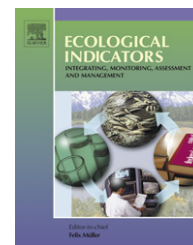


available at www.sciencedirect.comjournal homepage: www.elsevier.com/locate/ecolind

Deviances from expected Ellenberg indicator values for nitrogen are related to N throughfall deposition in forests

Walter Seidling*, Richard Fischer

Federal Research Centre for Forestry and Forest Products, Institute for Forest Ecology and Forest Inventories, 16225 Eberswalde, Germany

ARTICLE INFO

Article history:

Received 18 June 2007

Received in revised form

27 September 2007

Accepted 30 September 2007

Keywords:

Intensive forest monitoring

Plant available nitrogen

Soil acidity

Ground floor vegetation

ABSTRACT

The indication of environmental changes and their impacts on various compartments of ecosystems are high on the political and scientific agenda. Spatially and temporally different inputs of eutrophying nitrogen compounds into European forest ecosystems and their effects are still of concern. Tending floristic changes and respective changes of nitrogen indicator values are one of the suspected effects. Those can, however, not easily be discovered within any cross-sectional short-term approach. Since continuous long-term observations with a sufficiently large sample on an adequate geographical scale are not available, the investigation of deviations from a rather balanced and scientifically settled relationship between the soil acidity status and N mineralization rate is used to indicate additional nitrogen supply from atmospheric inputs. The suspected deviances show a significant statistical relationship with total N throughfall deposition (to a lesser degree also with oxidised and reduced nitrogen compounds), measured at the same locations. This suggests a higher N availability at sites with greater N deposition rates, causing a disproportion between site-specific mineralization rates and the effective amount of plant available nitrogen. In spite of some minor methodological restrictions, the approach might be an appropriate means to localise and regionalise eutrophying effects from atmospheric deposition of nitrogen on larger scales.

© 2007 Elsevier Ltd. All rights reserved.

1. Introduction

Information on state and condition of the environment is an essential basis for sound and effective policy making. The development of adequate monitoring systems is high on the agenda of environmental policy and has also been postulated in the Convention on Long-range Transboundary Air Pollution (CLRTAP) of the UNECE which led inter alia to the International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests). Originally designed to study effects of atmospheric deposition on forest condition, the monitoring system is today a provider for harmonized data on forest ecosystems (Bull et al., 2001). Ground vegetation data are recognized as a core contribution

of the programme. Among the EU headline biodiversity indicators is also one that refers to nitrogen inputs (ETC/BD, 2005).

Surveys of the floristic composition of the ground floor vegetation carried out on the intensive monitoring plots allow calculating indicator values according to Ellenberg (1992), which are based on empirical knowledge about the ecological behaviour of plant species. Such indicators deliver a rating of basic site qualities such as soil acidity, plant available nitrogen, soil moisture and light supply. Due to the considerable number of soil and deposition parameters being measured among parameters from other domains at the same plots (De Vries et al., 2003a), the exploration of appropriate relationships may contribute to an extensive

* Corresponding author. Tel.: +49 333465338; fax: +49 333465354.

E-mail address: wseidling@bfh-inst7.fh-eberswalde.de (W. Seidling).
1470-160X/\$ – see front matter © 2007 Elsevier Ltd. All rights reserved.
doi:10.1016/j.ecolind.2007.09.004

validation and eventually calibration of indicator values. Of particular interest within the forest monitoring under the umbrella of ICP Forests and respective EC policies are indicator values for soil reaction and availability of nitrogen, because atmospheric nitrogen inputs are currently assumed to specifically alter site conditions and subsequently species composition (e.g. Ellenberg, 1983; Kuhn et al., 1987; Van Dobben et al., 1999). This is of particular interest, as measurements and chemical analyses of deposition are quite intricate and can by no means be performed over large areas.

A well-defined relationship between pH of the soil solution and plant available nitrogen has already been reported (Möller, 1987; Seidling and Rohner, 1993) and expresses the dependency of quantity and quality of the nitrogen mineralization in forest soils from its acidity status (e.g. Runge, 1965; Gönnert, 1989) under otherwise equitable constraints. Any medium-scale disturbance may stimulate mineralization of organic substances and enhance nitrogen availability (Mladenoff, 1987) and subsequently cause floristic changes (Mellert et al., 1998; Jensch, 2004). While disturbances are rather discrete events accompanied by a multitude of physico-chemical changes, deposition of nitrogen is a sneaky process. Respective effects are much more difficult to detect, especially in the case of nitrogen, a nutrient with a complex interplay in terrestrial ecosystems. Apart from continuous laborious measurements of nitrogen concentrations in the soil solution at intensive monitoring sites (De Vries et al., 2003a,b), sound data about the actual availability of nitrogen in soils are difficult to achieve. Therefore indirect methods should not be neglected, especially not for large-scale surveying.

This paper is based on the hypothesis that due to deposition-caused enhanced nitrogen availability within forest ecosystems, the close relationship between nitrogen indicator values and parameters specifying the acidity status

might partially be uncoupled. Therefore the relationship between the residuals from the N indicator values against pH (or R indicator values as a surrogate) regressed against measured throughfall deposition is expected to be positive and should be meaningful. Besides this aspects of bioindication, any confirmation of effects of nitrogen inputs within ecosystems are valuable.

