PERSPECTIVE

Evaluation of forest nutrition based on large-scale foliar surveys: are nutrition profiles the way of the future?†

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This paper introduces the use of nutrition profiles as a first step in the development of a concept that is suitable for evaluating forest nutrition on the basis of large-scale foliar surveys. Nutrition profiles of a tree or stand were defined as the nutrient status, which accounts for all element concentrations, contents and interactions between two or more elements. Therefore a nutrition profile overcomes the shortcomings associated with the commonly used concepts for evaluating forest nutrition. Nutrition profiles can be calculated by means of a neural network, *i.e.* a self-organizing map, and an agglomerative clustering algorithm with pruning. As an example, nutrition profiles were calculated to describe the temporal variation in the mineral composition of Scots pine and Norway spruce needles in Finland between 1987 and 2000. The temporal trends in the frequency distribution of the nutrition profiles of Scots pine indicated that, between 1987 and 2000, the N, S, P, K, Ca, Mg and Al decreased, whereas the needle mass (NM) increased or remained unchanged. As there were no temporal trends in the frequency distribution of the nutrition profiles of Norway spruce, the mineral composition of the needles of Norway spruce needles subsequently did not change. Interpretation of the (lack of) temporal trends was outside the scope of this example. However, nutrition profiles prove to be a new and better concept for the evaluation of the mineral composition of large-scale surveys only when a biological interpretation of the nutrition profiles can be provided.

Introduction

Forests are complex ecosystems. Gaining an insight into the condition of forests and the assessment of the future development of forests under the present and predicted environmental scenarios requires large data sets from long-term monitoring programmes. At present several large-scale forest monitoring programmes exist globally, *i.e.* the International Cooperative Programme on the Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests) in Europe and North America, Forest Focus in the EU, the Acid Deposition Monitoring Network in East Asia, and the Forest Health Monitoring Programme in the USA. Owing to the relationships between the environment and the foliar mineral composition, these programmes monitor, among other ecosystem components, the mineral composition of tree foliage. As a result, these programmes have over the years built up large data sets of the mineral composition of tree foliage.

Experiments under controlled conditions have shown relationships between the mineral composition of tree foliage and, for example, N deposition,[1] and the ozone[2] and CO_2 concentration[3] in the environment. Carefully designed experiments allow the quantification of the joint effect of two or three environmental characteristics on the mineral composition of tree foliage, *e.g.* ozone and drought,[4] ozone and a limited N availability,[5] CO_2 and ozone,[6,7] SO_2 and NO_2,[8] and ozone, P and drought.[9] However, when long-term environmental changes are monitored, the controlled conditions of designed experiments are replaced with complex real-world conditions. The relationships between the environmental characteristics and the mineral composition of tree foliage are, to some extent, less clear in monitoring programmes under real-word conditions than in designed experiments.[10] Foliage analyses in monitoring programmes fall short of the expectations raised by foliage analyses in designed experiments. In monitoring programmes, the relationships observed in controlled experiments are probably buried in the variability caused by planning, sampling, sample preparation, instrumental analysis and data evaluation.[11] When a quality assurance programme eliminates these sources of variation, the significance of foliar mineral analysis as a tool for environmental monitoring largely depends on the concept used to evaluate the data, *i.e.* Critical Range, Nutrient–Element Balance, *etc.* At present, most of the commonly used concepts have one or several shortcomings (see further). Although, these shortcomings can be surmounted by the experimental control of designed experiments, they make evaluation of the mineral composition of foliage in monitoring programmes relatively problematic.

This study introduces the use of nutrition profiles as a first step in the development of a more complete concept to evaluate forest nutrition on the basis of large-scale foliar surveys. The aims are: (1) to define and explain the concept of the nutrition profile, and (2) to describe a mathematical method that can be used in calculating nutrition profiles. These ideas are then applied to describe the temporal variability in the mineral composition of a foliar survey of 16 Norway spruce (*Picea Abies* (L.) Karst) and 20 Scots pine (*Pinus sylvestris* L.) stands carried out in Finland between 1987 and 2000. The major questions to be addressed in this example are: (1) did the mineral composition of tree foliage change between 1987 and 2000 and, if so, (2) how did the foliar nutrient concentration change?

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Concepts for the evaluation of forest nutrition

