Oecologia (2006) 147: 315–326
DOI 10.1007/s00442-005-0269-z

ECOSYSTEM ECOLOGY

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Foliar pH as a new plant trait: can it explain variation in foliar chemistry and carbon cycling processes among subarctic plant species and types?

Received: 18 February 2005 / Accepted: 7 September 2005 / Published online: 11 October 2005

Abstract Plant traits have become popular as predictors of interspecific variation in important ecosystem properties and processes. Here we introduce foliar pH as a possible new plant trait, and tested whether (1) green leaf pH or leaf litter pH correlates with biochemical and structural foliar traits that are linked to biogeochemical cycling; (2) there is consistent variation in green leaf pH or leaf litter pH among plant types as defined by nutrient uptake mode and higher taxonomy; (3) green leaf pH can predict a significant proportion of variation in leaf digestibility among plant species and types; (4) leaf litter pH can predict a significant proportion of variation in leaf litter decomposability among plant species and types. We found some evidence in support of all four hypotheses for a wide range of species in a subarctic flora, although cryptogams (fern allies and a moss) tended to weaken the patterns by showing relatively poor leaf digestibility or litter decomposability at a given pH. Among seed plant species, green leaf pH itself explained only up to a third of the interspecific variation in leaf digestibility and leaf litter up to a quarter of the interspecific variation in leaf litter decomposability. However, foliar pH substantially improved the power of foliar lignin and/or cellulose concentrations as predictors of these processes when added to regression models as a second variable. When species were aggregated into plant types as defined by higher taxonomy and nutrient uptake mode, green-specific leaf area was a more powerful predictor of digestibility or decomposability than any of the biochemical traits including pH. The usefulness of foliar pH as a new predictive trait, whether or not in combination with other traits, remains to be tested across more plant species, types and biomes, and also in relation to other plant or ecosystem traits and processes.

Keywords Anti-herbivore defence · Litter decomposition · Functional trait · Leaf acidity · Specific leaf area

Communicated by Andrea Polle

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Introduction

Evidence is still mushrooming that plant species composition is a forceful control on ecosystem carbon and nutrient cycling (e.g. Hobbie 1992; Chapin et al. 1997; Tilman et al. 1997; Wardle et al. 1997; Berendse 1998; Binkley and Giardina 1998; Grime 2001; Eviner and Chapin 2003). The analysis of patterns in functional traits among plant species is an ever more popular tool (1) for describing recurrent patterns and trade-offs in plant design and function (Reich et al. 1992; Cornelissen et al. 2001; Grime 2001; Craine and Lee 2003; Díaz et al. 2004; Wright et al. 2004) and (2) for predicting

important carbon and nutrient cycling processes as well as their responses to environmental change (e.g. MacGillivray et al. 1995; Schulze et al. 1994; Wardle et al. 1998; Lavorel and Garnier 2002; Chapin 2003). In order for such a tool to be practical to various researchers and land managers with usually limited resources, and to be able to deal with multiple species in multiple ecosystems, many researchers have advocated the use of 'soft traits' (Hodgson et al. 1999; Weiher et al. 1999; Westoby et al. 2002; Cornelissen et al. 2003, Díaz et al. 2004). These are traits that are easy and inexpensive to measure for large numbers of plants and samples and which, at the same time, have good predictive power of other 'hard' plant traits or even of important ecosystem processes and responses themselves (Hodgson et al. 1999, Lavorel and Garnier 2002). Since leaves are the main plant modules for plant biomass production, and together an important resource for the consumer and decomposer subsystems, much focus has been directed towards soft leaf traits. Specific leaf area (SLA; fresh area per unit dry mass; or its inverse, leaf mass per area) has repeatedly been identified as an important trait by many of the above authors and others, particularly because of its predictive power of relative growth rate (Lambers and Poorter 1992; Cornelissen et al. 1996) and its trade-off against foliar lifespan (Reich et al. 1992; Wright et al. 2004), stress tolerance and defences against herbivores (Grime et al. 1997; Pérez-Harguindeguy et al. 2003). However, SLA generally explains at best half of the interspecific variation in growth rate or herbivory-related parameters in interspecific datasets.

Recently, soft leaf traits (e.g. SLA, toughness) have also been employed with partial success to predict leaf litter decomposability (Gallardo and Merino 1993; Cornelissen 1996; Cornelissen and Thompson 1997; Pérez-Harguindeguy et al. 2000a; Garnier et al. 2004), decomposition being a crucial control on carbon and nutrient cycling. Classical hard chemical traits such as leaf or litter C/N ratio, lignin/N ratio, lignin or phenolic concentrations remain widely used as predictors of litter decomposition rate (e.g. reviews by Swift et al. 1979; Parton et al. 1994; Aerts 1997; Cadisch and Giller 1997). However, they are relatively hard to measure for large numbers of species, and none of these parameters has emerged as a solid single predictor of decomposability across species, functional types and ecosystems. New combinations of soft and/or hard traits could help to improve predictive power (see Heal et al. 1978 for an early example).

Here we present leaf pH as a new plant trait and explore whether it should feature on the list of favourite traits or trait combinations for interspecific comparisons in the carbon or nutrient cycling context. It has been long known and well documented that bulk pH of the litter layer or upper soil horizon has important repercussions for decomposition and that this pH is partly a result of the composition of the green vegetation that produces this litter (e.g. Swift et al. 1979; Wardle et al. 1997; Finzi et al. 1998). Some early studies have suggested a possible correspondence between initial litter pH and decomposition rate among temperate forest tree species, however, without testing such correspondence quantitatively (Melin 1930; Matsson and Koutler-Andersson 1941). Also, some of the known predictors of variation in foliar anti-herbivore defence or litter decomposability among species, for instance basic cation concentration (Broadfoot and Pierre 1939; Swift et al. 1979; Cornelissen and Thompson 1997) and tannic and other phenolic acids (McKey et al. 1978; Swift et al. 1979; Coley 1988; Cadisch and Giller 1997), must also be strong determinants of leaf or litter pH (Broadfoot and Pierre 1939; Mattson and Koutler-Andersson 1941). It is therefore remarkable that, to the best of our knowledge, nobody has so far made direct and broad interspecific comparisons of leaf or leaf litter pH as a possible predictor of leaf or litter turnover processes. Foliar pH might be more than an indirect, easy predictor of other leaf traits and processes. For instance, decomposers are sensitive to the pH of the direct environment of their litter substrate, irrespective of the biochemistry that provides the H_3O^+ ions (Swift et al. 1979). Also, we have anecdotal information and observations suggesting that leaves that taste acidic to people, e.g. *Rumex acetosella*, are avoided by invertebrate herbivores. This could give foliar pH added value as a predictor of palatability or decomposability in combination with other traits.

