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Acta Oecologica 24 (2003) 209–219

ACTA OECOLOGICA
INTERNATIONAL JOURNAL OF ECOLOGY

www.elsevier.com/locate/actoec

Original article

Leaf structure vs. nutrient relationships vary with soil conditions in temperate shrubs and trees

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Received 18 June 2002; accepted 17 June 2003

Abstract

Often there are significant positive interspecific relationships between leaf area per unit dry mass (SLA) and foliar phosphorus and nitrogen concentrations ([P] and [N]). Most of these studies have been conducted on moderately acidic soils, and little is known of the generality of these relations as potentially affected by soil characteristics. We investigated foliage mineral composition in relation to leaf structure in a wooded meadow on calcareous alkaline soil, in a bog on strongly acidic soil, and in a flood plain on moderately acidic soil. Foliar nutrient contents and fertilization experiments indicated that foliage physiological activity was co-limited by both P and N availabilities in the wooded meadow, by P in the bog, and by N in the flood plain. In the wooded meadow and in the bog, there were positive relationships between SLA and P concentration ([P]), and no relationship between SLA and nitrogen concentration [N]. Given that the fraction of support tissues generally increases with decreasing SLA, the requirement for mineral nutrients is lower at low SLA. Thus, these contrasting relations between mineral nutrients and SLA suggest that P was distributed in a more "optimal" manner among the leaves with varying structure than N in P-limited communities. In the flood plain, SLA was positively related to both [P] and [N], possibly manifesting a strategy to cope with N limitations by enhancing N turnover, and accordingly, greater P requirement for nucleic acid formation in N-limited soils. Total variation in foliar structural and chemical characteristics was similar in all sites, and was mainly determined by variation among the species. Part of this variability was explained by life form and plant size. [P] was higher in trees than in shrubs, and [P] and P/N ratio increased with increasing total plant height, indicating that P nutrition was improved relative to N nutrition with increasing plant size. Since the capture of less mobile soil elements such as P is dependent on extensive root systems, but not that of readily mobile and temporarily variable elements such as N, this correlation was attributed to more extensive root systems in larger plants. Our study indicates that foliar structure vs. [N] and [P] relations may be separately regulated, but also that the generality of leaf structure vs. nutrient content relations may vary depending on soil conditions.

Keywords: Acidic soils; Alkaline soils; Leaf structure/nutrient relations; Leaf morphology; Nutrient limitation; Plant size

1. Introduction

The concentrations of foliar N ([N], Sobrado and Medina, 1980; Reich and Walters, 1994; Schulze et al., 1994; Niinemets et al., 2002) and P ([P], Sobrado and Medina, 1980; Bongers and Popma, 1990; Reich and Walters, 1994; Niinemets et al., 2001) often increase with increasing specific leaf area (SLA, leaf area per dry mass). Such relationships may partly be explained by a larger fraction of support structures in thicker and denser leaves that possess a lower SLA, and accordingly by a reduced requirement for mineral nutrients for construction of foliage with low SLA (Sobrado and Medina, 1980; Reich et al., 1992; Niinemets and Kull, 1998; Niinemets, 1999). Since the nutrient vs. structure relations are frequently observed, it has been suggested that they represent fundamental convergence in leaf formation and functioning (Reich et al., 1999). Provided such relationships occur for all combinations of environmental factors, they would have paramount significance in regional and global scaling of stand leaf area and foliage carbon gain capacities.

In some situations, SLA vs. nutrient relationships are poor, disagreeing with their fundamental nature. For instance, the strength of SLA vs. [N] relations may be different in communities of varying water availability (Wright et al., 2001). Such differences may partly be explained by modifications in support investments due to changes in water avail-

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doi:10.1016/S1146-609X(03)00094-8

ability (Niinemets, 2001). However, the hypothesis of the scaling of leaf nutrient concentrations with SLA due to alterations in fractional support investments does not explain why in some instances there are strong relationships of SLA with both [N] and [P], but in other cases only with one of these nutrients. Depending on nutrient supply from the soil, mineral nutrient contents may vary largely at a common SLA (e.g., Thompson et al., 1992). This probably arises from the circumstance that not all the foliage P and N are associated with cell metabolic functions. In fact, the nutrients in excess may be stored in the vacuoles (Rebeille et al., 1983; Leigh and Storey, 1991). This may further indicate that more severely limiting nutrients present in only functional cell compartments have the strongest relationships with SLA, while the concentrations of less limiting elements may more strongly fluctuate due to the presence of the non-metabolic storage.

Nitrogen is generally considered as the most limiting nutrient in earth ecosystems, but there is increasing evidence that phosphorus may be the primary limiting element in many communities on acidic soils. Severe P limitations have been observed in tropical forests on soils rich in iron and aluminum forming insoluble compounds with phosphate (Vitousek and Sanford, 1986; Reich et al., 1995), in temperate fens and bogs, where the availability of P is limited by slow turnover of organic P compounds (Wilson and Fitter, 1984; Wassen et al., 1995; Niinemets et al., 2001), in Mediterranean-type ecosystems (Niinemets et al., 1999) and in temperate forest communities (Prescott et al., 1992) where both P immobilization by soil micro-organisms and P occlusion on soil minerals may play a role. Phosphate salts with Ca and Mg are also poorly soluble at higher soil pH (Lindsay and Vlek, 1977), and accordingly, P availability may be low in alkaline calcareous soils as well (e.g., Clement and Gessel, 1985). However, little attention has been paid to this potential P limitation resulting from the low mobility of P in alkaline soils. So far, the leaf structure/nutrient relationships have been studied only in acidic soils, but gaining insight into the generality of these relations requires more advanced understanding of the potential variability of these relations in different soils.

To test the hypothesis that the correlations between foliar nutrient concentrations and SLA are dependent on the mineral nutrient supply from the soil, we studied foliar morphology and stoichiometry of mineral nutrients in widespread perennials in a wooded meadow on calcareous soils, in a bog on very acidic soils and in a flood plain on moderately acidic soils. Primary production of herbaceous vegetation has been previously shown to respond primarily to P rather than to N in the wooded meadow (Pork, 1979) and in the bog (Paavilainen, 1980; Finér, 1992), while the flood plain vegetation is mainly limited by N (Pork, 1963). Thus, we hypothesized (1) that P is present in limiting concentrations in the foliage in the bog and wooded meadow, but not in the flood plain, that [P] and [N] are positively correlated, and that other mineral elements are in a satisfactory supply. We further suggested (2) that there is a stronger positive relationship between [P] and SLA, than between SLA and other mineral nutrients in the P-limited ecosystems.

Within the same community, foliar nutrient concentrations vary largely among different species and among different individuals of the same species despite similar soil conditions (Ricklefs and Matthew, 1982; McJannet et al., 1995), but the plant and species characteristics responsible for this variability are still poorly understood. Although such species and plant effects may be superimposed by general constraints on variation of leaf structure and nutrient contents, they may significantly alter the strength and predictive ability of these relationships. Total height of sampled woody plants varied by two orders of magnitude across the species in the current study. Since the plant ability to capture less mobile soil nutrients such as phosphate strongly depends on extensive root systems exploring large soil volumes, but that of more mobile mineral nutrients such as nitrate does necessarily not (Sands and Mulligan, 1990), we suggested that (3) foliar concentrations of less-mobile soil mineral nutrients are greater in larger woody plants, and that (4) this pattern is more evident in the case of more limiting nutrients.