Irrespective of which statistical methods are used, *i.e.* analysis of variance, principal component analysis, cluster analysis *etc.*, the evaluation of foliar mineral composition is based on the well-known relationship between growth and the plant-available concentration of an element. This relationship has three regions: a deficient, an adequate and an excess range.[12] At a certain concentration of the element under study, the growth will be optimal when all other elements are available in non-limiting amounts. The element status of the plant is evaluated on the basis of the foliar concentration (x_1) of the element under study, and described as the vector $\boldsymbol{x} = [x_1]$, *e.g.* the Critical Range (CR) and Deviation from Optimal Percentage (DOP) concept.[13] When at least one element is limiting plant growth, alleviating the limiting growth factor results in a growth increase towards the optimal biomass. The interactions between elements are formalised as element ratios also known as the Nutrient–Element Balance concept.[14] An unbalanced ratio indicates that one of the factors is limiting growth. The element status of the plant is then evaluated by means of the ratios between two (x_1/x_2) or more ($x_1 + x_2/x_3$) foliar element concentrations, and it is described as the vector $\boldsymbol{x} = [x_1,x_2]$ or $\boldsymbol{x} = [x_1 + x_2,x_3]$. Diagnostic systems such as the Diagnosis and Recommendation Integrated System (DRIS)[15] and the Compositional Nutrient Diagnosis (CND)[16] are based on the concept that plant growth is controlled by the foliar concentrations of all the elements (x_1, x_2, x_3, ...x_d). DRIS and CND compute all the possible two-way nutrient ratios $\boldsymbol{x} = [x_2/x_1, x_3/x_1, \ldots x_d/x_1, x_3/x_2,\ldots x_d/x_2,\ldots x_{d-1}/x_d]$. Based on these ratios, DRIS calculates a single correction factor for all nutrients, whereas CND provides single correction factors for any nutrient ratio. When DRIS and CND are expanded to include nutrient concentrations, they can account for both the element concentrations and interactions between two elements. Although all of these concepts have proven to be useful, their use is limited by one or several conceptual shortcomings. The above-mentioned concepts either do not account for the interactions between elements and/or the fact that the growth of trees is controlled by the foliar concentrations (x_1, x_2, x_3, ...x_d) and contents of all elements ($x_1 \times$ FM, $x_2 \times$ FM, $x_3 \times$ FM,..., $xd \times$ FM), where FM is the foliar mass. As a consequence, we defined the nutrition profile of a tree or stand as the nutrient status, which accounts for all element concentrations, contents and interactions between two or more elements. The nutrition profile is formalised by the vector $\boldsymbol{x} = [x_1, x_2, x_3,\ldots, x_{d-1}, FM]$. Trees or stands with similar nutrition profiles form their own group. Each group k is characterised by a so-called group nutrition profile ($\bar{\boldsymbol{x}}_k$). The nutrition profile of evergreen trees $\boldsymbol{x} = [(x_1,\ldots,x_{d-1},FM)_C, (x_1,\ldots,x_{d-1}, FM)_{C+1},\ldots,(x_1\ldots,x_{d-1}, FM)_{C+N}]$ is more complicated than the profile of deciduous trees $\boldsymbol{x} = [x_1,\ldots,x_{d-1},FM]$ owing to the presence of a number of foliar age-classes (C, C + 1,..., C + N) in evergreens.

Method used to calculate the group nutrition profile ($\bar{\boldsymbol{x}}_k$)

A method that is suitable for calculating the group nutrition profile needs to account for all element concentrations, contents and interactions between two or more elements. Therefore it has to preserve the interactions between the elements of the vector $x = [x_1,x_2,x_3,\ldots,x_{d-1},FM]$. In other words, the method has to preserve the topology of the data set. If not, the aspect that makes the nutrition profile more complete than the other concepts is lost. We propose a clustering method[17] based on the distance matrix of a self-organizing map[18] as a method to calculate the group nutrition profile ($\bar{\boldsymbol{x}}_k$). The calculations are then as follows:

The data are normalized beforehand so that the mean of each variable is 0 and the variance becomes 1. The normalization method scales the data linearly, which preserves the structure of the absolute values of the measurements. The method which is used to normalize the data defines the distance between multidimensional vectors. For example, how should a change of 1 mg g^{-1} in nitrogen concentration be related to a change of 1 g in the weight of 1000 needles? Normalizing all the variances to unity solves this problem by defining that changes in different variables are equal if they are in equal proportion to their standard deviations. As a result, all variables have equal weights. This is technically convenient, but it has serious drawbacks in biological terms if the data processing methods seek an explanation of the variance, as in principal component analysis and other methods. However, the method applied in this study does not explain the variance of the data. The normalized data are only used to sort the observations. As further data processing and interpretation are based on the observed data, normalization does not have any drawbacks.

The normalized nutrition profile for each stand of the survey is described as $\boldsymbol{x}$. The vectors $\boldsymbol{x}$ are sorted with a self-organizing map (SOM).[18] Basically the SOM positions all the d-dimensional vectors $\boldsymbol{x}$ in a d-dimensional space. These positions in the d-dimensional space are projected on a 2-dimensional grid. A neighbourhood relationship controls the projection such that the topology of the data set is preserved. As a consequence vectors $\boldsymbol{x}$, which are close to each other in the d-dimensional space, will be close to each other in the 2-dimensional projection. The mathematical solution for the projection was formulated by Kohonen.[18] Usually, the SOM consists of a 2-dimensional regular grid of map units. Each map unit i is represented by a prototype vector, $\boldsymbol{m}_i = [m_{i1},\ldots,m_{id-1},FM_i]$, where d is the dimension of the input vector. The prototype vectors define a tessellation of the input space into a set of Voronoi sets $V_i = \{\boldsymbol{x} \| \|\boldsymbol{x} - \boldsymbol{m}_i\| < \|\boldsymbol{x} - \boldsymbol{m}_j\| \; \forall j \neq i\}$, where $\boldsymbol{x}$ are the data vectors and $\|\boldsymbol{x} - \boldsymbol{m}_i\|$ is the Euclidean norm. The SOM quantifies the training data set with a representative set of prototype vectors. Thus, each data vector belongs to the Voronoi set of the prototype vector to which it is most similar. The neighbourhood relationship, commonly a Gaussian neighbourhood function, controls the quantization process such that the topology of the data set is preserved. The whole algorithm can be regarded as a non-parametric, non-linear regression. Without the neighbourhood relationship the SOM algorithm reduces to the k-means clustering algorithm.[18]

The prototype vectors of the SOM are used to calculate a distance matrix, showing the median distances between neighbouring map units *i.e.* neighbouring nutrition profiles.

A clustering algorithm divides the vectors $\boldsymbol{x}$ into a limited number of groups. The U-matrix of the self-organizing map (SOM) is a commonly used tool to cluster the SOM visually.[19] Unfortunately, when humans identify clusters, the results obtained by different people are not necessarily the same. Therefore, an automated clustering algorithm which clusters the distance matrix of the SOM, is preferred:

(1) Local minima of the distance matrix are used as seed points for the base clusters. Local minima are the map units of which the median distance to neighbouring units is smaller than the median distance of any of the neighbouring units to their neighbours.