2. Data and evaluation methods

Unsynchronised vegetation records are available for a total of 720 ICP Forests Level II sites in Europe from 1994 to 2003 as a key component of the intensive monitoring programme at those sites (more general information in De Vries et al., 2003b; Lorenz et al., 2006). For 243 of these plots repeated assessments had been carried out, however, only one namely the latest relevé from each location was used. For this basically cross-sectional approach this is necessary in order to avoid pseudo-replication within the statistical modelling. To have a climatically and biogeographically more homogeneous sample and at the same time plots which differ distinctively with respect to deposition of nitrogen, the focus was put on plots from nemoral forest: all plot south of 46° latitude (species-rich systems, mainly transitions between maquis and open forests) and north of 61° latitude (monotonous species-poor systems) were a priori excluded as well as plots from altitudes above 750 m a.s.l. (often species-rich systems with fragments of Alpine meadows). Therefore, a total of 488 plots remained in the processed sample (Fig. 1).

Plot size is mostly around 400 m², however, can vary between 30 and 2000 m². All vascular plant species inclusive young trees, shrubs and lianas smaller than a height of 0.5 m within these permanently marked plots were sampled.

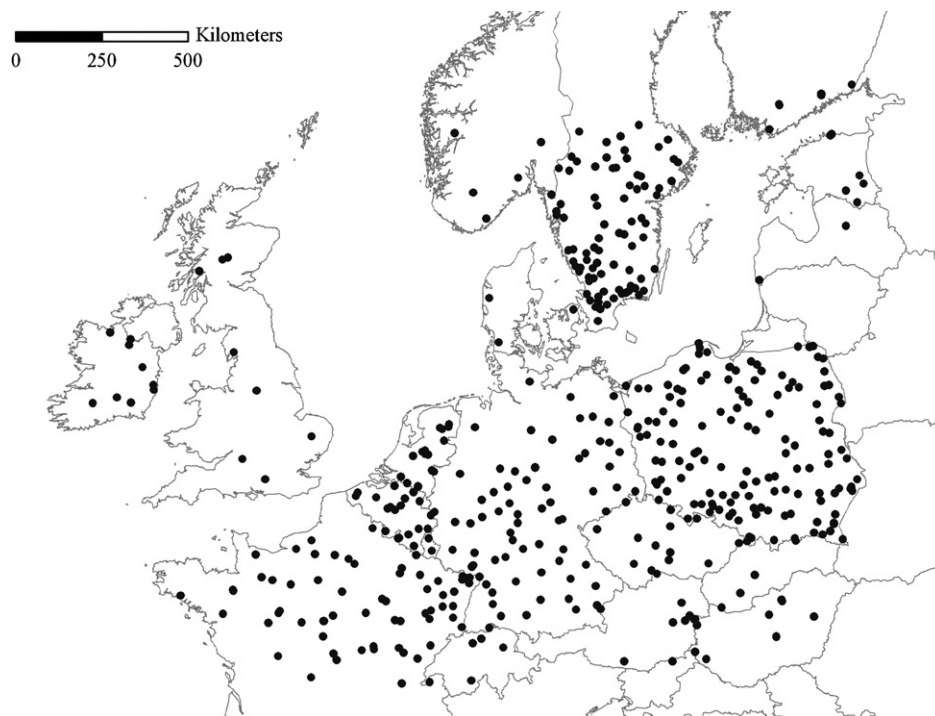


Fig. 1 – Map of the locations of the processed sample of Level II plots.

Table 1 – Soil and deposition parameters extracted from the Level II database of ICP Forests

| Parameter | Unit | Explanation |
|-------------------------------|-----------------------|--|
| Soil solid phase | | |
| C_m | $g\ kg^{-1}$ | Organic carbon concentration in the upper mineral soil layer |
| N_m | $g\ kg^{-1}$ | Total nitrogen concentration in the upper mineral soil layer |
| BCE_{m01} | $cmol\ (+)\ kg^{-1}$ | Sum of basic exchangeable cations in the upper 10 cm of the mineral soil layer |
| CEC_{m01} | $cmol\ (+)\ kg^{-1}$ | Cation exchange capacity of the upper 10 cm of the mineral soil layer |
| $Basesat_{m01}$ | % | Base saturation of the upper 10 cm of the mineral soil layer |
| C_{org_o} | $g\ kg^{-1}$ | Organic carbon concentration of the organic layer |
| C/N_{m01} | | C/N ratio of the upper 10 cm of the mineral soil layer |
| C/N_o | | C/N ratio of the organic layer |
| pH_o | | pH value in 0.01 M $CaCl_2$ of the organic layer |
| pH_{m01} | | pH value in 0.01 M $CaCl_2$ for the upper 10 cm of the mineral soil layer |
| Annual throughfall deposition | | |
| N_{depo} | $kg\ ha^{-1}\ a^{-1}$ | Mean annual nitrogen throughfall deposition |
| NH_4-N_{depo} | $kg\ ha^{-1}\ a^{-1}$ | Mean annual NH_4-N throughfall deposition |
| NO_3-N_{depo} | $kg\ ha^{-1}\ a^{-1}$ | Mean annual NO_3-N throughfall deposition |

Typical forest floor species were also included, even if they were larger than 0.5 m in height. Nomenclature follows Tutin et al. (1968/1980, 1993). Species abundance information was transformed into cover percentages according to the ICP Forests manual (Anonymous, 2002), if any of the various cover-abundance scales (e.g. Braun-Blanquet, 1964; Londo, 1976) was used. Epigeic mosses and lichens were also registered, however, not included.