2. Materials and methods

2.1. Study sites

The work was conducted in three sites of contrasting soil conditions in Estonia. The first site was an open woodland on calcareous alkaline soils in Laelatu (58°36' N, 23°35' E; elevation 2–5 m above sea level; Kull and Zobel, 1991). Species-rich herb layer is dominated by *Briza media* L., *Carex flacca* Schreb., *Festuca rubra* L., *Filipendula hexapetala* Gil., *Schorzonera humilis* L. and *Sesleria coerulea* (L.) Ard. (Kukk and Kull, 1997). Sparse shrub layer mainly consists of 2–4 m tall *Cornus sanguinea* L. and *Corylus avellana* L., while solitary or grouped individuals of *Betula pendula* Roth., *Fraxinus excelsior* L. and *Quercus robur* L. constitute the tree layer (height 6–12 m). The soil is a rendzic leptosol with two horizons. A thin (17–22 cm) humus horizon (A) lays directly on calcareous marine sediments and glacial moraines (C horizon). The bedrock, a Silurian limestone, is generally at a greater depth than 1 m and plays a minor part in soil formation processes (Sepp and Rooma, 1970). However, the bedrock is penetrated by numerous vertical cracks, and therefore, these soils are prone to drought. Soil pH is neutral to alkaline throughout the entire profile (Table 1), and was rich in organic matter (humus concentration 9.06 ± 0.29%) and total nitrogen (Table 1). Acetate (pH 3.75, ammonium acetate 0.1 M, acetic acid 0.3 M, lactic acid 0.1 M) soluble fractions of Ca (0.71 ± 0.01%) and Mg (0.38 ± 0.01%) were also high, but soluble K (0.144 ± 0.005 mg g^{-1}) and P (0.0207 ± 0.0013 mg g^{-1}, AL-method, Egner et al., 1960, Swedish standard SS 02 83 10) were relatively low. A fertilization experiment demonstrated that the herbaceous biomass responded both to

Table 1
Canopy characteristics and soil conditions (mean ± S.E.) of the three sites investigated

Site	Canopy height (m)		Coverage of woody vegetation (%)	Soil A horizon [a]			
	Herbaceous layer	Woody layer		pH [b]	Total N (%)	C/N mass ratio	*n*
Wooded meadow	0.3–0.5	2–12	30–50	6.92 ± 0.02 (6.7–7.5)	0.59 ± 0.01	9.58 ± 0.18	62
Bog	0–0.4	1.2–4	10–30	3.90 ± 0.15 (3–4.8)	2.65 ± 0.10	13.6 ± 0.8	30
Flood plain	0.3–1.1	0.8–2.3	5–15	5.10 ± 0.07 (4.9–5.3)	3.00 ± 0.38	12.5 ± 1.6	8

[a] Soil was sampled between 0 and 20 cm in the wooded meadow and between 0 and 30 cm in the two other sites.

[b] pH was measured in 1 M KCl solution. The values in parentheses provide the range observed.

N and P addition, with a strong combined effect of simultaneous addition of N and P (Niinemets and Kull, unpublished data).

The second site with contrasting soil conditions was an ombrotrophic bog in Ulila, Estonia (58°17' N, 26°12' E, elevation 50–55 m above sea level). *Andromeda polifolia* L., *Carex chordorrhiza* L. f., *Drosera rotundifolia* L., *Eriophorum vaginatum* L., *Ledum palustre* L., *Sphagnum* ssp., *Trichophorum alpinum* (L.) Pers. dominated the lower plant layer, while the tree layer was formed by sparsely growing 1–4 m tall individuals of *Betula humilis* Schrank, *Betula pubescens* Ehrh., *Pinus sylvestris* L. and *Salix rosmarinifolia* L. Due to the drainage of surrounding areas over 30 years ago, the upper peat horizons (0–30 cm) showed signs of mineralization due to decreased water table. Nevertheless, N content and C/N mass ratio of A_o horizon were still high (Table 1). The soil was acidic throughout the entire profile (Table 1). Despite the decreased water table, the bog was regulary flooded during most of the growing season.

The third site investigated was a flood plain of river Võhandu (58°5' N, 27°32' E, elevation 3–15 m). The grass layer is dominated by *Carex acuta* L., *Carex elata* Bell. and *Phalaris arundinacea* L., while the woody vegetation mainly consists of *Salix* spp. (Table 1). The soil is a moderately decomposed 0.5–1 m thick peat formed on an alluvial sand (Table 1). During the spring and fall months the river expands to its flood plain, and sediments carried by the flood are deposited on the flood plain. This leads temporarily to relatively high soil N and especially P availabilities typical to flood plain meadows of Estonia (Pork, 1963). The flood plain meadows extend in 200–300 m stripes along the riverbanks, and gradually transform to fens and further to minerotrophic open swamp forests or to heath forests along the toposequence from the river to the mainland.

2.2. Foliar sampling

The flora of shrubs and trees of the wooded meadow consists of 45 natural species, and is rich for temperate woodlands (Kukk and Kull, 1997). For the current analysis, we selected 25 widespread woody species. In addition, a hybrid *Salix* species was included in the dataset (Table 2). Together with the surrounding drained areas, there are 28 natural woody species in the bog (Niinemets, unpublished observations), but only seven dominate the natural bog ecosystem. Nine more frequent species were chosen for the study of foliar morphological and chemical variables (Table 2). In the flood plain, altogether 13 woody species from the genera *Alnus*, *Betula* and *Salix* occur, but 12 additional woody species may be found in the adjacent fens and open woodlands (Niinemets, unpublished observations). In the current analysis, we included eight species from this site.

In all locations, fully expanded mature leaves were sampled at the end of June and beginning of July. Leaves were taken from the distal twigs, either both from the upper and the lower third of the south-facing side of the canopy (tall trees) or from the middle of the canopy (small trees, shrubs and dwarf shrubs). Sample trees were chosen randomly, and the leaves of the same species were sampled from the trees growing in different parts of the study sites. On average 74 ± 10 (± S.E.) leaves per sampling location in the crown, and 7.1 ± 1.1 (wooded meadow), 5.5 ± 1.9 (bog) or 4.2 ± 1.2 (flood plain) sampling locations per species were analyzed.

To test for the generality of correlations between foliar nutrient concentrations during the season, freshly fallen leaves of seven species (*Betula pendula* Roth., *Cornus sanguinea* L., *Corylus avellana* L., *Fraxinus excelsior* L., *Populus tremula* L., *Quercus robur* L., *Sorbus aucuparia* L.) were collected in the wooded meadow.