(2) A region-growing algorithm[17] finds the unassigned map unit with the smallest distance to a cluster, and assigns it to the corresponding cluster. The continuity constraint is used to ensure that the clusters form continuous areas on the map. Therefore, only map units are considered for merging when they neighbour a cluster. Assigning the unassigned map units is continued until all the map units belong to a cluster. This procedure provides a partitioning of the map into a set of base

clusters. The number of clusters equals the number of local minima in the distance matrix.

(3) A cluster hierarchy may represent the true structure of the data better than a single-level partitioning. Therefore, an agglomerative clustering algorithm[20] is used to construct the cluster hierarchy from the base clusters. This produces a binary tree, which may contain unrepresentative base clusters. Unrepresentative base clusters occur when the distance matrix has some local minima, which are products of random variations in the data rather than real local maxima of the probability density function.

(4) Unrepresentative base and intermediate clusters are removed from the hierarchy. The pruning procedure, which removes unrepresentative clusters from the hierarchy, is discussed in detail by Vesanto and Sulkava.[17] This procedure gives a pruned cluster tree together with measures of the clustering quality of the sub-cluster sets of each node in the tree.

(5) The group nutrition profile ($\bar{\boldsymbol{x}}_k$) is calculated as the vector with the average values of the nutrition profiles ($\boldsymbol{x}$) of the members of group k. The group nutrition profiles are calculated on the basis of the observed data.

The Finnish example

The concept and mathematical procedure explained above were applied to an example of a large-scale foliar survey carried out in Finland from 1987 to 2000. The example introduces the foliar survey and demonstrates the procedure for calculating group nutrition profiles. The quality and robustness of the data and calculations are tested, and further data processing to describe the temporal dynamics of the nutrition profiles is demonstrated.

The large-scale foliar survey 1987–2000

The survey was initiated as a part of the UN/ECE International Co-operative Programme on Assessment and Monitoring of Air pollution effects on Forests (ICP Forests). Needle samples were collected from 36 plots of the Finnish Level I network of ICP Forests.[21] The 36 stands, which were located on mineral soils in background areas in different parts of the country, were sampled annually between 1987 and 2000. Sixteen of the stands were dominated by Norway spruce (*Picea abies* Karst. (L.)) and 20 by Scots pine (*Pinus sylvestris* L.). In 1990 and 1991 only 6 and 15 stands were sampled, respectively. Five stands were felled during the 14 year period, and could no longer be sampled. These stands were replaced by five other Level I plots in the vicinity of the original stand. Foliar N, S, P, K, Ca, Mg and Al concentrations were determined on 367 composite samples. This means that 27% of the maximum possible number of 504 composite samples (36 plots × 14 years) were missing. The needle mass of 1000 needles (NM) was not measured in the years 1990 and 1991 with the result that 6% of the measurement sets did not contain NM.

Every year between October and November, the same two persons collected the needle samples from dominant or co-dominant trees in the stands. Ten trees were selected in each stand, and three branches with current- and previous-year shoots were cut with an 18 m long pruning device from the top third of the crown of each sample tree. The branches were stored in a freezer (−18 °C) during the period between sampling and pre-treatment. Pre-treatment was performed as follows: the branches were cut up in order to separate the shoots with different needle-year classes. Shoots with the same needle-year class of each tree were pooled and further treated as a separate sample. Each sample was then divided into two parts: three pine shoots per tree or five spruce shoots per tree for determining the needle mass (NM), and the rest of the sample for determining the foliar element concentrations. Needle mass was determined as follows: 10 needles were removed from each shoot and the needles dried for 24 h at 105 °C. 300 Scots pine needles or 500 Norway spruce needles were then weighed (10 trees per plot × 3 or 5 shoots per tree × 10 needles per shoot), and the weight converted to a 1000-needle basis. The foliar element concentrations were determined as follows: the shoots were dried at 40 °C for 10 days and the needles were then removed from the shoots. The needles were then ground using an ultracentrifugal mill (Retsch type Zm 1). The mesh diameter of the ring sieve was 1 mm. All 10 samples from the same year class on each plot were pooled by combining equal weights of needle powder from each tree. The elemental composition (N, S, P, K, Ca, Mg and Al) was determined on the pooled samples. In 1987 and 2000 the 10 trees from each plot were also analysed separately.

The samples from all sampling years were analysed in the same laboratories of the Finnish Forest Research Institute (the Central Laboratory, Vantaa, and the Parkano Research Station) by the same personnel. The N concentration of the needles was determined by the Kjeldahl method (Tecator Digester and Distilling Unit) between 1987 and 1994, and without further pre-treatment on a CHN analyser from 1995 onwards (1995–1998: LECO CHN-600 Analyser, 1999–2000: LECO CHN-2000 Analyser). Boron was determined by Azomethin H-reagent and a UV-VIS spectrophotometer between 1987 and 1997. The S, P, K, Ca, Mg and Al concentrations in the needles were determined, following wet digestion in HNO_3/H_2O_2, by inductively coupled plasma atomic emission spectroscopy (ICP-AES). From 1987 until 1997, digestion was performed by the Open Wet Digestion method (Thermolyne 2200 Hot Plate), followed by determination on an ARL 3580 ICP-emission spectrometer. Since 1998 the needle samples were digested by the Closed Wet Digestion method in a microwave (CEM MDS 2000). The analyses were then performed on a TJA Iris Advantage ICP-emission spectrometer. Unwashed needles were analysed, and the results were expressed per 105 °C dry weight.