Mean indicator values for soil reaction (mR), the availability of soil nitrogen (mN), radiation (light, mL) and moisture (mF) were calculated for each relevé from all present vascular plant species for which an indicator value according to Ellenberg (1992) was available. Weighting by cover degrees did not improve any relationship, thus unweighted means of indicator values were used.

Parameters on key factors of the soil solid phase were extracted from the Level II monitoring data base (Table 1, see also De Vries et al., 2003a). Respective values were available for 472 plots from the finally used 488 plots with vegetation records, while measured throughfall deposition were available for 224 of these plots. Data transformations and statistical interference analyses among indicator values and between indicator values, respectively deviated items on one side and soils or deposition parameters on the other side were performed with SAS 9.1 using correlation analysis and simple or multiple regression.

3. Results

In total 810 vascular plant species were registered at the 488 relevés. Most relevés reveal species numbers below 30, while the maximum was 128 species (for more general results see Seidling et al., in review). Due to some species without respective indicator values and unidentified taxa the number of plots with mean indicator values is always smaller than 488 (cf. Table 2).

Significant correlations between the mean indicator values from all available plots reflect ties between certain ecosystem features (Table 2). The closest relationship exists between mR and mN, and only mR and mF show no significant relationship.

There are also a number of close correlations between all kinds of indicator values and measured soil and deposition parameters (Table 3). The mean indicators for soil reaction show significant correlations with the measured nitrogen concentration, and cation exchange capacity. With a correlation coefficient of 0.765 the relationship between mR and the pH in the organic layer is especially tight, as is the relationship between mR and base saturation. The closer examination of the mR and pH_o values shows, as to expect, a rather linear relationship over the total pH span (Fig. 2). mL is negatively correlated with soil parameters that indicate high nitrogen and base cation supply, such as pH, base saturation, and cation exchange capacity. This is in line with the correlations between mL on one side and the mR and mN on the other side (Table 2). The indicator for soil moisture is only weakly related to the measured soil and deposition parameters.

Mean nitrogen indicator values are significantly correlated with all measured parameters indicating dependencies of plant available nitrogen within the soil from a multitude of environmental factors. From soil parameters, the closest correlation was found between mN and pH in the organic layer. A more detailed examination of this relationship shows a constant increase from very acidic to slightly acidic soils and a flatter progression at higher pH values, which can be adequately described by a quadratic regression (Fig. 3). The correlation between mN and pH in the organic layer, respectively base saturation is closer than those between mN and N soil concentration. Among the fractions of N deposition, nitrate throughfall deposition reveals the closest

Table 2 – Correlation coefficients of mean indicator values calculated from 488 plots located in the nemoral zone of Europe

| | mF | mR | mN |
|----|-----------------|------------------|------------------|
| mL | -0.1413** (475) | -0.3880*** (482) | -0.4759*** (484) |
| mF | | 0.0166 (470) | 0.1843*** (473) |
| mR | | | 0.7954*** (481) |

() number of valid cases; (Prob > |r|) ≤ 0.05; ** (Prob > |r|) ≤ 0.01; *** (Prob > |r|) < 0.0001.

Table 3 – Correlation coefficients for mean indicator values calculated from 488 plots located in the nemoral zone of Europe and measured environmental factors of the soil solid phase and mean annual throughfall deposition; (): n of valid cases

| | mL | mF | mR | mN |
|---|------------------|-----------------|-----------------|-----------------|
| Soil solid phase | | | | |
| N_m | -0.3308*** (471) | 0.1329** (458) | 0.3328*** (466) | 0.3759*** (467) |
| BCE_{m01} | -0.2364*** (469) | -0.0345 (456) | 0.5311*** (464) | 0.3412*** (465) |
| CEC_{m01} | -0.2918*** (467) | 0.0679 (454) | 0.4250*** (462) | 0.3619*** (463) |
| $Basesat_{m01}$ | -0.2246*** (464) | -0.0544 (451) | 0.7555*** (459) | 0.5028*** (460) |
| pH_o | -0.3439*** (472) | -0.0249 (459) | 0.7648*** (466) | 0.5697*** (468) |
| pH_{m01} | -0.2064*** (472) | -0.1660** (459) | 0.5795*** (466) | 0.3426*** (468) |
| Mean annual throughfall deposition | | | | |
| xN_{depo} | 0.2423** (224) | 0.1740* (213) | 0.0795 (219) | 0.2402** (220) |
| xNH_4-N_{depo} | 0.2901*** (224) | 0.1833** (213) | 0.0384 (219) | 0.1794** (220) |
| xNO_3-N_{depo} | 0.0970 (224) | 0.1073 (213) | 0.1776** (219) | 0.3196*** (220) |

(Prob > |r|) ≤ 0.05; ** (Prob > |r|) ≤ 0.01; *** (Prob > |r|) < 0.0001.