2.3. Measurements of leaf morphology and chemistry

Leaf area was measured with an electronic-optical areameter (AAC-400, Hayashi Denkoh, Tokyo, Japan) and leaf dry mass was determined after oven drying at 90 °C for at least 48 h. In compound-leaved species, only leaflets were analyzed for area, but leaf laminas and petioles were not separated in simple-leaved species. Nitrogen and phosphorus contents were determined after standard Kjeldahl digestion by indophenol and molybdenum blue methods, respectively (Grimshaw et al., 1989). Ash content was found after combusting the sample in a muffle furnace at 500 °C for 4 h. The contents of Ca and K were determined by flame emission spectroscopy, and Mg by atom absorption spectroscopy using standard routines. Nutrient contents of compound leaved species were found as weighted averages of nutrient concentrations in leaflets and rachises.

2.4. Data analyses

Total variability, and intra- and interspecific variability among the sampling sites was characterized by the coefficient of variation (sample standard deviation divided by the mean value) as in Valladares et al. (2002, and the references

Table 2
Foliar nutrient concentrations and morphology (averages ± S.E.) of shrub and tree species studied at three sites of contrasting soil conditions

Site	Species	SLA [a] (cm^2/g)	Log (S, cm^2)	N (%)	P (%)	K (%)	Ca (%)	Mg (%)	Ash (%)
Wooded meadow	*Acer platanoides* L.	210 ± 5	3.95 ± 0.07	1.923 ± 0.035	0.1715 ± 0.0042	1.74 ± 0.08	1.69 ± 0.05	0.748 ± 0.022	8.68 ± 0.24
Wooded meadow	*Berberis vulgaris* L.	154 ± 20	0.91 ± 0.07	2.010 ± 0.032	0.1113 ± 0.0028	1.08 ± 0.05	1.422 ± 0.047	1.019 ± 0.05	7.22 ± 0.48
Wooded meadow	*Cornus sanguinea* L.	256 ± 22	2.83 ± 0.11	1.940 ± 0.039	0.1350 ± 0.0037	1.74 ± 0.17	2.56 ± 0.18	1.83 ± 0.18	11.9 ± 0.8
Wooded meadow	*Corylus avellana* L.	275 ± 17	3.27 ± 0.07	1.86 ± 0.05	0.167 ± 0.007	1.44 ± 0.07	1.608 ± 0.037	0.85 ± 0.05	8.17 ± 0.23
Wooded meadow	*Crataegus curvisepala* Lindm.	118 ± 11	1.00 ± 0.17	1.990 ± 0.022	0.1141 ± 0.0030	1.08 ± 0.08	1.73 ± 0.09	1.31 ± 0.09	7.94 ± 0.43
Wooded meadow	*Crataegus monogyna* N. J. Jacq.	100 ± 7	0.85 ± 0.48	1.96 ± 0.06	0.107 ± 0.006	1.53 ± 0.17	1.84 ± 0.06	0.952 ± 0.036	8.81 ± 0.37
Wooded meadow	*Daphne mezerum* L.	346 ± 37	1.70 ± 0.05	2.027 ± 0.019	0.161 ± 0.007	2.47 ± 0.30	2.033 ± 0.046	1.735 ± 0.19	12.5 ± 0.7
Wooded meadow	*Fraxinus excelsior* L.	120 ± 5	2.40 ± 0.06	2.042 ± 0.028	0.1425 ± 0.0027	2.55 ± 0.05	2.77 ± 0.05	1.071 ± 0.07	11.82±0.20
Wooded meadow	*Lonicera xylosteum* L.	267 ± 42	2.18 ± 0.13	2.105 ± 0.015	0.1367 ± 0.0018	2.13 ± 0.13	3.047 ± 0.017	1.243 ± 0.017	12.38±0.16
Wooded meadow	*Padus avium* Mill.	173 ± 7	2.332 ± 0.015	1.99 ± 0.05	0.147 ± 0.006	2.07 ± 0.19	3.61 ± 0.12	1.59 ± 0.11	13.75±0.36
Wooded meadow	*Quercus robur* L.	167.5±3.7	3.18 ± 0.07	2.109 ± 0.028	0.1713 ± 0.0026	1.435 ± 0.042	0.917 ± 0.019	0.546 ± 0.014	5.61 ± 0.12
Wooded meadow	*Ribes alpinum* L.	169 ± 20	1.67 ± 0.20	1.88 ± 0.05	0.141 ± 0.008	1.84 ± 0.18	1.610 ± 0.043	1.14 ± 0.07	8.94 ± 0.44
Wooded meadow	*Ribes nigrum* L.	213 ± 6	3.34 ± 0.17	1.97 ± 0.09	0.1295 ± 0.0015	1.885 ± 0.045	1.83 ± 0.12	0.885 ± 0.035	9.17 ± 0.10
Wooded meadow	*Rosa coriifolia* Fries.	192 ± 14	1.15 ± 0.05	2.04 ± 0.05	0.1280 ± 0.0033	1.22 ± 0.13	0.84 ± 0.12	0.94 ± 0.05	5.21 ± 0.07
Wooded meadow	*Rosa subcanina* (Christ.) Sarnth.	83 ± 7	1.05 ± 0.05	2.03 ± 0.06	0.1378 ± 0.0027	1.49 ± 0.10	1.43 ± 0.10	1.12 ± 0.07	6.74 ± 0.12
Wooded meadow	*Salix aurita* L.	106 ± 9	1.80 ± 0.21	2.009 ± 0.028	0.1749 ± 0.0038	1.710 ± 0.21	1.547 ± 0.038	0.945 ± 0.07	9.3 ± 0.6
Wooded meadow	*Salix aurita x S. cinerea*	126 ± 4	1.92 ± 0.27	2.013 ± 0.044	0.1644 ± 0.0020	1.88 ± 0.19	1.56 ± 0.06	0.883 ± 0.040	9.8 ± 0.7
Wooded meadow	*Salix caprea* L.	158 ± 17	2.61 ± 0.05	2.084 ± 0.036	0.1236 ± 0.0032	1.761 ± 0.041	1.771 ± 0.034	1.071 ± 0.023	9.98 ± 0.42
Wooded meadow	*Salix cinerea* L.	94.1 ± 3.0	1.472 ± 0.010	1.92 ± 0.06	0.1280 ± 0.0040	0.915 ± 0.035	1.72 ± 0.07	1.245 ± 0.035	8.0 ± 0.8
Wooded meadow	*Salix myrsinifolia* Sal.	130 ± 6	0.94 ± 0.16	1.995 ± 0.046	0.160 ± 0.014	1.070 ± 0.10	1.38 ± 0.05	1.36 ± 0.09	8.56 ± 0.36
Wooded meadow	*Salix phylicifolia* L.	103.3±4.4	1.38 ± 0.40	1.970 ± 0.032	0.1173 ± 0.009	0.913 ± 0.06	1.650 ± 0.017	0.93 ± 0.07	7.25 ± 0.12
Wooded meadow	*Salix rosmarinifolia* L.	141 ± 15	–0.386±0.005	2.160 ± 0.033	0.142 ± 0.005	0.85 ± 0.05	1.64 ± 0.14	1.02 ± 0.05	7.16 ± 0.15
Wooded meadow	*Syringa vulgaris* L.	107.4±1.4	2.68 ± 0.10	1.942 ± 0.032	0.1222 ± 0.0047	2.42 ± 0.19	1.69 ± 0.16	1.392 ± 0.027	9.53 ± 0.21
Wooded meadow	*Tilia cordata* Mill.	410 ± 26	3.28 ± 0.09	2.19 ± 0.05	0.184 ± 0.007	1.66 ± 0.16	1.92 ± 0.04	0.798 ± 0.015	9.23 ± 0.33
Wooded meadow	*Ulmus glabra* Huds.	175 ± 8	2.56 ± 0.10	2.100 ± 0.029	0.162 ± 0.006	2.85 ± 0.06	2.98 ± 0.13	1.169 ± 0.034	13.6 ± 2.0
Wooded meadow	*Viburnum opulus* L.	227 ± 24	3.15 ± 0.11	2.021 ± 0.042	0.1194 ± 0.0048	2.37 ± 0.24	1.92 ± 0.11	1.84 ± 0.11	11.40±0.36
Bog [b]	*Andromeda polifolia* L.	75.0 ± 1.0	–0.51 ± 0.22	1.500 ± 0.049	0.083 ± 0.008	0.458 ± 0.013	0.800 ± 0.050	0.510 ± 0.010	4.21 ± 0.20
Bog	*Betula humilis* Schrank	96 ± 21	0.67 ± 0.20	2.033 ± 0.049	0.097 ± 0.011	0.395 ± 0.028	0.88 ± 0.08	0.92 ± 0.09	5.68 ± 0.49
Bog	*Betula pubescens* Ehrh.	114.6±3.4	1.842 ± 0.046	1.914 ± 0.029	0.107 ± 0.008	0.335 ± 0.005	0.95 ± 0.06	1.17 ± 0.07	5.05 ± 0.26
Bog	*Ledum palustre* L.	154 ± 19	–1.21 ± 0.07	1.970 ± 0.028	0.130 ± 0.014	0.585 ± 0.024	0.660 ± 0.021	0.700 ± 0.045	5.43 ± 0.38
Bog	*Salix cinerea* L.	109 ± 8	0.877 ± 0.037	1.711 ± 0.037	0.1153 ± 0.0019	0.381 ± 0.040	0.856 ± 0.045	0.368 ± 0.007	4.44 ± 0.23
Bog	*Salix lapponum* L.	113 ± 7	0.61 ± 0.05	1.83 ± 0.08	0.1263 ± 0.0042	0.424 ± 0.008	0.81 ± 0.08	0.253 ± 0.013	3.96 ± 0.24
Bog	*Salix myrsinifolia* x *S. lapponum*	101 ± 6	–0.630±0.040	1.88 ± 0.07	0.0900 ± 0.019	0.278 ± 0.046	1.18 ± 0.29	0.51 ± 0.14	6.57 ± 0.26
Bog	*Salix rosmarinifolia* L.	108.1±4.2	–0.21 ± 0.20	2.155 ± 0.030	0.120 ± 0.027	0.373 ± 0.025	1.54 ± 0.26	0.48 ± 0.13	5.9 ± 1.0
Bog	*Salix starkeana* Willd.	96 ± 14	0.235 ± 0.030	1.73 ± 0.25	0.086 ± 0.011	0.25 ± 0.06	1.45 ± 0.28	0.52 ± 0.10	6.6 ± 0.9
Flood plain [c]	*Arctostaphylos uva-ursi* (L.) Sprengel	68.6 ± 2.9	–0.108±0.032	0.99 ± 0.06	0.132 ± 0.009	0.304 ± 0.035	0.70 ± 0.06	0.191 ± 0.023	3.66 ± 0.19
Flood plain	*Aronia melanocarpa* (Michx.) Elliott	98 ± 6	0.822 ± 0.041	1.664 ± 0.025	0.162 ± 0.007	0.369 ± 0.026	2.17 ± 0.08	0.948 ± 0.038	8.4 ± 0.7
Flood plain	*Betula pubescens* Ehrh.	194.3±4.5	n.d. [d]	3.09 ± 0.05	0.275 ± 0.031	n.d.	n.d.	n.d.	4.30 ± 0.16