Quality control

Between 1987 and 1995 the quality of the analytical methods was checked by means of method blanks, repeated measurement of internal reference samples, repeated measurement of certified reference samples and participation in inter-laboratory tests. The laboratories participated in 8 international (IUFRO International Forestry Sample Exchange) and 5 national (Finnish Forest Research Institute Inter-Calibration) inter-laboratory tests. In 1995 the quality assurance system was extended to include the repeated measurement of certified reference samples (CRM 101). Between 1995 and 2000, the laboratories participated in 14 international (International Plant-Analytical Exchange Programme, and ICP-Forests inter-laboratory ring tests) and one national (Finnish Forest Research Institute Inter-Calibration) inter-laboratory test. The methods used on the current and earlier instruments and equipment were validated with standards and older samples from inter-laboratory proficiency tests.

In total, the laboratory analysed 9 plant samples in national and 120 plant samples in international inter-laboratory tests between 1987 and 2000. The limited number of outliers (not given) showed that the relative quality, compared with other analytical laboratories working in the field of plant analysis, is good. During the same period the relative standard deviation (RSD), based on repeated measurements of 11 different internal control samples and a measure of the precision of the methods, ranged between 0.7 and 1.8% for N, 1.5 and 5.1% for S, 1.5 and 4.1% for P, 1.7 and 7.5% for K, 1.5 and 4.5% for Ca, 1.1 and 4.3% for Mg and 1.6 and 4.5% for Al. Since 1995, the accuracy of the analytical methods was determined by repeated measurements of a certified reference sample. The

Table 1 Average value ± half width of the 95% confidence interval of CRM 101 certified reference sample. N, S, P, Mg and Ca are expressed as $mg.kg^{-1}$ dry mass and Al as $\mu g.kg^{-1}$ dry mass

	N	S	P	Mg	Ca	Al
CRM 101						
Certified	18.89 ± 0.18	1.70 ± 0.04	1.69 ± 0.04	0.62 ± 0.09	4.28 ± 0.08	173 ± 5
1995 (4/10)[a]	17.7 ± 1.8	1.80 ± 0.09	1.81 ± 0.09	0.62 ± 0.04	4.10 ± 0.25	124 ± 11
1996 (10/10)[a]	18.6 ± 0.6	1.78 ± 0.04	1.77 ± 0.08	0.62 ± 0.04	4.31 ± 0.22	127 ± 11
1997 (7/5)[a]	18.8 ± 2.2	1.73 ± 0.14	1.81 ± 0.08	0.61± 0.10	4.39 ± 0.16	123 ± 16
1998 (5/14)[a]	18.8 ± 0.8	1.65 ± 0.16	1.75 ± 0.14	0.60 ± 0.06	4.09 ± 0.29	126 ± 9
1999 (23/23)[a]	19.2 ± 1.0	1.66 ± 0.09	1.79 ± 0.12	0.61± 0.02	4.22 ± 0.31	119 ± 17
2000 (10/10)[a]	19.1 ± 0.8	1.60 ± 0.06	1.74 ± 0.08	0.60 ± 0.02	4.15 ± 0.28	117 ± 15

[a] (number of repetitions for nitrogen/number of repetitions for S, P, Mg, Ca and Al).

accuracy for N, S, P, Ca and Mg satisfies the needs of this study (Table 1). The trend in the accuracy of the methods for determining S (Table 1) may have overestimated a decreasing trend in foliar S concentrations by 12% between 1995 and 1999. The recovery of Al was 30% too low compared with the certified Al concentration (Table 1). The low Al recovery is caused by not using HF in the sample digestion method. Nevertheless, the precision for Al (RSD of 4.5%) satisfies the needs of this study.

Calculation of the nutrition profiles

By definition, nutrition profiles contain the element concentration of all elements and the total foliar biomass (FM). Needle samples were analysed for N, S, P, K, Ca, Mg and Al, in this survey. Therefore, a nutrition profile with the N, S, P, K, Ca, Mg, Al concentrations and FM is likely to best represent the structure of the data set. However, the number of repetitions (367) is too low to construct reliable 8-dimensional nutrition profiles because the data would be overfitted. We decided to calculate the nutrition profiles based on N, S, P and FM only, thus excluding K, Ca, Mg and Al. The K, Ca, Mg and Al concentrations were added in the presentation of the profiles. This approach prevented overfitting of the data. By definition, nutrition profiles should also contain the total foliar biomass (FM). Total foliar mass is the logical growth response to be used together with foliar concentrations. However, as total foliar mass data were not available for the monitored plots, we used the mass of 1000 needles (NM) as a substitute for the total needle mass. We were not able to find any study which supported or tackled the relationship between the mass of 1000 needles and the total needle mass. It is not clear which processes are measured by the mass of 1000 needles. Although the mass of 1000 needles lacks physiological meaning, it accounts for some dynamics and its use is reported to improve the interpretation of the nutrient status of tree foliage.[22–27] As a result, the mass of 1000 needles was considered to be an acceptable substitute for the total needle mass in the nutrition profiles of this study. When available, basal area increment could also substitute total foliar biomass.[28] Despite these departures from the concept of the nutrition profile, the main features of the concept were respected, *i.e.* the data evaluation method accounted for the element concentrations, contents and interactions between two or more elements. Nutrition profiles containing current-year N, S and P concentrations and NM from 1987 to 2000 from all the 36 plots were submitted to the SOM. A map consisting of a regular hexagonal grid with six by nine map units was used in the SOM. The map was trained using the batch algorithm[18] in two rough training epochs and five fine-tuning epochs. The final neighbourhood width was 1 in order to ensure good quality quantization. The SOM Toolbox,[29] available at http://www.cis.hut.fi/projects/somtoolbox was used to train the SOM and calculate the distance matrix.