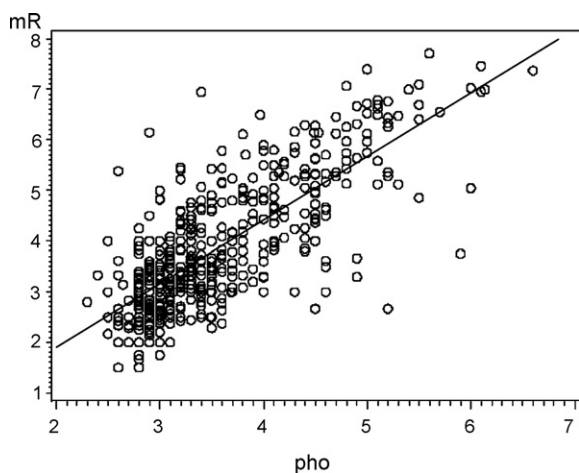


Fig. 2 – Relationship between mean indicator values for soil reaction and pH_o for $n = 466$ plots, $R^2 = 0.5849$, regression: $mR = -0.6260 + 1.2602pH_o$.

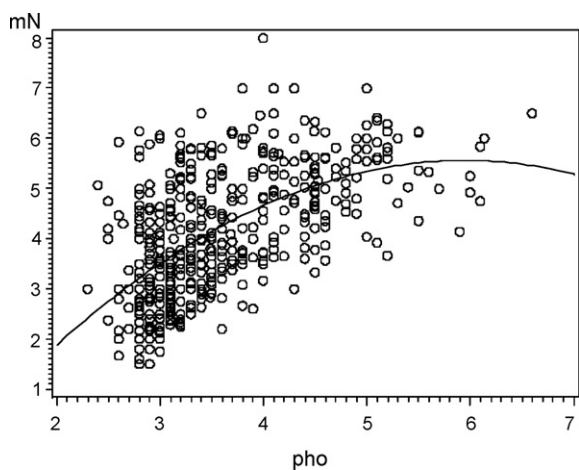


Fig. 3 – Relationship between mean indicator values for nitrogen and pH_o for $n = 468$, $R^2 = 0.3443$, regression: $mN = -2.7799 + 2.8000pH_o + 0.2352pH_o^2$.

relationships with mN. The respective relationship with bulk nitrogen deposition (not shown) is considerably weaker.

In a further step the residuals from the linear – and even more suitable – quadratic regression between mN and pH_o were calculated. These were regressed against soil and deposition parameters (Table 4). The closest relationship was found between these residuals from a quadratic regression and total N throughfall deposition (Fig. 4). Separate correlations for nitrate and ammonium were slightly weaker, however, distinctively closer than the relationship between mean N indicator values and total N deposition (Table 4). Residuals from the relationship between mN and mR values (the latter as a surrogate for the pH_o) were also regressed against nitrogen throughfall deposition. The correlations were significant as well, but less tight.

4. Discussion

Two questions have critically been annotated in connection with the use of indicator values. The first concerns the calculation of arithmetic means from ordinal numbers as species-specific Ellenberg values. The application of medians or indices derived from frequency distributions of indicator values instead of means has at times been recommended (Möller, 1987, 1992, 1997; Kowarik and Seidling, 1989) and was sometimes applied (e.g. Kreyer and Zerbe, 2006). Since median values produce additional stochastic noise due to their rough scaling, weighted median values or robust mean values (like Tukey's biweight) are rather sophisticated and may differ in most cases only slightly from mean values. Therefore there is practically no substantial argument against the use of average values. The calculation of unweighted mean values (without consideration of cover degrees) is most customary (Diekmann, 2003) and especially recommended, if data are collected by different surveyors (see Lepš and Hadinocová, 1992 for interpersonal differences of cover degree estimates) and, moreover, on plots of different sizes like in the case of these Level II data (De Vries et al., 2003a; Seidling, 2005).

The question of the applicability of Ellenberg indicator values over geographically huge areas has often been raised, because the values were originally designed for central

Table 4 – Correlation coefficients for residuals from the linear and quadratic regression models of mean N indicator values and pH_o on one side (indicator values were derived from the vegetation assessments; all records from the nemoral forest region, if more than one record per plot was taken, the last record has been chosen) and key factors characterising the soil solid phase (organic layer and upper mineral layer) and mean throughfall deposition on the other side

| | Residuals of mN on pH _o | |
|-------------------------------------|------------------------------------|---------------------------------|
| | From linear regression model | From quadratic regression model |
| Mean annual throughfall deposition | | |
| xN _{depo} | 0.4000*** (210) | 0.4310*** (210) |
| xNH ₄ -N _{depo} | 0.3644*** (210) | 0.3899*** (210) |
| xNO ₃ -N _{depo} | 0.3860*** (210) | 0.4194*** (210) |

*(Prob > |r|) ≤ 0.05; ***(Prob > |r|) < 0.0001.

Germany (Ellenberg, 1992). As species-habitat relations are not totally constant over geographical space (Walter and Walter, 1953), alternative systems have been developed (e.g. Zolyomi et al., 1967; Landolt, 1977; Böhling et al., 2002) or regional modifications have been proposed (e.g. Ertsen et al., 1998; Diekmann, 1995; Hill et al., 2000). Nonetheless, mainly original values are applied at least in nemoral and boreal Europe. Godefroid and Dana (2007) reported on problems with light, temperature, and moisture values within the Mediterranean region. As soil-related indicator values refer to comparatively general ecological features, the indicator system seems to inhere a considerable generality across phytogeographical units or habitat types and might be interpreted as a kind of simplified enumeration of niche theory (cf. Hill et al., 2000). The ecological behaviour of different plant species seems at least not to deviate systematically over geographical space, thus obviously levelling off respective deviances due to single species in the nemoral and subboreal part of Europe. As shown for the trans-national Level II data set, the original mean Ellenberg indicator values for soil conditions are as closely related to measured soil parameters as in regional studies (Seidling and Rohner, 1993; Härdtle et al., 2004). Also the above presented results reveal that respective plot-related mean

indicator values seem to indicate sufficiently accurate over wide geographical scales, justifying their use at least over large non-Mediterranean parts of Europe.