Here we explore the extent to which interspecific variation in green leaf pH or (pre-decomposition) leaf litter pH across a broad range of species correlates with variation in other traits, and with variation in two important carbon and nutrient cycling processes: leaf digestion by herbivores and litter decomposition. Specifically we test the following hypotheses:

(1) There is an interspecific correlation between green leaf pH or leaf litter pH and biochemical and structural foliar traits that have a key role in biogeochemical cycling.
(2) There is consistent variation in green leaf pH or leaf litter pH among plant types relevant to biogeochemical cycling.
(3) Green leaf pH can predict a significant proportion of variation in leaf digestibility among plant species and types.
(4) Leaf litter pH can explain a significant proportion of variation in leaf litter decomposability among plant species and types.

For hypotheses (3) and (4) we also compare the predictive power of foliar or litter pH with regard to leaf digestibility or litter decomposability with the predictive power of SLA. To test our hypotheses, we developed an assay to measure leaf pH rapidly for large numbers of small samples and linked our new pH data for a wide range of subarctic plant species and types to existing data for foliar chemistry, leaf digestibility and litter decomposability of the same species.

Methods

Details about the study area, species included, leaf and litter sampling, biochemical analyses and digestibility and decomposability tests were given in two previous papers (Quested et al. 2003; Cornelissen et al. 2004). In the following, we only give the minimum information necessary in the context of pH in this paper.

Study area, plant species and types

We collected green leaves and leaf litter of up to 73 plant species (67 seed plants, 2 ferns, 1 horsetail, 2 clubmosses, 1 moss) from their typical subarctic terrestrial ecosystems within a 25 km radius around Abisko, North Sweden (68°21′N, 18°49′E). Emphasis was on low-altitude ecosystems (altitudes 300–600 m), which included (1) birch (*Betula pubescens* ssp. tortuosa) woodland (4 m tall) with ericaceous dwarf shrub understorey; (2) mesic woodland (4 m tall) with birch, willow (*Salix* spp.), grey alder (*Alnus incana*) and perennial forbs; (3) treeless tundra with ericaceous dwarf shrub species, sedges (*Carex* spp.), rushes (*Juncus* spp.), *Calamagrostis lapponica* grass and forbs; (4) mires with sedges (*Eriophorum* spp., *Carex* spp.); (5) grassy ruderal sites, while a few species were collected from (6) river banks and (7) coniferous patches (*Pinus sylvestris*, *Picea abies*/*obovata*). Ten species were collected from (8) forb-rich sub-alpine meadows and (9) fellfields at higher altitudes (600–1,100 m). Together the species collected included most of the dominant constituents of these ecosystems. All species except three of the seven hemiparasites were perennial, which reflects the fact that annual species are relatively uncommon and low in biomass in the predominant subarctic ecosystems. The selected species also represented the predominant plant types (see the *X*-axis in Fig. 1) in terms of higher taxonomy and N uptake strategy, which we expected to be the most differentiating factors with respect to leaf and litter quality, including pH. Leaf quality and litter decomposability have previously been linked to hemiparasitism and nitrogen fixing (Quested et al. 2003) and to mycorrhizal strategy (Cornelissen et al. 2001). Summergreen versus evergreen habit, another known important parameter in this context (Cornelissen 1996), was not used explicitly for our classification, but all groups consisted exclusively or predominantly of one or the other (see below). Higher taxonomy distinguished bryophytes, fern allies, gymnosperms, monocot angiosperms and dicot angiosperms. Nutrient uptake strategy distinguished hemiparasitism (all herbaceous), N_2 fixing capacity (herbaceous except for the deciduous tree *A. incana*) and carnivory (both herbaceous; Quested et al. 2003); and three mycorrhizal association types (mostly assigned using data by Michelsen et al. 1996, 1998) with respect to predominant N uptake from inorganic versus organic sources. These types were (1) non-mycorrhizal or arbuscular-mycorrhizal (mostly herbaceous plus the deciduous shrub *Ribes spicatum* and the tree *Sorbus aucuparia*); (2) ecto-mycorrhizal (all deciduous woody plants except for semiwoody, deciduous *Dryas octopetala* and the forb *Bistorta viviparum*); (3) ericoid (dwarf shrubs only; five evergreen, two deciduous). *Orthilia secunda* could not be classified with certainty, while *Arctostaphylos alpinus* was classified as ectomycorrhizal since its predominantly arbutoid mycorrhiza is considered to be functionally close to ectomycorrhiza (Smith and Read 1997).

Leaf and litter sampling

We collected fresh, mature green leaves of 73 species during summer 1999. Usually leaves from at least five plants were pooled, but from only two trees in *P. abies x obovata* and *P. sylvestris*. Fresh, undecomposed leaf litter of the same 73 species was collected in 1998, mostly during September. About two-thirds were collected from the same sites as the green leaves. A subset of 33 species