The quality of the SOM quantization was measured using the average quantization error, which is the average distance from each data vector to the closest prototype vector. The average quantization error was 0.82, which is an acceptable value for this error given the number of map units (six by nine). The average number of measurements per map unit was 6.8. Increasing the map size could have decreased the quantization error but could also have led to overfitting of the data in specific too few measurements per map unit. Preservation of the topology of the maps was measured by means of the topographic error. This is the percentage of data vectors for which the best matching unit and the second best matching unit are not neighbouring map units.[30] The topographic error was 5.5%. Due to the low number of topographic errors, the topology of the data set was preserved well in the quantization process. Therefore, clustering the distance matrix of the SOM was expected to give reliable results. The distance matrix was clustered with an agglomerative clustering algorithm with pruning. The quality of the clustering was measured with the gap index I_{gap}. The I_{gap} value for the final clustering was 1.67. This means that the cluster was better than a random clustering with a probability of 0.7, and the quality of the clustering is therefore considered to be good. In addition, each cluster contained more than 25 samples. Although the data set was small for the applied methods, which could affect the generalization property of the results, the quality indices given in this section indicate a realistic representation of the structure of data set. Due to the pruning algorithm, cluster 2 was pruned out of the hierarchy, and bottom-level clusters 1 and 4 were combined into cluster 10 in the final clustering. As a result, 6 groups, each represented by a group nutrition profile, were retained. The topology of the group nutrition profiles, named 3, 5, 6, 7, 8 and 10, is presented in Fig. 1. The element

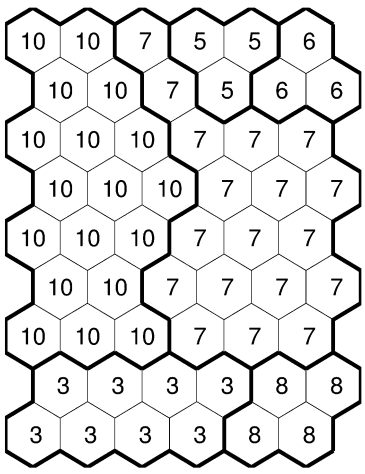

Fig. 1 Two dimensional projection on 6 by 9 map units of the *4*-dimensional vectors $\boldsymbol{x}$ which were sorted in a *4*-dimensional space with a self-organizing map. A neighbourhood relationship controlled the projection such that the topology of the data set is preserved. As a consequence, vectors $\boldsymbol{x}$, which are close to each other in the *4*-dimensional space, are close to each other on the map. In this figure the element concentrations of the vectors $\boldsymbol{x}$ were replaced by the number (3, 5, 6, 7, 8 or 10) of the most similar group nutrition profile.

Table 2 Mean values and standard deviations of the N, S, P, K, Mg, Ca and Al concentration ($mg.g^{-1}$), Mg:N, Ca:Al and S:N ratios (dimensionless) and needle mass (g per 1000 needles) for the six group nutrition profiles of Norway spruce and Scots pine in Finland

Nutrition profiles						
	3	5	6	7	8	10
Norway spruce						
N	13.7 ± 2.63	11.4 ± 0.99	10.2 ± 0.36	12.4 ± 0.96	13.3 ± 1.33	n.a. ± n.a.
S	1.06 ± 0.09	0.82 ± 0.06	0.86 ± 0.05	0.94 ± 0.09	1.10 ± 0.10	n.a. ± n.a.
P	1.75 ± 0.11	1.19 ± 0.15	1.62 ± 0.24	1.53 ± 0.21	2.02 ± 0.22	n.a. ± n.a.
K	7.15 ± 0.40	6.19 ± 0.76	6.48 ± 1.26	6.39 ± 1.16	6.66 ± 1.03	n.a. ± n.a.
Mg	1.18 ± 0.11	1.10 ± 0.12	1.17 ± 0.13	1.19 ± 0.16	1.30 ± 0.15	n.a. ± n.a.
Ca	3.97 ± 0.56	4.23 ± 1.18	3.73 ± 1.09	5.00 ± 1.35	5.00 ± 1.14	n.a. ± n.a.
Al	0.05 ± 0.02	0.03 ± 0.02	0.03 ± 0.01	0.04 ± 0.02	0.06 ± 0.03	n.a. ± n.a.
Mg:N	0.09 ± 0.02	0.10 ± 0.01	0.16 ± 0.01	0.10 ± 0.01	0.10 ± 0.02	n.a. ± n.a.
Ca:Al	100 ± 50.0	173 ± 113	117 ± 37.0	144 ± 95.9	101 ± 57.2	n.a. ± n.a.
S:N	0.08 ± 0.02	0.07 ± 0.01	0.08 ± 0.01	0.08 ± 0.01	0.08 ± 0.02	n.a. ± n.a.
NM	5.60 ± n.a.	4.04 ± 0.58	4.33 ± 0.79	4.23 ± 0.73	4.66 ± 0.86	n.a. ± n.a.
Scots pine						
N	13.6 ± 0.86	11.2 ± n.a.	9.65 ± 0.63	12.3 ± 0.71	13.6 ± 0.71	11.9 ± 1.10
S	1.09 ± 0.09	0.79 ± n.a.	0.87 ± 0.10	0.96 ± 0.08	1.13 ± 0.12	0.89 ± 0.08
P	1.81 ± 0.16	1.19 ± n.a.	1.60 ± 0.15	1.46 ± 0.13	2.05 ± 0.15	1.46 ± 0.13
K	5.68 ± 0.41	4.58 ± n.a.	6.43 ± 0.66	5.18 ± 0.70	5.88 ± 0.46	5.11 ± 0.53
Mg	1.18 ± 0.17	1.00 ± n.a.	1.11 ± 0.15	1.08 ± 0.08	1.13 ± 0.06	1.06 ± 0.13
Ca	2.41 ± 0.41	2.35 ± n.a.	2.95 ± 1.02	2.12 ± 0.43	2.26 ± 0.18	2.00 ± 0.40
Al	0.34 ± 0.10	0.28 ± n.a.	0.10 ± 0.09	0.26 ± 0.08	0.37 ± 0.05	0.24 ± 0.08
Mg:N	0.09 ± 0.02	0.09 ± n.a.	0.12 ± 0.02	0.09 ± 0.01	0.08 ± 0.01	0.09 ± 0.01
Ca:Al	8.14 ± 3.95	8.27 ± n.a.	40.4 ± 17.2	10.2 ± 2.74	6.23 ± 1.40	9.03 ± 3.17
S:N	0.08 ± 0.01	0.07 ± n.a.	0.09 ± 0.01	0.08 ± 0.01	0.08 ± 0.12	0.08 ± 0.01
NM	12.5 ± 2.70	n.a. ± n.a.	5.27 ± 1.74	8.14 ± 0.46	8.35 ± 0.95	11.5 ± 2.43