The intercorrelations between different mean Ellenberg indicators reflect ties between certain ecosystem features within forests. Besides the examples given in the result part, stands with better water supply (higher mF) coincide with low mL probably due to denser crown layers. For wet and very wet soils this relationship is reversed, therefore the respective over-all relationship is weak. The similar relationships exist between mL and mR respectively mN. On soils rich in basic cations or rich in available nitrogen tree crowns should be denser resulting in less light reaching the forest floor.

A very strong relationship ($r = 0.795$) exists between mR and mN. Analogue relationships have previously been found (e.g. Ellenberg, 1992; Seidling and Rohner, 1993) and was similarly already described by Schönhar (1952). The relationship is almost linear from very acidic to weakly acidic soils. For weakly acidic to neutral soils this relationship flattens and becomes even reversal at the alkaline side of this gradient. This relationship is physically based on the complex interplay between N mineralisation and the availability of base cations (e.g. Runge, 1965; Kriebitzsch and Bühmann, 1978). Very acidic soils with usually poor nitrogen supply (mainly as ammonia) store over time considerable amounts of organically bound N due to impeded mineralization. Relative high N-mineralisation (predominantly as nitrate) is found in slightly acidic, base rich soils. On calcareous soils typically decreasing nitrification rates are found.

The close relationship between mean indicators for acidity and nitrogen availability is fairly confirmed by the found relationships between respective indicator values and measured soil parameters. The close correlation between mR and pH especially of the organic layer and base saturation of the upper soil is a strong support for the empirically derived Ellenberg indicators for soil reaction even on a scale across large parts of Europe. Typically, mN values are also closely related to pH. This relationship confirms the principally close causal relationships between N mineralization and soil acidity status. Even the separation of calcifuge and calcicole species may partly depend on the availability of ammonia on one side and nitrate on the other side respectively their ratios (Schäfer, 1989; Diekmann and Falkengren-Grerup, 1998). The discussion, what ecophysiologically separates calcifuge and calcicole species has a long tradition (Ellenberg, 1964; Runge, 1965; Kinzel, 1983), however, shall not be deepened here. A rather weak relationship exists between mN and the N concentration

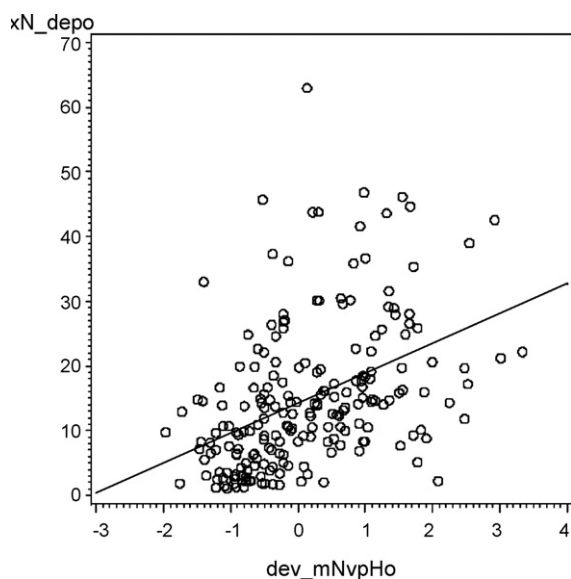


Fig. 4 – N throughfall deposition [kg ha⁻¹ a⁻¹] over residuals from the quadratic regression model between N indicator values and pH in the organic layer; R² = 0.186; n = 210; regression: xN_{depo} = 14.246 + 4.620 dev_{mNvpHo}.

in the solid phase of soils. This apparent contradiction is based on immobilisation of N in unproductive acidic soils leading to high stocks of organically bound N within the upper soil and litter layer, but low availability of mineralised N.

There is a number of plots with acid substrates where indicators of the ground vegetation suggest unexpected high nitrogen availability. This has led to the idea to relate residuals from the regression between mean nitrogen indicator values and measured pH of the soil (or reaction indicator values as a substitute). Under natural/undisturbed conditions, there should be the described close and steady relationship between the amount and quality of mineralised nitrogen and soil pH. Even if reasons for deviations of both nitrogen availability and N indicators can be manifold, positive deviances (residuals) from a respective regression should at least partly indicate any surplus of nitrogen availability for plants in comparison to the natural/unchanged N status. In this context, the input of air-borne nitrogen should also enhance the availability of nitrogen in forest soils (e.g. Gundersen et al., 1998; Van Dobben et al., 1999; Strengbom et al., 2003) a process quoted as eutrophication and frequently brought in connection with ecosystem changes. Also any kind of small- to medium-scale disturbance, especially when accompanied by higher radiation reaching the forest floor due to canopy opening (effects covered partially by the intermediate disturbance hypothesis of Connell (1978)) as well as other impacts like liming may foster N mineralisation in soils (Marschner et al., 1992; Dulière et al., 1999). Response of the phytocoenosis/plants which finally leads to an increase of N indicating plants might be based on different processes like activation of the soil seed bank (Hintikka, 1987), availability of open space, or shifts of competitive relationships among present plant species (ruderals sensu Grime, 1979; see also Jensch, 2004). These will subsequently lead to an increase of the number of N indicating plants. Contrariwise, erosion or historic respectively recent litter racking can be taken as processes, which may lower the N status of a site in comparison to its potential nutrient status and should finally lead to negative residuals.