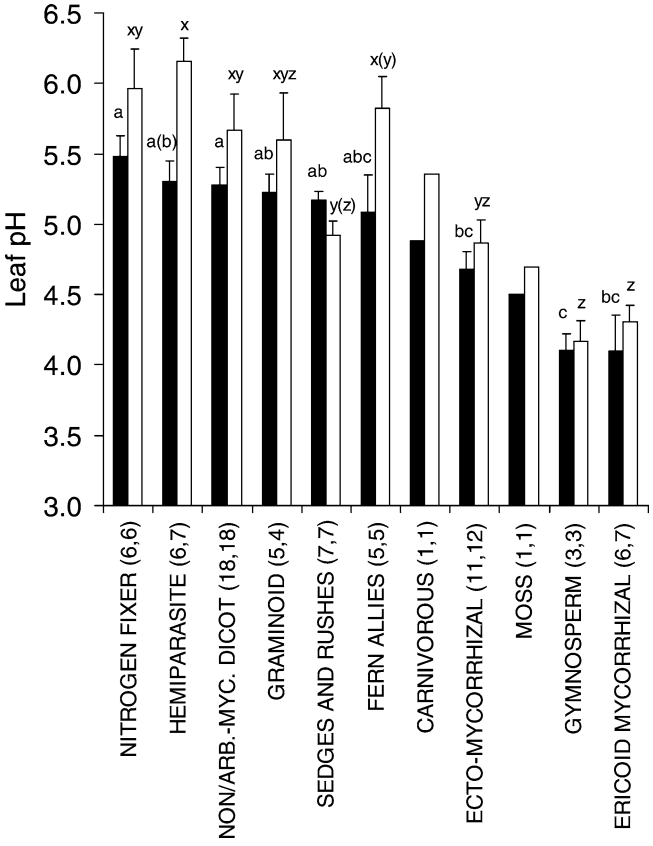

Fig. 1 Variation in pH of green leaves (*black bars*) or leaf litter (*white bars*) among plant types. NON/ARB.-MYC. DICOT: non-mycorrhizal and arbuscular-mycorrhizal dicotyledons. Numbers of species included are given in parentheses for green leaves and leaf litter, respectively. Standard errors are given one-sided. Means sharing a similar letter are not significantly different (i.e. $P > 0.05$) in Games-Howell posthoc tests (with separate tests for green leaves and litter). *Letters in parentheses* indicate $P = 0.05$

(also including *S. phylicifolia*, for which litter was not collected in 1998) was collected again in 1999, so as to have a direct comparison of green leaves and litter of the same cohorts, and to test the robustness of interspecific variation in litter quality. Leaves and litter of the 1999 cohorts were collected from the same sites for virtually all of the species. Both leaves and litter were stored air-dried and dark until the treatments and analyses.

pH analysis

For each ground green leaf or leaf litter sample (i.e. pooled leaves or litter of a species), we took four subsamples for pH measurement. These had been used previously for [N] and [C] analyses, for which they had been oven-dried (see below). The use of dried leaves makes the method robust to transport and storage of material, as is often necessary in fieldwork campaigns. While we assume the pH ranking of species to be similar for dried (and subsequently rehydrated) and fresh tissues, and for different particle sizes after cutting or grinding, we recommend empirical calibration of such factors in future studies of leaf pH. Each subsample consisted of 150 ± 50 mm^3 air-dried sample and 1,200 mm^3 (1.2 ml) deionised water (i.e. volume ratio 1:8) in a 2.5 ml eppendorf tube. Extensive initial checks showed that pH measurements were robust to substantial deviations from this 1:8 volume ratio (data not shown). The mixtures were shaken at 250 rpm for 1 h, then centrifuged at 13,000 rpm for 5 min. pH of the fluid was measured using a narrow (5 mm diameter) SenTix Mic electrode connected to an Inolab Level 2 pH meter (both: WTW, Weilheim, Germany). We calibrated the pH meter against buffer solutions (pH 4 and 7) before each measurement series. Variability around the mean for the four subsamples was generally small (standard errors on average 0.05 pH unit), as it was for repeated measurements on the same subsamples (deviations on average < 0.05 pH unit; data not shown).

Other analyses of leaf and litter quality

Air-dried leaf or litter samples were ground and oven-dried (60°C, 48 h) before chemical analyses. For lignin concentration, three (in a few cases two) 2 g subsamples of each leaf population were analysed with the Van Soest assay as described by Allen et al. (1989) and discussed by Palm and Rowland (1997). For total phenol concentration and foliar C and N concentrations, we weighed four subsamples (~2.5 mg), to the nearest µg, placed into tin elemental analysis cups. Mass-based C and N concentrations were determined using an isotope ratio mass spectrometer (Tracermass Europa Scientific Ltd, Crewe, UK). We used a combination of methanol extraction and the Folin-Ciocalteau assay to determine mass-based total soluble phenol concentrations of leaves (Waterman and Mole 1994; Palm and Rowland 1997). See Cornelissen et al. (2004) for the rationale of using these relatively crude lignin and phenol analyses, with known limitations, for broad interspecific comparisons.

SLA (fresh lamina area over lamina dry mass) was measured on ten leaves per species (but not on mosses or clubmosses), which was possible from several different plant individuals. We measured leaf area with an Area Meter (Delta-T, Burwell, Cambridge, UK) and leaf dry mass after 72 h at 60°C. We also used green leaf SLA in relation to litter decomposition, since litter SLA is difficult to measure in many species whose leaves shrivel up during senescence.

Digestibility of green leaves was analysed as in vitro cow's rumen juice digestibility, based on the method of Tilley and Terry (1963). Three 0.5 g subsamples of each leaf population were ground and incubated with buffered cow's rumen juice for 48 h, then with acid-pepsin solution for an additional 48 h. Dry-matter digestibility (digested mass per unit initial mass, milligram per gram) was calculated using the dry mass of the residue.

Litter decomposition

We took leaf litter subsamples at random from each pooled species collection and weighed 1.0 ± 0.1 g of air-dried material to the nearest mg. We estimated initial true (oven-dried) mass from the water content of subsamples. We sealed the sample into a nylon litterbag with 0.3 mm mesh, which allowed exchange of micro-organisms and small soil invertebrates. Interspecific ranking of litter decomposability was shown previously to be robust to mesh size, litterbag size or initial mass (Cornelissen 1996,; Quested et al. 2003). We remoistened the litterbag samples, then incubated them in an outdoor litter bed in a nursery at the Abisko Scientific Research Station, following the Cornelissen (1996) approach. This litter bed was exposed to the natural macroclimate (for climate and weather data, see Quested et al. 2003) and was in a sheltered spot, where snow cover lasted almost continuously from November through May in the period 1998–2000. The main litter bed consisted of wooden frames enclosing a free-draining foundation of grit stones, on top of which we put the incubation medium, being a loose 100-mm layer of thoroughly mixed (fresh and partly decomposed) litter taken from nearby typical birch heath-woodland. Different compartments of the frame hosted different litterbags (subsamples) of the same species and incubation period. On 6 October 1998 we positioned all litterbags flat and without overlap, approx. 3–4 cm below the surface of the incubation matrix. After compaction of the litter matrix, incubation depth was gradually reduced to 2 cm. This is deeper than the natural depth of most fresh litter, which serves to approximately double decomposition rates and reduce variability due to variability in surface temperatures and moisture (authors' unpublished results based on comparison with surface-placed litterbags of three of the species). Thus this experiment can be seen as a semi-

standardised 'outdoor laboratory test'. For each species a subset of five litterbags was retrieved on 15 September 1999 (1-year incubation). Then, a thin layer of fresh litter was added to the top of the matrix holding the second subset of five litterbags, which was retrieved on 18 September 2000 (2-year incubation).