Table 2 (continued)

Site	Species	SLA [a] (cm ^{2} /g)	Log (S, cm ^{2})	N (%)	P (%)	K (%)	Ca (%)	Mg (%)	Ash (%)
Flood plain	*Chimaphila umbellata* (L.) Nutt.	91.3 ± 2.9	0.203 ± 0.047	1.68 ± 0.10	0.120 ± 0.009	0.468 ± 0.035	1.56 ± 0.09	0.442 ± 0.023	6.94 ± 0.39
Flood plain	*Salix myrsinifolia* Sal.	88 ± 7	0.046 ± 0.17	1.53 ± 0.12	0.145 ± 0.009	0.668 ± 0.029	1.59 ± 0.14	0.440 ± 0.020	7.12 ± 0.23
Flood plain	*Salix triandra* L.	129 ± 13	0.84 ± 0.13	2.21 ± 0.09	0.200 ± 0.013	0.74 ± 0.08	0.97 ± 0.06	0.319 ± 0.037	6.29 ± 0.54
Flood plain	*Vaccinium myrtillus* L.	123 ± 6	–0.143±0.035	1.47 ± 0.09	0.161 ± 0.012	0.638 ± 0.035	1.20 ± 0.09	0.380 ± 0.023	6.07 ± 0.37
Flood plain	*Vaccinium vitis-idaea* L.	80.1 ± 2.9	–0.253±0.045	1.17 ± 0.10	0.121 ± 0.009	0.334 ± 0.035	0.96 ± 0.06	0.300 ± 0.023	4.81 ± 0.29

[a] SLA—specific leaf area (leaf surface area per unit dry mass). S, area per leaf, was transformed using natural logarithmic transformation. In compound-leaved species, leaflet is considered as the functional analogue of simple leaf, and the areas for the leaflets are depicted.

[b] Bog with adjacent drained peat lands.

[c] Flood plain meadow with fens and open swamp and heath woodlands.

[d] n.d.—not determined.

therein). Within species variability for each site and for a specific leaf variable was found as an average of species-specific coefficients of variation for this leaf variable.

Linear correlation and regression techniques were used to analyze the relationships between foliage chemical and morphological parameters. To reduce the influence of within canopy and within habitat variabilities on these statistical relations, all data per species were averaged before the regression analyses. This routine generally improved the r^2s of the statistical dependencies, but did not alter the conclusions qualitatively.

Differences between the sites in mean leaf morphological characteristics, mineral nutrient concentrations and coefficients of variation between the sites, and between trees and shrubs in the wooded meadow were compared by ANOVA analyses. Average leaf area was not normally distributed, and Kruskal–Wallis non-parametric ANOVA was used to test for differences in leaf size. All comparisons between habitats were conducted with data averaged per species, and all relations were considered significant at $P < 0.05$ (SAS Institute Inc., 1990).