Combined evaluations of mN and mR indicator values have already been suggested by Möller (1987). However, he concentrates on multiplicative effects of both features brought in relation to decomposition within soils like urease activity. Only residuals of the relationship between soil acidity and nitrogen availability, either expressed as mN–pH_o or as mN–mR relationship as a substitute, can be regarded as a measure for any surplus of the availability of nitrogen. These residuals were significantly related to nitrogen deposition which supports the hypothesis that nitrogen deposition can enhance N availability. Mean N indicator values itself were not as closely related to nitrogen deposition as the above denoted residuals. This shows that mN values alone do not allow a differentiation of the underlying mechanisms of nitrogen surplus supply in soils, as they are mainly related to natural and undisturbed site conditions and their specific N status.

5. Outlook

Environmental policy does not only require data on atmospheric deposition, but information on effects of these inputs as

well. There is no doubt that sampling and chemical analysis of soil condition and deposition and the simultaneous assessment of biological ecosystem components such as ground vegetation allow for a comparatively accurate quantification of actual inputs (Draaijers and Erisman, 1995) and assessments of different biotic responses. However, such extensive investigations will remain limited to intensive monitoring plots. Only indirect methods are applicable at larger numbers of plots or – in connection with up-scaling approaches – even for areas. Based on the plotwise deviation from the mN–pH_o relationship this study suggests an estimation of N deposition and its effects on vegetation based on a simple soil parameter in combination with vegetation data, without actually measuring deposition itself, even if deposition is certainly not the only possible reason for deviations from this naturally close relationship. It might even be possible to rate deposition effects based solely on ground vegetation assessments by establishing a mN–mR relationship. However, in this case some additional statistical noise has to be accepted.

Vegetation data collected within the forest condition monitoring under ICP Forests and EU provides a large potential to further verify this approach. Within the ongoing BioSoil demonstration project, surveys of the soil solid phase and ground vegetation are performed at ca. 5000 representatively arranged forest monitoring sites in Europe. The approach presented in this study is recommended to be applied to such data. Additional applications for the presented method are integrated evaluations, examining the relations of the described residuals to other indicators for forest condition, such as data on forest growth or defoliation. Cross-checks with evaluation from other large-scale environmental programmes like the initiative of ICP Vegetation (WGE, 2004) to measure nitrogen contents of mosses collected at Level II forest sites (Schröder et al., 2007), might also be adapted to perform cross-checks of results achieved with the method described above. If the shown relationships can further be substantiated, we may obtain a rather comfortable means to calculate changes from nitrogen inputs on forests and probably other land use types over large areas in the future.

Acknowledgements

The project was subsidised by the European Commission under its Forest Focus regulation (EC) Nr. 2152/2003. Dr. Volker Mues and Oliver Granke are acknowledged for extracting respective data from the ICP Forests data base and Oliver Granke for providing a map, Dr. Wolf-Ulrich Kriebitzsch for his constructive statements on an earlier version of this paper and two anonymous reviewers for valuable comments.

REFERENCES

-
- Anonymous, 2002. Assessment of ground vegetation. In: PCC (Programme Co-ordinating Centre, 1998 and later up-dates): manual on methodologies and criteria for harmonised sampling, assessment, monitoring and analysis of the effects of air pollution on forests, fourth ed., UNECE, Hamburg, Part 8.