In order to test for possible interactions of interspecific decomposition rankings and incubation environment, we incubated litterbags of a subset of 11 diverse species also in an adjacent smaller litterbed, filled with an incubation matrix consisting of ruderal, presumably high-nutrient species from a local playground. Otherwise these litterbags were treated similarly and incubated simultaneously with the ones in the main litterbed for one year. Matrix samples of both litterbeds were taken in September 1999 for pH analysis. Litter decomposability was expressed as 1-year or 2-year mass loss percentage as calculated from initial and final dry mass.

Statistics

Prior to parametric statistical analyses below, data were ln-transformed (some of the biochemical parameters) or arcsine [square-root ($x/100$)] transformed (litter mass loss percentage), which was necessary to improve frequency distributions and homogeneity of variances. Because cryptogams (both fern allies and the moss *Polytrichum*) consistently had low leaf digestibility or litter decomposability at a given pH, we carried out most of the analyses mentioned below with and without these outliers. We employed Pearson's correlation to test for correspondence of interspecific rankings of pH with other leaf or litter quality traits as well as for correspondence of interspecific pH rankings of different leaf or litter samplings. We tested variation in mean leaf or litter pH among plant types using one-way analysis of variance followed by post-hoc Games-Howell comparisons between individual types. We used linear regression to predict variation in green leaf digestibility among plant species or types from that in green leaf chemical or structural traits. We also used linear regression to predict variation in litter decomposability among plant species or types from that in each of several litter traits. For analyses at the species level, we also added pH as a second term to the regression model, in order to test whether pH could add significantly to the predictive power of other commonly used leaf or litter traits. We considered Pearson's correlation coefficients of $r > 0.5$ (Table 1) as indications of collinearity between pairs of independent variables. Generally, cases of collinearity corresponded with a lack of contribution of pH as a second variable to regressions. Finally, we compared regressions between litter pH and mass loss for incubations in the main birch heath litterbed and the ruderal litterbed, respectively. All analyses were carried out in SPSS version 10.1 (SPSS, Inc.).

Results

Variation in foliar pH among plant species and types

Generally across most species except sedges and rushes, green leaves were slightly more acidic than leaf litter (Fig. 1). However, the ranking of species by pH was broadly maintained between green leaves and leaf litter (1999 cohort for green leaves versus 1999 cohort for litter: $r = 0.74$, $N = 33$, $P < 0.001$; 1999 cohort for green leaves versus 1998 cohort for litter: $r = 0.71$, $N = 68$, $P < 0.001$). The species ranking according to litter pH was also rather robust to interannual variation, based on

Table 1 Interspecific Pearson's correlations (r) between pH and other traits of green leaves and leaf litter shed in 1998 and 1999, respectively, in the Abisko subarctic flora

	Green leaves		1998 litter		1999 litter	
	N[a]	r[b]	N	r	N	r
pH versus [N]	33	0.55** [c]	72	0.48***	32	0.64***
	31	0.54**	66	0.51***	31	0.65***
pH versus [C]	33	-0.65***	72	-0.63***	32	-0.57**
	31	-0.67***	66	-0.65***	31	-0.58**
pH versus C:N ratio	33	-0.63***	72	-0.56***	32	-0.71***
	31	-0.63***	66	-0.59***	31	-0.71***
pH versus [lignin]	33	-0.54**	41	-0.12^{NS}	32	0.05^{NS}
	31	-0.60***	35	-0.22^{NS}	31	-0.02^{NS}
pH versus [cellulose]	33	-0.03^{NS}	41	-0.22^{NS}	32	0.05^{NS}
	31	-0.04^{NS}	35	-0.31^{NS}	31	0.05^{NS}
pH versus [phenol]	29	-0.30^{NS}	–	–	–	–
	27	-0.36^{NS}	–	–	–	–
pH versus SLA	33	0.59***	–	–	–	–
	31	0.57**	–	–	–	–

Bottom lines of relationship refer to seed plants only (excluding fern allies and mosses)
NS not significant
[a]Number of species
[b][C], pH and SLA untransformed, all other parameters ln-transformed prior to analysis
[c]Significance levels: $*P < 0.05$; $**P < 0.01$; $***P < 0.001$

data from 30 vascular seed plant species sampled in subsequent years (1998 versus 1999 cohort for leaf litter: $r = 0.95$, $N = 30$, $P < 0.001$). There was significant variation in pH among plant functional types as defined by a combination of higher taxonomy and nutrient uptake strategy (Fig. 1), both for green leaves ($F = 7.57$, $N = 67$, $P < 0.001$) and for leaf litter ($F = 6.58$, $N = 69$, $P < 0.001$). Relatively high pH was seen among nitrogen fixers, hemiparasites, other non-mycorrhizal or arbuscular mycorrhizal dicots, graminoids and ferns and horsetails, intermediate pH among sedges, rushes and ecto-mycorrhizal plants and low pH among gymnosperms, clubmosses and ericoid mycorrhizal plants (Fig. 1).

Correlations between pH and other leaf or litter quality traits across plant species and types

There were significant correlations among species between green leaf pH and green leaf [N], [C], C:N ratio, [lignin] or SLA, respectively. (Table 1). [C] and C:N ratio were the strongest correlates with pH, while [cellulose] was a particularly poor correlate. However, for none of the correlations did r^2 approach 0.5 (50% of interspecific trait variation explained by the other trait), either for all plants or for the seed plants only. The same relationships for leaf litter gave broadly comparable correlations as for green leaves, although both [lignin] and [cellulose] gave coefficients close to zero (Table 1). In contrast, the correlation between pH and C:N ratio was particularly strong within the 1999 leaf litter cohort, with r^2 just exceeding 0.5. The somewhat different patterns for 1998 and 1999 litter were probably due to the larger species set in the former, some of which (e.g. *Drosera rotundifolia*, *Trollius europaeus*) increased the scatter around the trendline. However, the 1998 and 1999 species sets were broadly comparable in terms of functional and taxonomic spectra (cf. Quested et al. 2003; Cornelissen et al. 2004).

pH as a (joint) predictor of green leaf digestibility or leaf litter decomposability

Green leaf pH alone explained up to a third (seed plants only) of the interspecific variation in leaf digestibility (Table 2). Only leaf [C] and SLA were better predictors. Remarkably, pH had similar predictive power as leaf C:N ratio or [lignin]. The best predictive power (R^2 between 0.4 and 0.5) was reached when pH was added as a second term to the model with [cellulose] as the first independent variable. In cases where pH showed low collinearity with the first independent trait, it generally strengthened the regression considerably when added as a second independent variable.