concentration and NM for each group nutrition profile is given in Table 2. The N, S, P, K, Mg concentrations and Mg:N ratio were similar for the same profiles in both Norway spruce and Scots pine. Due to the autecology of the tree species, however, the values for Ca, Al, Ca:Al, S:N and NM were very different for Scots pine and Norway spruce needles. The topology from Fig. 1 is reflected in the values of the nutrition profiles in Table 2.

A 14 year sequence with the group nutrition profiles that best represented the data for N, S, P and NM was made for each plot (Table 3). The variation in the chemical composition of the foliage is now captured by the group nutrition profiles for Scots pine and Norway spruce separately. However, the temporal and spatial variability in forest nutrition is not yet described. This example was limited to a description of the temporal variability. The temporal variability was described by means of an individual transition matrix for both tree species (Table 4). The analysis could be extended to a spatio-temporal analysis by calculating individual transition matrices for different regions. A transition matrix indicates the probability of switching from one profile to another between two consecutive years. The transition matrices were calculated as follows. First, the number of data vectors Z_k belonging to a group nutrition profile $\bar{\boldsymbol{x}}_k$ was counted for each of the profiles $k = 1,..., 6$. Then the number of Z_{kl} was counted; these are observations that belong to profile k in year t and belong to profile l in year $t + 1$. The maximum likelihood estimates of the transition probabilities ($\hat{a}_{kl}$) for the temporal variation of the nutrition profiles were calculated by $\hat{a}_{kl} = Z_{kl}/Z_k$, where k and l are the number of group nutrition profiles, *i.e.* 6. The transition matrix is a probabilistic model of the temporal variation of the nutrition profiles and allows, by means of iteration, calculation of the frequency distribution of the nutrition profiles at steady state.

The accuracy of the analytical methods sometimes equalled or even exceeded the differences in concentrations between nutrition profiles. Therefore, it cannot be ruled out, for these shifts and nutrients, that the shift from one year to another is caused by the analytical method and not by a real change in the needle composition. The robustness of the nutrition profiles to changes in a single element concentration was tested for N, S and P. The changes in the element concentration were within the limits of the accuracy of the N, S and P analysis. Nutrition profiles 3, 5, 6, 8 and 10 were robust for 79 to 96% of the changes in the N, S and P concentration. Profile 7 was robust for 87 % of the changes in N concentration. However, profile 7 was robust for only 65 of the changes in the S and 73% of the changes in P. Despite the fact that for a single element the accuracy of the analytical methods can be equal or even exceed the differences in concentrations between some group nutrition profiles, shifts between group nutrition profiles usually represent a real change in nutrient concentrations and/or NM.

Temporal variation of the foliar nutrient concentrations

The questions that we wanted to answer in this example were: (1) did the mineral composition of Norway spruce and Scots pine change between 1987 and 2000 and, if so, (2) how did the foliar nutrient concentrations change?

(1) The observed frequency distribution of the profiles was counted from the 36 14 year sequences (Table 2). Profiles 3, 5, 6, 7, 8 and 10 occurred 4, 28, 13, 84, 23 and 0 times, respectively, for Norway spruce, and 39, 1, 13, 20, 4 and 139 times for Scots pine (Table 5). The observed frequency distribution of the profiles is not uniform for Norway spruce (Chi-square, $p = 0.00$) or for Scots pine (Chi-square, $p = 0.00$). The observed frequency distribution showed that, given the environmental conditions between 1987 and 2000 in Finland, profile 7 dominated the chemical foliar composition of Norway spruce and profile 10 dominated the composition of Scots pine needles.

The transition matrix (Table 4), which describes the probabilities that the chemical composition of the needles shifts from one profile to another, is a probabilistic model of the temporal variation of the nutrition profiles. The probabilistic model can be used to calculate the frequency distribution of the nutrition profiles at the steady state. At the steady state the frequency distribution of the nutrition profiles is constant over time. Note that these calculations are valid predictions only if the transition matrix does not change during the period needed to converge on the steady state. This assumes that the future environmental conditions will be similar to the conditions experienced between 1987 and 2000. This is an

Table 3 Group nutrition profiles, which best represent the observed N, S, P concentrations and NM, for each monitored plots from 1987 to 2000. The plot numbers are the numbers used in the ICP Forest level I programme. Ns denotes plots dominated by Norway spruce, Sp plots dominated by Scots pine, and n.a. years and plots without data. The numbers refer to the group nutrition profiles