3. Results

3.1. Nutrient concentrations in relation to foliar morphology

In the wooded meadow, foliar [P] and SLA were positively correlated (Fig. 1), but the concentrations of other mineral nutrients were not related to SLA. [N] varied little among all plants, and was considerably less at higher values of SLA than expected on the basis of a general relationship derived from the data covering six earth biomes (Reich et al.,

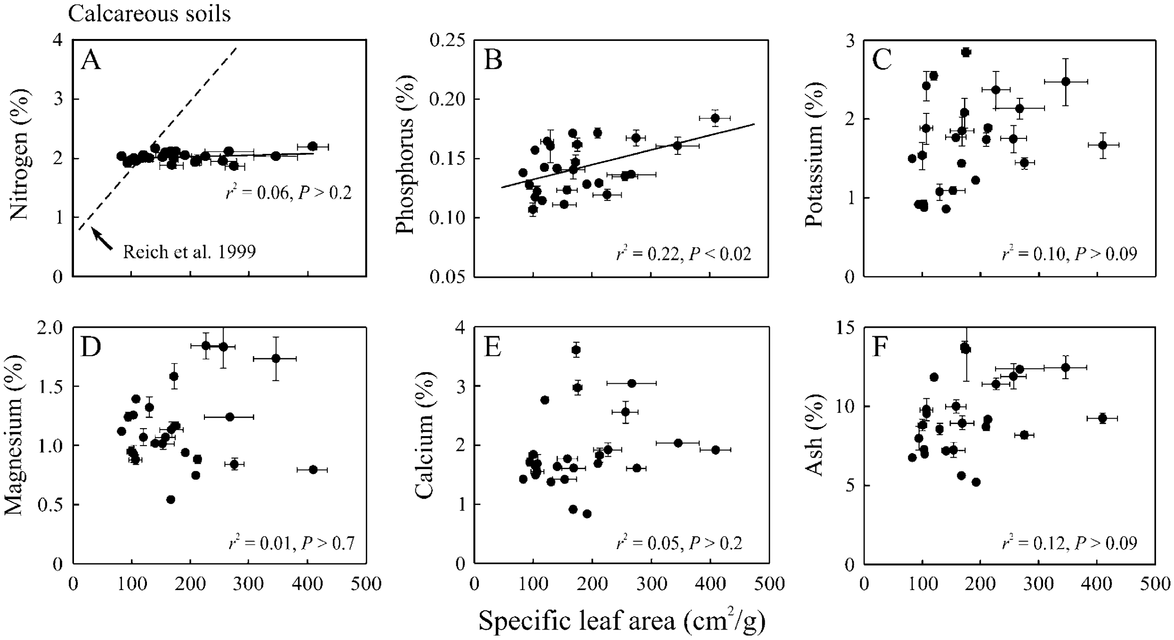

Fig. 1. Interrelationships between foliar nutrient concentrations and leaf specific area (SLA) in 26 woody species sampled in the wooded meadow on calcareous soils. Each point stands for a species (Table 2). r^2-s are calculated for a linear dependence. Error bars give ± S.E. Local woody flora consisted of 45 species, of which more widespread species were included in the analysis. The dashed line in A provides a general regression equation fitted to the data from six earth biomes (Reich et al., 1999; $r^2 = 0.72$, $P < 0.001$, $n = 110$).

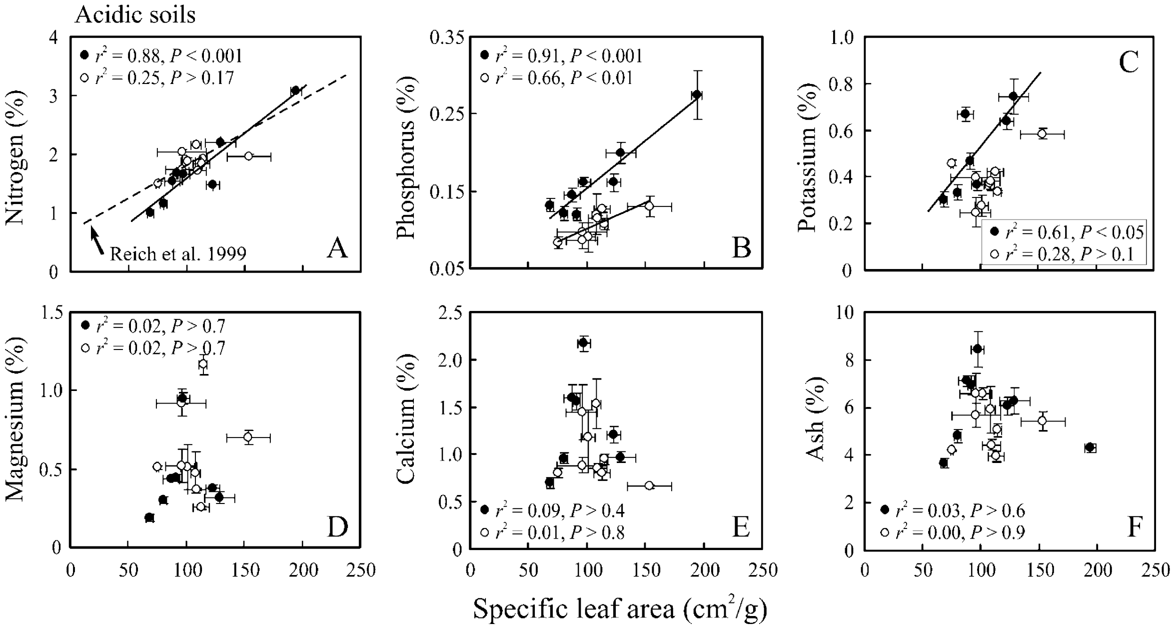

Fig. 2. Foliar nutrient concentrations in relation to SLA in nine species from the oligotrophic bog (open symbols), and in eight species from a flood plain (filled symbols). Each point is an average per species (Table 2). r^2-s are calculated for a linear dependence, and error bars give ± S.E. The bog is on strongly acidic peat, while the flood plain meadows and adjacent heath and swamp forests are on moderately acidic soils (Table 1). In (A), the general relationship of Reich et al. (1999) is also depicted.

1999). The concentrations of foliar Ca, Mg and K varied two- to fourfold across the species and foliar morphologies (Fig. 1), suggesting either widely differing species requirements for these nutrients or that there was a large soil microheterogeneity in the availability of these elements.

Statistical significance of the correlations between foliar nutrients and SLA was similar in the bog plants (Fig. 2). However, there were additional significant relationships between [N] and SLA, and [K] and SLA in the flood plain (Fig. 2). In fact, the relationship of [N] vs. SLA observed in the flood plain was very similar to the general relationship demonstrated by Reich et al. (1999). Although the N data of bog plants also virtually fitted the same broad pattern (Fig. 2A), the interaction term (SLA X site) was significant (P < 0.02) in a separate slope ANCOVA model comparing these two sites. This demonstrates that the bog and flood plain data were not part of the same relationship. Similarly to N, the slope of [P] vs. SLA was also larger in the flood plain than in the bog (P < 0.03).

The leaves were significantly larger and had also greater values of SLA in the wooded meadow species than in the other two sites (Table 3). Foliar [N] was similar between the sites (Table 3), but Ca, K, Mg and ash concentrations were significantly higher in the wooded meadow than in the other two sites (Table 3). [P] was the lowest in the bog, while P/N ratio increased in the order of bog < wooded meadow < flood plain (Table 3).

