Phytometric assessment of the fertility of undrained rich-fen soils. *J. Appl. Ecol.* **29**: 466–475.