Most litter traits as well as SLA were better predictors of 1-year litter mass loss than of 2-year mass loss, except [lignin], which predicted slightly more variation in 2-year than of 1-year mass loss (Table 3). Litter pH alone could explain only up to a quarter of the interspecific variation in litter decomposability. However, for the species subset with seed plants only, it significantly improved all trait–decomposition regressions when added as a second independent variable, except for the relationships between [C] or SLA and 2-year mass loss. In contrast, pH generally added little or no significant explanatory power to relationships between [N], [C], C:N ratio or SLA and litter mass loss. These four independent variables were also the ones that showed strong collinearity with pH (Table 1). Both for litter [lignin] and [cellulose], the addition of pH as a variable increased the strength of the regressions drastically, pushing R^2 well above 0.5 in all regressions involving seed plants only as well as in regressions against 1-year mass loss for all plants (Table 3).

The positive relationship between pH and (1-year) litter mass loss was robust to the litter environment (matrix) in which the litter bags were incubated, as tested for a subset of 11 species common to both litterbeds. Litter pH versus 1-year mass loss in birch heath litterbed (matrix pH = 5.65 ± 0.05) gave $R^2 = 0.55$ ($P < 0.01$), while

Table 2 Regressions of chemical and structural parameters against digestibility of green leaves without and with the contribution of leaf pH as a second independent variable

	R^2 using single parameter		R^2 adding pH	
pH versus digestibility	0.261**[a]	(0.338**)	–	–
[N] versus digestibility	0.158*	(0.183*)	0.280**	(0.355**)
[C] versus digestibility	0.350**	(0.438***)	0.377**	(0.472***)
C:N ratio versus digestibility	0.228**	(0.267**)	0.301**	(0.376**)
[Lignin] versus digestibility	0.261**	(0.266**)	0.339**	(0.381**)
[Cellulose] versus digestibility	0.152*	(0.145*)	0.402***	(0.464***)
[Phenol] versus digestibility	0.074^{NS}	(0.066 ^{NS})	0.217*	(0.273*)
SLA versus digestibility	0.321**	(0.403***)	0.370**	(0.474***)

R^2 is underlined if pH added significant ($P < 0.05$) explanatory power as an added independent variable. Results in parentheses: exclusion of the two fern allies. For signs (+/-) of the relationships see Table 1

$N = 33$ vascular species (29 in analyses with [phenol])

[N], C:N ratio, [lignin], [cellulose] and [phenol] were ln-transformed prior to analysis

NS not significant

[a]Significance levels: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

Table 3 Regressions of chemical parameters of leaf litter (1998 cohort) or green specific leaf area (SLA) against leaf litter decomposability (as 1-year or 2-year mass loss), without and with the contribution of leaf pH as a second independent variable. See Table 2 for explanation

		R^2 using single parameter		R^2 adding pH	
pH	versus 1-year mass loss percentage	0.175***[a]	(0.253***)	–	–
	versus 2-year mass loss percentage	0.112**	(0.193***)	–	–
[N]	versus 1-year mass loss percentage	0.162***	(0.151**)	0.229***	(0.277***)
	versus 2−year mass loss percentage	0.096**	(0.085*)	0.141**	(0.199**)
[C]	versus 1-year mass loss percentage	0.183***	(0.258***)	0.219***	(0.310***)
	versus 2-year mass loss percentage	0.130**	(0.223***)	0.149**	(0.253***)
C:N ratio	versus 1-year mass loss percentage	0.207***	(0.206***)	0.246***	(0.291***)
	versus 2-year mass loss percentage	0.127**	(0.128**)	0.154**	(0.208**)
[Lignin]	versus 1-year mass loss percentage	0.342***	(0.261***)	**0.521***	(**0.601***)
	versus 2-year mass loss percentage	0.367***	(0.284**)	0.482***	(**0.591***)
[Cellulose]	Versus 1-year mass loss percentage	0.413***	(0.354***)	**0.543***	(**0.627***)
	versus 2-year mass loss percentage	0.297***	(0.234**)	0.387***	(**0.519***)
SLA	versus 1-year mass loss percentage	0.282***	(0.358***)	0.335***	(0.417***)
	versus 2-year mass loss percentage	0.229***	(0.331**)	0.258**	(0.364***)

Results in parentheses: exclusion of cryptogams. R^2 values exceeding 0.5 are in bold script. For signs (+/-) of the relationships see Table 1
$N = 72$ or 73 species (41 in analyses involving [lignin] or [cellulose])
[N], C:N ratio, [lignin], [cellulose] were ln-transformed, mass loss percentage of arcsine($\sqrt{(x/100)}$) transformed
NS not significant
[a]Significance levels: $*P < 0.05$; $**P < 0.01$; $***P < 0.001$

litter pH versus 1-year mass loss in the ruderal litter bed (matrix pH = 6.46 ± 0.02) gave $R^2 = 0.66$ ($P < 0.01$).