- Böhling, N., Greuter, W., Raus, T., 2002. Zeigerwerte der Gefäßpflanzen der Südägäis (Griechenland). *Braun-Blanquetia* 32, 108.
- Braun-Blanquet, J., 1964. Pflanzensoziologie. Grundzüge der Vegetationskunde. 3. Aufl. Springer, Berlin, 865 pp.
- Bull, K.R., Achermann, B., Chrast, R., Fenech, G., Forsius, M., Gregor, H.-D., Guardans, R., Haussmann, T., Hayer, F., Hettelingh, J.-P., Johannessen, T., Krzyzanowski, M., Kucera, V., Kvaeven, B., Lorenz, M., Lundin, L., Mills, G., Posch, M., Skjelvåle, B.L., Ulstein, M.J., 2001. Coordinated effects monitoring and modelling for developing and supporting international air pollution control agreements. *Water Air Soil Pollut.* 130, 119–130.
- Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. *Science* 199, 1302–1310.
- De Vries, W., Vel, E.M., Reinds, G.J., Deelstra, H., Klap, J.M., Leeters, E.E.J.M., Hendriks, C.M.A., Kerkvoorden, M., Landmann, G., Herkendell, J., Haußmann, T., Erisman, J.W., 2003a. Intensive monitoring of forest ecosystems in Europe. 1. Objectives, set-up and evaluation strategy. *For. Ecol. Manage.* 174, 77–95.
- De Vries, W., Reinds, G.J., Posch, M., Sanz, M.J., Krause, G.H.M., Calatayud, V., Renaud, J.P., Dupouey, J.L., Sterba, H., Vel, E.M., Dobbertin, M., Gundersen, P., Voogd, J.C.H., 2003b. Intensive Monitoring of Forest Condition in Europe: Technical Report 2003. UN-ECE, EC, Brussels, Geneva, 161 pp.
- Diekmann, M., 1995. Use and improvement of Ellenberg's indicator values in deciduous forests of the Boreo-nemoral zone in Sweden. *Ecography* 18, 178–189.
- Diekmann, M., 2003. Species indicator values as an important tool in applied plant ecology—a review. *Basic Appl. Ecol.* 4, 493–506.
- Diekmann, M., Falkengren-Grerup, U., 1998. A new species index for forest vascular plants: development of functional indices based on mineralization rates of various forms of soil nitrogen. *J. Ecol.* 86, 269–283.
- Draaijers, G.P.J., Erisman, J.W., 1995. A canopy budget model to estimate atmospheric deposition from throughfall measurements. *Water Air Soil Pollut.* 85, 2253–2258.
- Dulière, J.-F., Carnol, M., Dalem, S., Remacle, J., Malaisse, F., 1999. Impact of dolomite lime on the ground vegetation and on potential net N transformations in Norway spruce (*Picea abies* [L.] Karst.) and sessile oak (*Quercus petraea* [Matt.] Lieb.) stands in the Belgian Ardenne. *Ann. For. Sci.* 56, 361–370.
- ETC/BD, 2005. EU Headline Biodiversity Indicators Monitoring Programmes in Europe. Final Draft Report. ECNC (European Centre for Nature Conservation), Tilburg (The Netherlands), 72 p.
- Ellenberg, H., 1964. Stickstoff als Standortfaktor. *Ber. Dt. Bot. Ges.* 77, 82–92.
- Ellenberg, H., 1992. Zeigerwerte der Gefäßpflanzen ohne Rubus. *Scripta Geobot.* 18, 9–166.
- Ellenberg Jr., H., 1983. Gefährdung wildlebender Pflanzen in der Bundesrepublik Deutschland. Versuch einer ökologischen Betrachtung. *Forstarchiv* 54, 127–133.
- Ertsen, A.C.D., Alkemade, J.R.M., Wassen, M.J., 1998. Calibrating Ellenberg indicator values for moisture, acidity, nutrient availability and salinity in The Netherlands. *Plant Ecol.* 135, 113–124.
- Godefroid, S., Dana, D., 2007. Can Ellenberg's indicator values for Mediterranean plants be used outside their region of definition. *J. Biogeogr.* 34, 62–68.
- Gönnert, T., 1989. Ökologische Bedingungen verschiedener Laubwaldgesellschaften des Nordwestdeutschen Tieflandes. *Dissertationes Botanicae* 136, 1–224.
- Grime, J.P., 1979. *Plant Strategies and Vegetation Processes*. Wiley, Chichester.
- Gundersen, P., Emmett, B.A., Kjonaas, O.J., Koopmans, C.J., Tietema, A., 1998. Impact of nitrogen deposition on nitrogen cycling in forests: a synthesis of NITREX data. *Forest Ecol. Manage.* 101, 37–55.
- Härdtle, W., von Oheimb, G., Friedel, A., Meyer, H., Westphal, C., 2004. Relationship between pH-values and nutrient availability in forest soils—the consequences for the use of ecograms in forest ecology. *Flora* 199, 134–142.
- Hill, M.O., Roy, D.B., Mountford, J.O., Bunce, R.G.H., 2000. Extending Ellenberg's indicator values to a new area: an algorithmic approach. *J. Appl. Ecol.* 37, 3–15.
- Hintikka, V., 1987. Germination ecology of *Galeopsis bifida* (Lamiaceae) as a pioneer species in forest succession. *Silva Fennica* 21, 301–313.
- Jensch, D., 2004. Der Einfluss von Störungen auf Waldbodenvegetation. *Diss. Bot.* 386, 388.
- Kinzel, H., 1983. Influence of limestone, silicates and soil pH on vegetation. *Encyclopedia Plant Physiol.* NS 12c, 201–244.
- Kowarik, I., Seidling, W., 1989. Zeigerwertberechnungen nach Ellenberg – zu Problemen und Einschränkungen einer sinnvollen Methode. *Landschaft und Stadt* 21, 132–143.
- Kriebitzsch, W.-U., Bühmann, H., 1978. Stickstoff-Mineralisation im Boden eines Eichen-Buchen-Waldes und eines Kiefernforstes in der nordwestdeutschen Tiefebene. *Forstwiss. Cbl.* 108, 255–270.
- Kreyer, D., Zerbe, S., 2006. Short-lived tree species and their role as indicators for plant diversity in the restoration of natural forests. *Restoration Ecol.* 14, 137–147.
- Kuhn, N., Amiet, R., Hufschmid, N., 1987. Veränderungen in der Waldvegetation der Schweiz infolge Nährstoffanreicherung aus der Atmosphäre. *Allg. Forst- u- Jagd-Ztg.* 158, 77–84.
- Landolt, E., 1977. Ökologische Zeigerwerte zur Schweizer Flora. *Veröff. Geobot. Inst. ETH Stiftung Rübel* 64, 1–208.
- Lepš, J., Hadinocová, V., 1992. How reliable are our vegetation analyses? *J. Veg. Sci.* 3, 119–124.
- Londo, G., 1976. A decimal scale for relevés of permanent quadrats. *Vegetatio* 33, 61–64.
- Lorenz, M., Fischer, R., Becher, G., Mues, V., Seidling, W., Riedel, T., Kraft, P., 2006. Forest condition in Europe. Technical Report of ICP Forests. *Work Report Institute for World Forestry* 2006/1, 113 p.
- Marschner, B., Stahr, K., Renger, M., 1992. Lime effects on pine forest floor leachate chemistry and element fluxes. *J. Environ. Qual.* 21, 410–419.
- Mellert, K.-H., Kölling, C., Rehfuess, K.E., 1998. Vegetationsentwicklung und Nitrataustrag auf 13 Sturmflächen in Bayern. *Forstarchiv* 69, 3–11.
- Mladenoff, D.J., 1987. Dynamics of nitrogen mineralization and nitrification in hemlock and hardwood treefall gaps. *Ecology* 68, 1171–1180.
- Möller, H., 1987. Beziehungen zwischen Vegetation und Humuskörper in der Eilenriede (Hannover), einem Stadtwald mit menschlich beeinflussten Böden. *Tuexenia* 7, 427–446.
- Möller, H., 1992. Zur Verwendung des Medians bei Zeigerwertberechnungen nach Ellenberg. *Tuexenia* 12, 25–28.
- Möller, H., 1997. Reaktions- und Stickstoffzahlen nach Ellenberg als Indikatoren für die Humusform in terrestrischen Waldökosystemen im Raum Hannover. *Tuexenia* 17, 349–365.
- Runge, M., 1965. Untersuchungen über die Stickstoff-Nachlieferung an nordwestdeutschen Waldstandorten. *Flora* 155, 353–386.
- Schäfer, H., 1989. Untersuchungen zur potentiellen Stickstoffnettomineralisation in nordhessischen und südniedersächsischen Buchenwäldern. *Verh. Ges. Ökol.* 17, 353–363.