3.2. Correlations between mineral nutrients

[N] and [P] were not correlated in mid-season in either the wooded meadow (Fig. 3A) or in the bog plants (Fig. 4A). However, there was a strong correlation between [N] and [P] in the flood plain (Fig. 4A). Poor correlations were found

Table 3
Average (± S.E.) leaf area (S, cm^2), specific leaf area (SLA, cm^2/g), mineral nutrient concentrations (%), and P/N mass ratio in leaves of woody species from the wooded meadow (calcareous soil, 26 species), oligotrophic bog (acidic soil, nine species) and flood plain (acidic soil, eight species)

Variable	Wooded meadow	Bog	Flood plain
S	14.1 ± 2.4 ^{a}	2.7 ± 0.9 ^{b}	2.7 ± 1.1 ^{b}
SLA	177 ± 16 ^{a}	107 ± 7 ^{b}	109 ± 14 ^{b}
N	2.010 ± 0.016 ^{a}	1.86 ± 0.07 ^{a}	1.73 ± 0.23 ^{a}
P	0.1416 ± 0.0042 ^{a}	0.106 ± 0.006 ^{b}	0.164 ± 0.018 ^{a}
P/N	0.0705 ± 0.0020 ^{a}	0.0571 ± 0.0028 ^{b}	0.097 ± 0.006 ^{c}
K	1.66 ± 0.11 ^{a}	0.386 ± 0.033 ^{b}	0.50 ± 0.06 ^{b}
Ca	1.87 ± 0.13 ^{a}	1.01 ± 0.10 ^{b}	1.31 ± 0.18 ^{b}
Mg	1.15 ± 0.06 ^{a}	0.60 ± 0.10 ^{b}	0.43 ± 0.09 ^{b}
Ash	9.24 ± 0.46 ^{a}	5.32 ± 0.33 ^{b}	6.0 ± 0.6 ^{b}

Significant differences (P < 0.05) are denoted by a letter code. Kruskal–Wallis ANOVA was used to test for site differences in S, while a standard ANOVA analysis followed by Bonferroni test was used for all other variables.

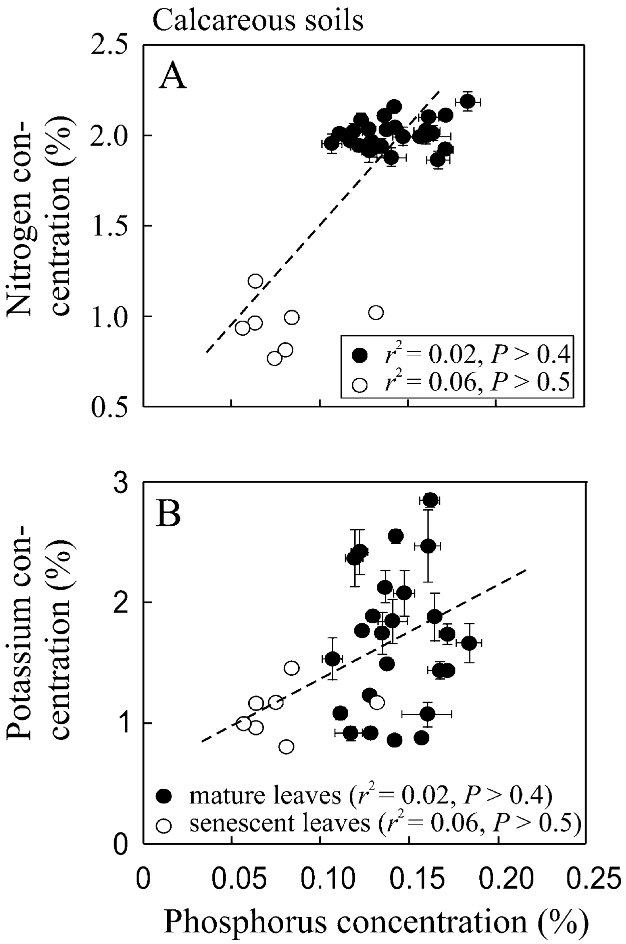

Fig. 3. Correlations between foliar N and P (A), and K and P (B) concentrations in woody species in the wooded meadow in mature (filled symbols, Table 2) and freshly fallen leaves (open symbols; seven species collected at the end of the growing season). Error bars give ± S.E. Dashed lines demonstrate the correlations for the mid- and late-season data pooled ($r^2 = 0.59$, $P < 0.001$ for N vs. P and $r^2 = 0.17$, $P < 0.02$ for K vs. P).

between foliar [P] and [K] in mid-season in all individual sites (Figs. 3B and 4B).

When the late-seasonal data from the wooded meadow were pooled with the mid-seasonal values, a positive relationship between foliar [N] and [P] was found (Fig. 3A), indicating that both elements declined in a similar manner during foliar senescence. [K] and [P] (Fig. 3B), and [K] and [N] ($r^2 = 0.19$, $P < 0.05$) were also correlated in the pooled set of data. Thus, apparently balanced changes in foliage elemental composition occurred with leaf senescing.

In mid-season, Mg, Ca and ash concentrations were generally positively related in all sites with the average r of the significant correlations of 0.77 ($P < 0.001$). The only exceptions were correlations between [Mg] and [Ca] ($P > 0.7$), and [Mg] and ash ($P > 0.5$) in the bog.

3.3. Sources of variation in nutrient contents

There was a large variation among foliar structural characteristics, while foliage element concentrations varied less

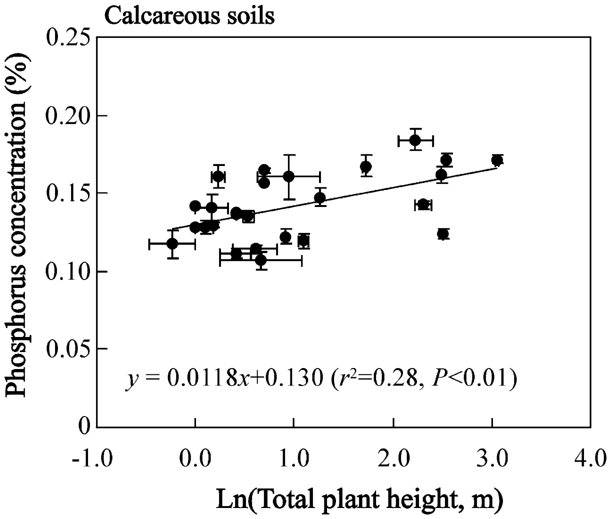

Fig. 4. Relations between foliar N and P (A), and K and P (B) concentrations in the bog (open symbols, Table 2) and the flood plain (filled symbols, Table 2) species. Error bars give ± S.E. The values of r^2s are calculated for linear dependencies.

(Table 4). The average total variability tended to be larger in the flood plain than in the other sites ($P = 0.078$). In particular, foliage nutrient concentrations and average leaf area varied more, but SLA less in the flood plain than in the other sites (Table 4).

Total variability consists of interspecific and within species variability. In the current study, interspecific variability was generally larger than intraspecific variability in all sites, indicating that the total variability was mainly determined by the variability among the species rather than within species (Table 4).