For those chemical or structural parameters that gave the best predictive power of biogeochemical processes, we aggregated the data as means for each plant type in subsequent regressions (excluding fern allies and mosses, which tended to deviate from the patterns for seed plants). The R^2 of these relationships were generally much higher than those at the species level, both for trait-digestibility regressions of green leaves (Fig. 2) and for trait-decomposition regressions of litter (Fig. 3). Green leaf pH predicted almost half of the variation in

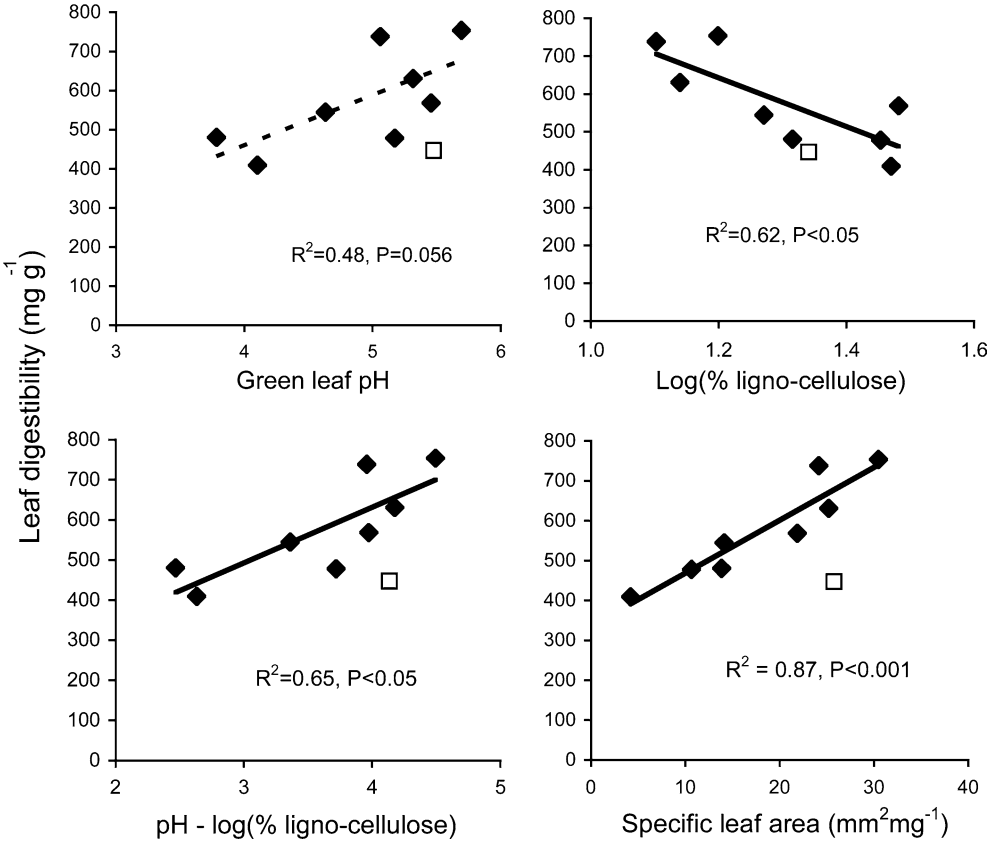

Fig. 2 Green leaf digestibility as predicted by four other green leaf parameters among plant types (as in Fig. 1; carnivorous plants and mosses excluded. ♦ Seed plants; □ Fern allies. Regressions are only given for the seed plants. All graphs used a total of 33 species underlying the means for plant types. For the mean green leaf pH of individual plant types, see the *black bars* in Fig. 1