- Schönhar, W., 1952. Untersuchungen über die Korrelation zwischen der floristischen Zusammensetzung der Bodenvegetation und der Bodenazidität sowie anderen Bodenfaktoren. *Mitt. Ver. forstl. Standortskartierung* 2, 1–23.
- Schröder, W., Hornsmann, I., Pesch, R., Schmidt, G., Markert, B., Fränze, S., Wünschmann, S., Heidenreich, H., 2007. Nitrogen and metals in two regions in central Europe: significant differences in accumulation in mosses due to land use? *Environ. Monit. Assess.* 133, 495–505.
- Seidling, W., 2005. Ground floor vegetation assessment within the intensive (Level II) monitoring of forest ecosystems in Germany: change and challenges. *Eur. J. Forest Res.* 124, 301–312.
- Seidling, W., Fischer, R., Granke, O., in review. Forest floor vegetation on ICP Forests monitoring plots in Europe and its relation to atmospheric deposition, *Int. J. Environ. Stud.*
- Seidling, W., Rohner, M.-S., 1993. Zusammenhänge zwischen Reaktions-Zeigerwerten und bodenchemischen Parametern am Beispiel von Waldbodenvegetation. *Phytocoenologia* 23, 301–317.
- Strengbom, J., Walheim, M., Näsholm, T., Ericson, L., 2003. Regional differences in the occurrence of understorey species reflect nitrogen deposition in Swedish forests. *Ambio* 32, 91–97.
- Tutin, T.G., Heywood, V.H., Burges, N.A., Moore, D.M., Valentine, D.H., Walters, S.M., Webb, D.A., 1968–1980. *Flora Europaea*. vol. 2–5, Cambridge University Press, Cambridge.
- Tutin, T.G., Burges, N.A., Chater, A.O., Edmondson, J.R., Heywood, V.H., Moore, D.M., Valentine, D.H., Walters, S.M., Webb, D.A., 1993. *Flora Europaea*, vol. 1. Cambridge University Press, 581 pp.
- Van Dobben, H.F., ter Braak, C.J.F., Dirksen, G.M., 1999. Undergrowth as a biomonitor for deposition of nitrogen and acidity in pine forests. *For. Ecol. Manage.* 114, 83–95.
- Walter, H., Walter, E., 1953. Einige allgemeine Ergebnisse unserer Forschungsreise nach Südwestafrika 1952/53. *Das Gesetz der allgemeinen Standortskonstanz; das Wesen der Pflanzengemeinschaften*. *Ber. Dt. Bot. Ges.* 66, 228–236.
- WGE (Working Group on Effects), 2004. Review and assessment of air pollution effects and their recorded trends. Working Group on Effects, Convention on Long-range Transboundary air pollution. National Environment Council, United Kingdom, 56 p.
- Zolyomi, B., Barath, Z., Fekete, G., Jakucs, P., Karpati, I., Kovacs, M., Mate, I., 1967. Einreihung von 1400 Arten der ungarischen Flora in ökologische Gruppen nach TWR-Zahlen. *Fragm. Bot. Mus. Hist. Nat. Hung.* 4, 101–142.