Plot		87	88	89	90	91	92	93	94	95	96	97	98	99	00
426	Ns	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	5	7
532	Ns	8	8	8	n.a.	8	7	7	8	7	6	7	8	7	7
556	Ns	8	8	8	n.a.	n.a.	7	7	8	7	7	6	7	7	7
581	Sp	3	3	10	n.a.	3	7	3	10	10	10	3	3	10	10
685	Sp	n.a.	n.a.	n.a.	n.a.	n.a.	10	10	3	3	10	10	3	10	3
819	Ns	8	8	8	n.a.	7	7	7	7	7	7	7	7	7	7
1078	Ns	7	7	7	n.a.	7	8	7	7	7	6	5	7	5	7
1104	Sp	7	3	10	n.a.	7	10	10	10	10	10	10	10	10	10
1108	Ns	7	7	7	n.a.	7	7	5	7	7	5	5	5	n.a.	3
1112	Sp	7	3	7	n.a.	3	7	7	7	10	10	10	10	10	10
1117	Ns	8	8	8	n.a.	3	7	7	8	7	7	7	7	5	7
1121	Ns	7	7	7	n.a.	7	5	5	5	5	5	5	5	5	5
1190	Sp	10	3	10	n.a.	10	10	10	10	10	10	10	10	10	10
1194	Ns	7	8	7	n.a.	3	7	7	7	7	7	5	7	5	n.a.
1198	Ns	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	8	7
1591	Ns	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	5	5
1721	Ns	7	3	7	n.a.	n.a.	7	5	6	7	6	7	7	n.a.	n.a.
1840	Sp	7	8	10	n.a.	n.a.	10	10	10	10	10	10	10	n.a.	n.a.
1901	Sp	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	10	10
1927	Ns	7	7	7	n.a.	n.a.	7	5	7	7	7	7	7	5	7
2018	Sp	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	10
2100	Sp	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	10	10
2151	Sp	7	3	10	n.a.	10	10	10	10	10	10	10	10	n.a.	n.a.
2709	Sp	10	3	10	n.a.	n.a.	10	10	10	10	10	10	10	10	10
2841	Ns	8	8	8	n.a.	n.a.	7	5	7	6	7	7	7	6	7
3103	Ns	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	6	6	6	7
3163	Ns	6	7	6	n.a.	n.a.	6	5	5	5	n.a.	n.a.	n.a.	n.a.	n.a.
3259	Sp	10	3	10	n.a.	n.a.	7	10	10	10	10	10	10	10	10
3350	Sp	10	10	10	0	n.a.	10	10	10	10	10	10	10	10	10
3606	Sp	6	3	3	7	7	10	3	3	10	3	10	10	10	10
3612	Sp	6	6	6	n.a.	n.a.	6	6	6	6	6	6	6	6	10
3690	Sp	6	3	10	5	10	10	10	10	10	3	10	10	10	10
3708	Sp	3	3	3	10	10	10	3	3	3	3	3	10	10	10
3819	Sp	7	3	10	7	n.a.	7	7	7	7	10	10	10	10	10
3894	Sp	7	10	10	10	n.a.	10	3	10	10	10	10	10	10	10
3961	Sp	8	3	3	10	n.a.	10	8	10	8	3	3	10	10	3

Table 4 The transition matrices for Norway spruce and Scots pine between 1987 and 2000. The transition matrix shows the probability of switching from one specific profile in year t (row) to a specific nutrition profile in the consecutive year $t + 1$ (column)

	Year $t + 1$											
	Norway spruce						Scots pine					
Year t	3	5	6	7	8	10	3	5	6	7	8	10
3	0.00	0.00	0.00	1.00	0.00	0.00	0.38	0.00	0.00	0.11	0.00	0.51
5	0.00	0.50	0.08	0.42	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
6	0.00	0.10	0.20	0.70	0.00	0.00	0.17	0.00	0.75	0.00	0.00	0.08
7	0.04	0.13	0.11	0.60	0.11	0.00	0.28	0.00	0.00	0.33	0.06	0.33
8	0.00	0.00	0.00	0.37	0.63	0.00	0.50	0.00	0.00	0.00	0.00	0.50
10	0.00	0.00	0.00	1.00	0.00	0.00	0.11	0.01	0.00	0.01	0.02	0.86

unrealistic assumption. Therefore, the difference between the observed frequency distribution (1987–2000) and the frequency distribution at the steady state are only presented as measures of the temporal variation in the nutrition profiles and not as predictions. The steady state frequency distribution for Norway spruce (Table 5) was derived from the transition matrix for Norway spruce. Evidence is, however, missing (Chi-square, $p = 0.90$) to show that the observed frequency distribution and the frequency distribution at the steady state are different for Norway spruce. It was concluded that there were no significant temporal dynamics in the frequency distribution of the group nutrition profiles of Norway spruce between 1987 and 2000. For Scots pine, the frequency distribution at the steady state (Table 5) is different from the

Table 5 The observed and the steady state distribution frequency (%) of the nutrition profiles. Frequencies of the steady state distribution were calculated with a transition matrix

	Norway spruce						Scots pine					
	3	5	6	7	8	10	3	5	6	7	8	10
Observed freq. (%)	2.6	18.4	8.5	55.3	15.2	n.a.	18.1	0.4	6.0	9.3	1.9	64.3
Steady state freq. (%)	2.6	15.8	9.2	55.3	17.1	n.a.	16.7	0.9	0	3.7	1.4	77.3

observed frequency distribution of the nutrition profiles (Chi-square, $p = 0.00$). The temporal trends in the frequency distribution of the group nutrition profiles of Scots pine indicated an increasing importance of profile 10, accompanied by a decreasing importance of all other profiles between 1987 and 2000.