3.4. Can the species-to-species differences in foliar structure and chemistry be explained?

In the wooded meadow, plant life form significantly affected foliar [P]. Phosphorus concentration was larger ($P < 0.05$) in trees (0.157 ± 0.008%) than in shrubs (0.1357 ± 0.0043%). There were also trends of greater [N] (2.062 ± 0.033%) and [K] (2.01 ± 0.19%) in trees than in shrubs (1.990 ± 0.017% for [N] and 1.54 ± 0.13% for [K]), but these were not significant ($P > 0.07$ for [N] and $P > 0.06$ for [K]). Despite this, foliar P/N and P/K ratios were not significantly different between shrubs and trees ($P > 0.09$ for P/N and $P > 0.2$ for P/K). SLA and concentrations of other chemical elements were also not affected by plant life form ($P > 0.2$).

There was a positive correlation between total plant height and foliar [P] (Fig. 5) as well as between foliar P/N ratio and total plant height ($r^2 = 0.21$, $P < 0.02$). Other mineral elements and SLA were not affected by plant size ($P > 0.06$ for a positive relationship with [K] and $P > 0.2$ for the relationships with SLA and other elements).

Table 4
Total, among species, and within species variability of eight foliar structural and chemical characteristics in shrubs and trees at three sites of contrasting soil conditions. Variability was estimated by the coefficient of variation (S.D./mean)

Site and group	Coefficient of variation								
	Area per leaf	Specific leaf area	Mineral concentration						Mean
			N	P	K	Ca	Mg	Ash	
Total variability (*n* = 275 samples)									
Wooded meadow	0.847	0.478	0.071	0.191	0.350	0.351	0.417	0.285	0.374
Bog	0.752	0.339	0.099	0.258	0.241	0.328	0.470	0.221	0.338
Flood plain	0.906	0.293	0.313	0.471	0.358	1.256	0.584	0.272	0.556
Variability among species (*n* = 43 species)									
Wooded meadow	0.977	0.460	0.040	0.169	0.339	0.344	0.332	0.249	0.364
Bog	1.010	0.232	0.078	0.168	0.228	0.301	0.471	0.184	0.334
Flood plain	1.117	0.374	0.381	0.314	0.353	0.560	0.565	0.269	0.492
Variability within species (*n* = 2–21 samples per species)									
Wooded meadow	0.278	0.175	0.046	0.086	0.169	0.089	0.126	0.112	0.135
Bog	0.258	0.162	0.079	0.222	0.155	0.204	0.220	0.157	0.182
Flood plain	0.291	0.128	0.045	0.086	0.123	0.076	0.128	0.150	0.129

The means were not significantly different among the sites in any of the comparisons ($P > 0.05$, ANOVA).

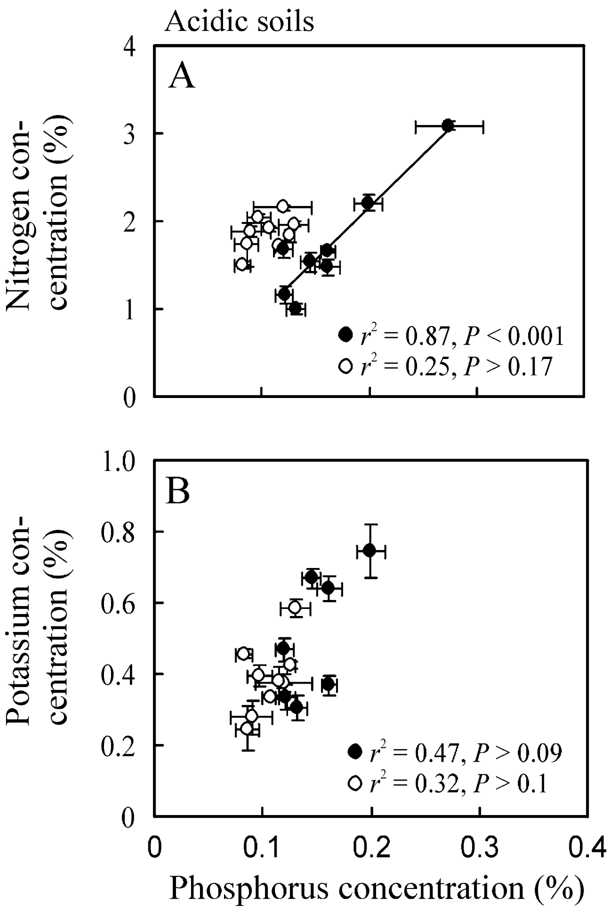

Fig. 5. Foliar phosphorus concentration in relation to total plant height in woody species in the wooded meadow (Table 2). Data presentation as in Fig. 1.

4. Discussion

4.1. Foliage nutrient concentrations in calcareous and acidic soils

In the wooded meadow, average [P] was just above the level (0.125–0.135%) considered limiting for tree species, foliar [N] was relatively low as well, but Ca, K and Mg concentrations (Table 1) were several-fold higher than the limiting concentrations (cf. Rode, 1993, for a review of leaf nutrients in temperate trees). Ca concentrations exceeded the limiting range by threefold, K by twofold, and Mg by ninefold. Clearly, the cation supply was lower in bog and flood plain plants, but it was still higher than that considered limiting for plant growth in the case of Mg and Ca, and slightly below the limiting range in the case of K in the bog (Table 3). In the bog, very low values were observed for P as well as for P/N ratio, indicating that P is the primary limiting nutrient (Table 3). In contrast, P/N ratio was the largest in the flood plain, suggesting that plant growth is primarily limited by N supply in this site (Table 3).

4.2. Is P a limiting nutrient in both acidic and calcareous soils?

Foliar analyses demonstrate that plant P status is optimal in moderately acidic soils as the flood plain in our study, but P availability declines with both decreasing (Binkley and Vitousek, 1989) and increasing soil pH (Bard, 1945; Clement and Gessel, 1985). Lowered P mobility in calcareous soils and low mineralization rates in bogs provide an explanation for the P deficiency in these communities (cf. Section 1). Moreover, soil pH may alter plant P status more than is necessarily evident in soil phosphate concentrations, because of the direct effects of pH on P uptake. Phosphate uptake is largest at nutrient solution pH values around 5 (Baligar, 1987; Breeze et al., 1987).

Typical P/N ratios in P-limited tropical rain forests on acidic soils and in several temperate fens and bogs are on the order of 0.04–0.05 (cf. Vitousek and Sanford, 1986; Wassen et al., 1995, for review). Wassen et al. (1995) suggest that P/N ratios >0.07 in mire vegetation hint at N limitation. Thus, the situation of limiting P seems to be clear in bog plants, where both foliar P and P/N ratio were lower than those considered limiting. Average P/N ratio of 0.0705 ± 0.0020 (varying from 0.055 to 0.090) in the wooded meadow was higher than that observed for the ecosystems with solely P limitation. Nevertheless, the utility of P/N ratio in indicating nutrient imbalances depends on the absolute concentrations of both P and N. P in nucleic acids constitutes a larger fraction of total leaf P than the fraction of total N in nucleic acids. This suggests that the initial requirement for P for non-zero protein synthesis is comparatively larger than in N. Accordingly, P/N ratio may be relatively large even if P is the limiting nutrient. In a number of mire communities, N and P appear to co-limit production over a range of P/N ratios of 0.059–0.200 (Hayati and Proctor, 1991), and P/N ratio in leaves of P-limited *Pinus taeda* stands varies from 0.059 to 0.098 (Adams and Allen, 1985).