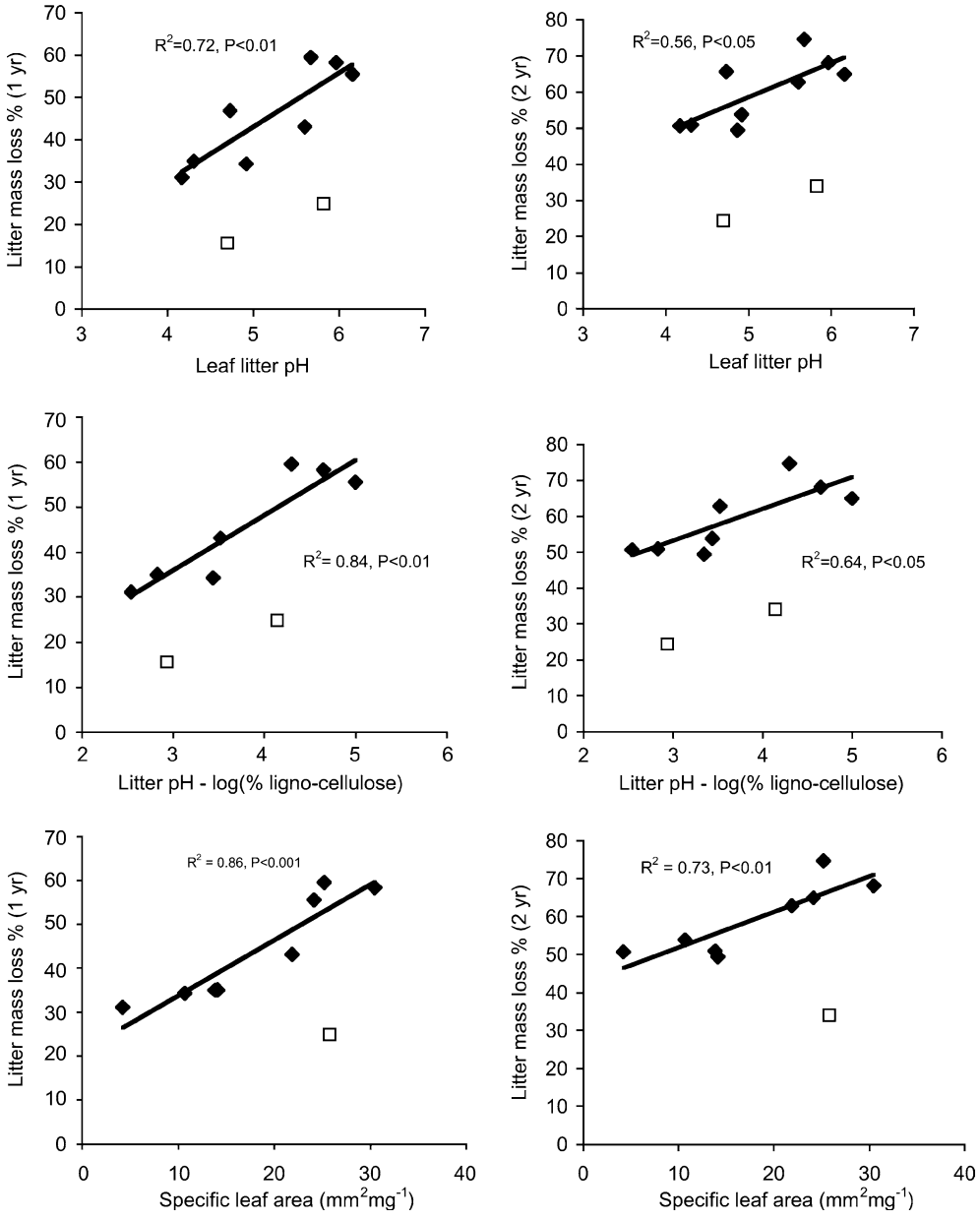

Fig. 3 Litter decomposability as 1- or 2-yr mass loss percentage as predicted by litter parameters or green leaf SLA among plant functional types (as in Fig. 1). Underlying data for pH are based on 72 species, for pH –log(percentage of lignocellulose) on 41 and for SLA on 69 species. ♦ Seed plants; □ Fern allies and moss. Regressions are only given for the seed plants. Mass loss percentage data were arcsine[$\sqrt{(x/100)}$] transformed prior to regressions. For the mean leaf litter pH of individual plant types, see the *white bars* in Fig. 1. For comparison, the regression between log(percentage of lignocellulose) and 1-year mass loss percentage (not shown) gave $R^2 = 0.51$ ($P < 0.05$) and that between log(percentage of lignocellulose) and 2-year mass loss percentage (not shown) gave $R^2 = 0.33$ (not significant) with only seed plants included

leaf digestibility among seed plant types (Fig. 2a). Based on the above regressions at the species level (Table 2), and the fact that pH represents -log[H+], we combined pH and the log-transformed summed concentration of lignin plus cellulose into one variable: pH-log(percentage of lignocellulose). This compound parameter explained more of the variation in leaf digestibility among seed plant types (Fig. 2c) than log(percentage of lignocellulose) (Fig. 2c) or any of the simple chemical traits alone (data not shown). However, SLA was still better at predicting leaf digestibility (Fig. 2d) and in this case compound traits involving pH and SLA did not improve the regression (data not shown). Similarly, litter pH itself was a reasonable predictor of 1-year (Fig. 3a) or 2-year mass loss (Fig. 3b), at least among seed plant types only. Also in these regressions, using pH-log(percentage of lignocellulose) as opposed to log(percentage lignocellulose) or any of the simple traits improved the predictive power substantially (Fig. 3c, d and data not shown). Again, however, green leaf SLA was still a marginally better predictor of 1-year (Fig. 3e) or 2-year mass loss (Fig. 3f) compared to pH-log(percentage of lignocellulose).

Discussion

Our results for a subarctic flora demonstrate that the pH of leaves or leaf litter has a useful complementary role to play as a new, easy-to-measure trait predicting species contributions to key carbon and nutrient turnover processes. Foliar pH is a complex trait that depends on the concentrations, mobilities and interactions of multiple chemical compounds, which in turn are highly variable

in space and time, also within species. Ontogenetic factors, leaf age and infection by endophytic fungi or pathogenic microbes might all be further sources of variability in leaf pH. Our approach in this paper has been to measure leaf or litter pH from a wide range of plant species and types in their natural environments, and to interpret clear and significant relationships with other traits or biogeochemical processes as evidence that the predictive power of foliar pH is robust to such intraspecific variability. Indeed, we found that pH of leaves or leaf litter can predict a substantial proportion of the variation in biochemistry, leaf digestibility to ruminant herbivores and litter decomposability among plants in a subarctic flora. In support of our hypothesis (1), we showed that interspecific variation in both green leaf pH and leaf litter pH correlated significantly, and in some cases substantially, with that in key biochemical and structural foliar traits, the best correlates being C concentration and C:N ratio. Interestingly, green leaf pH correlated reasonably well with SLA, a 'soft' trait of proven usefulness. We also found consistent variation in green leaf pH or leaf litter pH among plant types relevant to biogeochemical cycling, providing support for hypothesis (2). It is well known that ecosystems with a predominance of ericoid and/or ecto-mycorrhizal plants, including gymnosperms such as pine and spruce species, tend to feature strongly organic soils with high C:N ratios, low N availability, and poor quality litter of low pH (Swift et al. 1979; Read 1991; Cornelissen et al. 2001; see also Finzi et al. 1998). Our results extend the latter pattern to the green foliage, and the litter this turns into, of individual plant species and types, and will help to disentangle the pH contributions of different plant types to the overall soil litter pH.

We demonstrated that green leaf pH was itself a reasonable predictor of leaf digestibility of 33 diverse subarctic species as tested in fresh rumen juice of ruminants (cows) that had not previously been exposed to this foliage; this supports our hypothesis (3). However, more substantial interspecific variation in leaf digestibility was predicted by coupling pH with leaf [cellulose] or, to a lesser extent, with C:N ratio or [lignin]. It was remarkable that SLA alone did almost as good a job of predicting interspecific variation in leaf digestibility as [cellulose] and pH combined. At the seed plant type level, SLA was by far the best predictor of leaf digestibility. We have to be aware, though, that plant types were not weighted for species numbers and that there were only few species representing some of the plant types. Also, the relationship at this level may be sensitive to the plant type classification employed. Indeed, the relationship between SLA and leaf digestibility was much less tight when a somewhat different classification, incorporating growth form and leaf lifespan, was used (Cornelissen et al. 2004).

In support of our hypothesis (4), we found that leaf litter pH could explain a significant proportion of variation in leaf litter decomposability among plant species, particularly for the first year of decomposition. However, again the most powerful contribution of litter pH was that it greatly improved the predictive power of litter [lignin] or [cellulose] when added to the regression model as a second independent variable. In this case, the combination of [lignin] with pH or [cellulose] with pH greatly exceeded the predictive power of SLA in relation to litter decomposability, whether or not pH was coupled with SLA as a second variable. Corresponding with the above link between traits and leaf digestibility, the power of green SLA as a predictor of litter decomposability among (means for) seed plant types exceeded that of any of the other simple traits. SLA was even a slightly better predictor than the compound trait combining pH, [lignin] and [cellulose]. In this regression the plant types were represented by more species, suggesting that SLA is a particularly useful soft predictor of litter decomposition at this level of species aggregation, at least in the subarctic flora that was analysed.