(2) The temporal trends in the frequency distribution of the group nutrition profiles of Scots pine indicated an increasing abundance of profile 10, accompanied by a decreasing importance of all other profiles. This means that between 1987 and 2000 the N, S, P, K, Ca, Mg and Al decreased, whereas the NM increased or remained unchanged. As there were no temporal trends in the frequency distribution of the group nutrition profiles of Norway spruce, the mineral composition of the needles of Norway spruce needles subsequently did not change between 1987 and 2000. The same questions were addressed with the Critical Range and Nutrient-element Balance concept. The similarities and differences between these concepts and the nutrition profiles can be derived from this study and Lorenz *et al.*[31] It should be noted that foliar surveys can be used to ascertain which elements are in short or excessive supply within the plant, but the cause of the problem cannot be determined without additional data. Interpretation of the (lack of) temporal trends was outside the scope of this example.

Perspective

Although Critical Range (CR), Deviation from Optimal Percentage (DOP), Nutrient–Element Balance, Diagnosis and Recommendation Integrated System (DRIS) and the Compositional Nutrient Diagnosis (CND) concepts have proven to be useful for evaluating the mineral composition of tree foliage, their use is limited especially in monitoring programmes, by one or several conceptual shortcomings. CR and DOP do not account for the interactions between elements. In addition to these concepts Nutrient–Element Balance, DRIS and CND do not account for the fact that the growth of trees is controlled by the foliar concentrations and contents of all elements. As a consequence, we defined the nutrition profile of a tree or stand as the nutrient status, which accounts for all element concentrations, contents and interactions between two or more elements. Trees or stands with similar nutrition profiles form their own group. Each group is characterised by a so-called group nutrition profile. The approach, which we called nutrition profiles, differs from commonly used concepts in the following characteristics:

(1) Most studies, apart from a few exceptions,[32–34] limit the evaluation of large-scale foliar surveys to evaluating the foliar element concentrations. There is, however, clear evidence that element concentrations alone do not fully characterize plant element turnover.[35] Therefore, it is desirable to evaluate foliar surveys by simultaneously comparing the element concentration, the element content, and the growth response.[27] A nutrition profile contains explicitly the element concentration and foliar mass, and thus implicitly the element content and ratios. Owing to the neighbourhood relationship in the self-organizing map (SOM), which was used to calculate the group nutrition profiles, the relationships between the element concentrations and foliar mass are preserved. As a consequence, group nutrition profiles represent the element concentration, content and ratios, and thus allow simultaneous comparison of the element concentration, content, ratios and the growth response.

(2) Nutrition profiles contain untransformed data and therefore have the potential for a straightforward interpretation. Due to the fact that a group nutrition profile represents a group of stands, the interpretation of the group profile serves all the stands characterised by this profile. Nutrition profiles are based on the relationship between growth and the element concentrations in the plant. Therefore, existing threshold and classification values for element concentrations, contents and ratios can be used to interpret the nutrition profile. In addition, because nutrition profiles capture the relationships between elements, the interpretation can be based on the relationships between elements and, through this, largely overcome the problems associated with the use of threshold values.[12,35,36] To benefit from the multi-dimensionality of the nutrition profiles, a set of threshold values, classification values, ratio and relationships between elements, should be used to describe a so-called *fingerprint* of a specific environmental condition, for example, a fingerprint for elevated N deposition, elevated CO_2 concentrations, elevated ozone concentrations *etc.* It should be noted that a successful interpretation of the nutrition profile largely depends on the accuracy of the threshold and classification values with which the analytical results are compared. Unfortunately, little is known about nutrient stress conditions in most natural environments[35,36] and establishing threshold and classification values is complicated by experimental difficulties.[12] However, nutrition profiles allow simultaneous comparison of the element concentration, content and foliar mass. Therefore, vector analysis[26,27] can be used to interpret the temporal or the spatial variation of the nutrition profiles. When a biological interpretation of the nutrition profiles can be provided, nutrition profiles might prove to be a new and better concept for the evaluation of the mineral composition of large-scale surveys.

(3) A group nutrition profile ($\bar{\boldsymbol{x}}_k$) describes the characteristic nutrient status (in the example the average one) of a group of trees or stands with similar nutrition profiles ($\boldsymbol{x}$). This means that there is variation in the element concentrations and foliar mass within a profile. This variation within the profile is no longer considered when the spatial and/or temporal variation of group nutrition profiles is studied. Temporal or spatial variation within a group profile will remain undetected. In this respect group nutrition profiles act as a smoothing agent.

(4) It is the number of replicate samples in the monitoring program that determines the maximal dimension of the group nutrition profiles. The number of replicate samples is the number of plots multiplied by the number of years, minus the missing values. In the example, 367 replicate samples were used to calculate 4 dimensional group nutrition profiles (N, S, P and NM). Reliable group nutrition profiles, which contain ten or more elements, should be calculated from large-scale foliar surveys with thousands of replicate samples.

Although the example demonstrated the potential of the concept, it does not fully explore the possibilities of this technique:

(1) Element concentrations and needle mass from current and previous-year needles could be included in the profile $\boldsymbol{x} = [(x_1,...,x_{d-1},FM)_C,(x_1,...,x_{d-1},FM)_{C+1}]$. This could help to show the dynamics of elements and to improve the interpretation of the nutrition profile under conditions in which threshold and classification values are lacking.

(2) The spatial variation was not described in the example. However, the temporal variation was described by means of annual changes. More complex models of the spatial and temporal variability could describe the spatial-temporal history of the tree or stand's foliage. Modelling the spatial and temporal variation could help to understand the processes underlying the changes in nutrition profiles.

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