Although nutrient ratios are often used as the criterion to identify nutrient imbalances, there is a general difficulty in distinguishing between N and P limitations. The low availability of only one of these essential elements may slow down the soil turnover, and lead to the shortage of the other too, due to enhanced immobilization of nutrients in soil organic matter. Since both P and N were low in the wooded meadow (Table 1), and given that low P supply may bring about low rates of protein synthesis and nitrogen uptake (Clement and Gessel, 1985), the moderate P/N ratio observed in the shrubs and trees in the wooded meadow does not run counter to the hypothesis that P availability is limited in this site. The results of fertilization experiments of the herb vegetation also indicate that P and N may curb the primary production in this wooded meadow (Pork, 1979; Niinemets and Kull, unpublished). Other experiments in calcareous grasslands indicate that the plant productivity does respond to P, but also that it likely interacts with N supply in a complex manner (Niklaus et al., 1998; Stöcklin et al., 1998).

4.3. Interplay between foliar morphology and nutrient concentration

As numerous studies indicate, foliar morphology and nutrient concentrations may be correlated. In the current study, SLA was used as a quantitative variable characterizing foliar morphology. Since the fractional investment of foliar biomass in support biomass is negatively related to SLA (Niinemets, 1999), the requirement for mineral nutrients for foliage construction is lower at low SLA (cf. Medina et al., 1990; Reich et al., 1992; Niinemets and Kull, 1998). The relationship between structural carbon compounds and SLA is likely to provide a mechanistic explanation for the positive relations between foliar mineral nutrient concentration and SLA as frequently observed.

In our study, N was almost invariable in mid-season in the wooded meadow (Figs. 1A and 3A) and in the bog (Figs. 2A and 4A), and we found only a positive relationship between SLA and [P], and none between [SLA] and [N] in these sites (Figs. 1A and 2A). This contrasts to the strong [N] vs. SLA relationship in the flood plain (Fig. 2A), and to the studies where SLA correlates with both [N] and [P] as discussed in Section 1. The patterns observed in the wooded meadow and in the bog (Figs. 3 and 4) were also not in agreement with the positive correlations between the concentrations of elements that are readily retranslocated from the senescent leaves, e.g., P and N (Loveless, 1961; Sobrado and Medina, 1980; Bongers and Popma, 1990; McJannet et al., 1995) or K and N (Bongers and Popma, 1990; Simon et al., 1990). Given that the relationships between leaf structure and [N] and [P] likely depend on the potential availability of the specific nutrient in the plant, conflicting leaf morphology vs. N and P relationships may indicate that P was in a relatively shorter supply than N in both wooded meadow and bog plants. Literature data of the strength of nutrient/structure relationships are in accord with this explanation. The relationship between [N] and SLA was poor in P-limited ecosystems (Reich and Walters, 1994), and SLA was more strongly correlated with [P] than with [N] in P-limited *Eucalyptus grandis* (Kirschbaum and Tompkins, 1990). In contrast, [N] and [K] were better correlates with SLA in another tropical rain forest (Bongers and Popma, 1990), and in temperate bogs and marshes (recalculated from Small, 1972) where P did not play a role as limiting nutrient. This evidence suggests that the strength of leaf structure vs. nutrient relationships may vary depending on the availability of specific nutrients relative to other physiologically important elements.

Our hypothesis agrees with SLA vs. [N] and [P] relations in the wooded meadow and in the bog, where the plant species maximized leaf-level P-use-efficiency. Although [N] was likely more limiting in the flood plain (Table 3), both [N] and [P] were strongly associated with SLA in this site (Fig. 2A). This discrepancy may indicate that different combinations of species colonizing habitats of varying nutrient availability exhibit various strategies to cope with nutrient shortages. It is unclear what is the role of enhanced leaf P in the flood plain. In conditions of large phosphorus availability, [P] is poorly correlated with foliar photosynthetic capacity (Reich and Schoettle, 1988; Wright et al., 2001). However, a large P pool may be necessary to increase the content of nucleic acids, thereby allowing to enhance the rate of protein turnover (Usuda, 1995; Usuda and Shimogawara, 1995). Such an effect of P on the rate of protein turnover may partly compensate for low soil N availability in perennials competing in the flood plain.

4.4. Plant life form and size effects on foliar nutrient concentrations

In our study, interspecific variability in foliar structure and nutrient concentrations was the primary determinant of total variability (Table 4). Part of this variability was explained by life-form differences. We observed that foliar P concentrations were greater in trees than in shrubs, and that foliar P as well as P/N ratio increased with increasing plant size (Fig. 4). This was not due to changes in foliar morphology, since SLA was not related to plant stature. Given that acquisition of relatively immobile phosphate strongly relies on plant's ability to build an extensive root system exploring large soil volumes, but effective capture of mobile ions such as nitrate is less heavily dependent on extensive root systems (Norby et al., 1986; Sands and Mulligan, 1990; BassiriRad et al., 1997), we suggest that improved P nutrition relative to N nutrition is indicative of larger root systems in greater plants. An increased investment in below-ground biomass in response to nutrient deficiency is a general plant strategy to increase plant internal nutrient concentrations (e.g., Poorter and Nagel, 2000). Moreover, as the woody plants increase in size, the fractional biomass allocation in foliage decreases but that in supporting tissues—branches, stems, and roots—increases (Magnani et al., 2000). As the current study demonstrates, P limitation may effectively be overcome by increased biomass investment in roots, and also that the limitations imposed by different nutrients may vary widely among the plants growing in the same soil.

Given the importance of life-form and plant size in determining foliar nutrient contents, it may be argued that we did not observe significant correlations between [N] and SLA in the wooded meadow and bog because our dataset did not include herbaceous plants that inherently possess larger SLA and nitrogen contents (e.g., Reich, 1993). However, the general relationship of [N] vs. SLA observed for the data from six biomes (Reich et al., 1999) is actually not dependent on whether ($r^2 = 0.72$, $P < 0.001$) or whether not ($r^2 = 0.58$, $P < 0.001$) herbaceous species are included in the dataset. The data sampled from the flood plain (Fig. 2A) also agreed with the general relationship of Reich et al. (1999), while [N] contents did not essentially vary in the wooded meadow and in the bog. This suggests that lack of herbaceous species in our dataset did not modify the statistical significance of leaf structure vs. chemistry relationships.

Taken together our data demonstrate that [N] and [P] vs. SLA relations vary significantly among sites of differing soil conditions. Although there is strong evidence of the convergence of leaf trait relationships due to fundamental trade offs between foliar structure, chemistry and physiology (Reich et al., 1997, 1999), current results suggest that the broad patterns in leaf structure vs. nutrient relations consist of a series of viable scaling solutions.

Acknowledgements

Financial support was provided by the Estonian Science Foundation (Grants 859 and 2661 to K.K., and 4584 to Ü.N.) and the Estonian Ministry of Education and Science (grant 0182468As03). We thank Tiina Elvisto for providing the unpublished data of late-season foliar nutrient contents, and Angelika Portsmuth, Juhani Püttsepp and Ülle Püttsepp for assistance with plant and soil sampling. Thoughtful suggestions of the reviewers have significantly contributed to maturation of this paper.

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