It is important to note that the above regressions involving leaf digestibility or litter decomposability were mostly stronger if cryptogams, i.e. a moss, two club-mosses, a horsetail and two ferns, were excluded from analysis, except in the cases of [lignin] and [cellulose]. The deviation of cryptogams from the seed plant regressions was particularly striking at the plant type level: at a given leaf (or litter) pH or SLA, the fern allies and the moss *Polytrichum* generally had poor leaf digestibility and low litter decomposability compared to seed plants. The generally low decomposability of fern litter compared to that of seed plants was also revealed in a subtropical flora in Argentina, and tentatively linked to particularly powerful secondary metabolites in ferns (Pérez-Harguindeguy et al. 2000b). From the sparse information available, the low decomposability of *Polytrichum* in this study may also be representative of a general pattern for bryophytes. For instance, *Hylocomium splendens*, a common circumarctic moss, has slow litter decomposition (Hobbie 1996, Quested and Cornelissen, unpublished data). There are not enough data available to test whether low decomposability in mosses is linked to low pH. Our data for *Polytrichum* would contradict this. However, it is well known that *Sphagnum* peat mosses generally combine (very) low pH with slow litter decomposition (Clymo and Hayward 1982; Aerts et al. 1999). Perhaps most mosses contain relatively high concentrations of anti-microbial secondary chemistry, but the composition and acidic potential of this chemistry may differ among species.

Now that we have demonstrated consistent albeit not very tight relationships between leaf or litter pH and carbon turnover processes, the question arises whether similar relationships can be detected in other biomes with different types of plant species. For a preliminary comparison with a contrasting flora in warm-temperate Argentina, we recollected fresh leaf litter (1999/2000) of some of the same species for which litter decomposability had been tested previously (1995/1996; Pérez-Harguindeguy et al. 2000a) and measured litter pH of bulk species samples according to the method described

Table 4 Linear regression relationships between initial leaf litter pH and litter mass loss % as calculated from literature data for northern temperate forests (all laboratory incubations) and from the authors' unpublished data for an Argentine flora (outdoor study)

Site	Plant species	Decomposability test [a]	R^2
Temperate forests in W-Virginia, USA[c]	15 woody angiosperms, 4 gymnosperms	IJ, 120 days (27.5°C)	0.21* [b]
Temperate forests in W-Virginia, USA[c]	15 woody angiosperms, 4 gymnosperms	IJ, 180 days (27.5°C)	0.26*
'Several habitats' in NW-USA[d]	2 angiosperm trees, 10 gymnosperm trees	ID, 100 days (10°C)	0.44*
'Several habitats' in NW-USA[d]	2 angiosperm trees, 10 gymnosperm trees	ID, 100 days (25°C)	0.37*
Woods, parks, farm in S-Sweden[e]	7 angiosperm trees, 1 gymnosperm, wheat	IJ, 365 days (temp.?)	0.31^{NS}
Forests in NE-USA[f]	10 woody angiosperms, 5 gymnosperms	IJ-CO_2, 27 days (25°C)	0.14^{NS}
Diverse ecosystems Central-W Argentina[g]	16 herbaceous and woody angiosperms	Litterbed, 63 days (summer)	0.08^{NS}

Decomposability is expressed as mass loss percentage unless stated otherwise. All regression slopes were positive
NS not significant
[a]IJ incubation in jar (mass loss); ID incubation in dish (mass loss); IJ-CO2 incubation in jar (CO_2 production)
[b]* $P < 0.05$
[c]Broadfoot and Pierre (1939), [d]Daubenmire and Prusso (1963), [e]Mattson and Coutler-Andersson (1941), [f]Melin (1930), [g]Unpublished pH data by *N*. Pérez-Harguindeguy, J.H.C. Cornelissen combined with Pérez-Harguindeguy et al. 2000a)

above. For 16 wide-ranging seed plant species (including 2 woody plants, 4 forbs, 7 graminoids, 1 stem succulent, 2 bromeliads), there were some significant correlations between litter pH (1999/2000 material) and other litter chemistry parameters (1995/1996 material): litter pH versus ln(C/N), $r = -0.67$, $P < 0.01$; litter pH versus litter [C], $r = -0.60$, $P < 0.05$; litter pH versus litter [N], $r = 0.63$, $P < 0.01$. However, the regression between litter pH and litter decomposability (9 weeks in outdoor litterbed under summer monsoon conditions) was poor and non-significant (Table 4). It appeared that the well-represented graminoids combined poor decomposability with relatively high litter pH, a pattern that was also somewhat apparent in the subarctic dataset. For green leaves of 42 wide-ranging species in the same Argentine flora, pH of newly collected leaves only correlated significantly with [C] of previously collected leaves ($r = -0.57$, $P < 0.001$), but not with ln(C/N) or [N].

Although interspecific variation in foliar litter pH has not been applied before as a predictor of carbon turnover processes such as litter decomposition, some underlying data, collected for other purposes, are available from older forestry-related studies. For different sets of temperate woody species, initial leaf litter pH predicted on average about a third of the variation in litter mass loss during laboratory incubations between 100 and 365 days of duration (Table 4). Thus, the interspecific relationship for the subarctic flora is extended to the northern temperate woody flora, but not to a contrasting, more xerophytic flora in warm-temperate Argentina. We hypothesise that the relationship between litter pH and decomposability is generally stronger in biomes with strong (variation in) organic matter accumulation, where there is a strong representation of species with substantial concentrations of organic acids.

Concluding remarks

From our results, we can conclude that in a subarctic flora, species leaf and litter pH, respectively, have a role to play as easy-to-measure predictors of key carbon turnover processes such as leaf digestion in the ruminant gut and leaf litter decomposition. The main contribution of pH as a foliar trait could be to improve the predictive power of foliar lignin and/or cellulose concentrations across species in relation to these processes. When species are aggregated into plant types as defined by higher taxonomy and nutrient uptake mode, green SLA appears to be at least as powerful a predictor of the same processes as any of the biochemical traits, at least in the subarctic flora. So, while the usefulness of SLA is extended by this study, the usefulness of foliar pH as a new plant trait remains to be tested across more plant species, types and biomes, and perhaps also as a predictor of other ecosystem traits or processes. Another challenge with respect to relationships between foliar pH and species traits or ecosystem processes, is to disentangle the separate and interactive contributions of innate species or population pH, phenological patterns, ontogenetic variation and environment-induced phenotypic variation in plant pH. Field and 'common garden' studies with controlled soil biochemistry and pH could be employed to these purposes.

Acknowledgement We thank Alexandra Kondratchuk, Miranda de Beus, Merijn van Leeuwen, Fernanda Vendramini, Sven Jonasson, Ellen Dorrepaal and several staff at Abisko Research Station, Sweden for their significant help with particular aspects of this study. We declare that the work reported here complies with the current laws of the countries in which it was performed.

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