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Energy requirement for foliage formation is not constant along canopy light gradients in temperate deciduous trees

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SUMMARY

Foliage construction cost (glucose requirement for formation of a unit foliar biomass, G, kg glu kg^{-1}), chemical composition and morphology were examined along a light gradient across the canopies in five deciduous species, which ranked according to increasing shade-tolerance as *Populus tremula* < *Fraxinus excelsior* < *Tilia cordata* = *Corylus avellana* < *Fagus sylvatica*. Light conditions in the canopy were estimated by a hemispheric photographic technique, allowing ranking of sample locations according to long-term light input incident to the sampled leaves (relative irradiance). G and foliage carbon concentration increased with increasing relative irradiance in *F. excelsior*, *T. cordata* and *C. avellana*, but were independent of irradiance in *F. sylvatica* and *P. tremula*. However, if G of non-structural-carbohydrate-free dry mass was considered, it also increased with increasing relative irradiance in *P. tremula*. A positive correlation between the concentration of carbon-rich lignin and irradiance, probably a result of the acclimation to greater water stress at higher light, was the major reason for the light-dependence of G. Lignin concentrations were highest in more shade-tolerant species, resulting in greatest carbon concentrations in these species. Since carbon concentration and G are directly linked, the leaves of shade-tolerant species were also more expensive to construct. As the result of these effects, G increased faster with increasing leaf dry mass per area which was mainly determined by relative irradiance, in shade-tolerators. Given that shade-tolerant species had lower leaf dry mass per area at common irradiance and that this saturated at lower relative irradiance than leaf dry mass per area in the intolerant species, it was concluded that enhanced energy requirements for foliage construction might constrain species morphological plasticity and the upper limit of leaf dry mass per area attainable at high light.

Key words: carbon, foliar construction cost, irradiance, lignin, nitrogen, non-structural carbohydrates, shade-tolerance, structural carbohydrates.

INTRODUCTION

Leaf morphology is sensitive to daily light receipt during foliage growth and development. Leaf dry mass per area (LMA) consistently increases with increasing irradiance (Ellsworth & Reich, 1993; Niinemets, 1995, 1997c). This is a relevant adaptive response optimizing plant carbon assimilation potentials, because high LMA enables increased carbon acquisition in high light, while low LMA enhanced light harvesting in low light, changes that collectively lead to an improvement of the carbon gain of the whole plant (Björkman, 1981; Gutschick & Wiegel, 1988; Niinemets & Tenhunen, 1997).

The alterations in leaf morphology in response to light gradients are also paralleled by modifications in foliar chemistry. The concentrations of the immediate products of CO_2 assimilation, soluble carbohydrates and starch, are frequently greater in leaves growing at higher irradiance (Fjeld, 1992; Niinemets, 1997a,c). In several instances, the stoichiometry of foliage structural components is modified by light gradients along the forest canopies as well, probably because the gradients in other stress factors also generally accompany light gradients (e.g. Eliáš, 1979; Chiariello, 1984). In a previous study of five temperate deciduous species, we found that lignin concentrations increased at the expense of cellulose and hemicellulose in all species with increasing irradiance (Niinemets & Kull, 1998). This was considered to be an important acclimation response which improved mechanical properties of foliage and thereby the ability to tolerate water stress, which was expected to be more severe at higher irradiance. Given that lignin is carbon-rich (63.3%, calculated according to Nimz, 1974) in comparison with cell-wall polysaccharides (44.4%, using cellulose as model compound), and that leaf

carbon concentration is directly proportional to the energy requirement for foliage construction (G, kg glu kg^{-1}; Vertregt & Penning de Vries, 1987), enhanced investment of foliar biomass in lignin might increase G. However, the strong increase in foliar non-structural carbohydrates with low carbon content decreases G, and a careful analysis is required to predict the summary effect of the outlined changes in foliar chemistry. Studies using a few fixed light levels in temperate, Mediterranean as well as in tropical species (Dadykin & Kononenko, 1975; Steubing *et al.*, 1979; Frey & Ivask, 1983; Runge, 1986; Larcher & Thomaser-Thin, 1988) consistently show that foliar heat of combustion (ΔH) scales positively with irradiance. Since ΔH can be used as an alternative variable for deriving foliar G (Williams *et al.*, 1987; Griffin, 1994), these data suggest that there is a basic positive relationship between G and irradiance. Though potentially extremely relevant in affecting the amount of foliar biomass which can be constructed from a certain amount of carbon, few studies have been conducted to examine the variability in G between different light treatments (Sims & Pearcy, 1991, 1994; Poorter & Villar, 1997) or over a wide natural light gradient (Williams *et al.*, 1989; Niinemets, 1997b), and to analyse the implications of the variability in G for foliage structure and function.

In our previous study, shade-tolerant species had higher lignin concentrations at common irradiance than intolerant species (Niinemets & Kull, 1998). This was attributed to their lesser ability osmotically to adjust leaf water potential by carbohydrates due to lower rates of photosynthesis (Bazzaz, 1979; Björkman, 1981; Abrams & Mostoller, 1995; Niinemets *et al.*, 1998), and consequently to the requirement for more advanced structural modifications of cell walls to tolerate low leaf water potentials. Higher lignin concentrations in the foliage of shade-tolerators also suggest that the leaves of these species should contain more carbon and be more expensive to construct. This would have important implications on whole-canopy foliar area development and biomass costs of light harvesting.

From another perspective, foliar growth might depend directly on lignification and G, because both enhanced cell-wall lignification and carbohydrate requirements for biomass construction might bring about increased diffusive limitations for carbohydrate transport to the sites of incorporation in cells. Moreover, extensively lignified cell walls might constitute a significant barrier for CO_2, and thereby curb assimilation. Accordingly, a negative relationship might exist between leaf growth and G. In the previous study, shade-tolerant species had lower LMA at common irradiance, and their LMA saturated at a lower irradiance than that in intolerant species (Niinemets & Kull, 1998).

In this paper, foliage chemical and morphological data reported in Niinemets & Kull (1998) were further analysed by asking the following questions. (1) What is the significance of altered stoichiometry of foliage chemicals in terms of the energy requirements for foliage construction? Do the changes in foliar chemistry lead to a positive correlation between G and irradiance? (2) Do species differ in G? (3) Is leaf dry mass per area related to G? If so, are the relationships consistent between the species?

MATERIALS AND METHODS

Species and study sites

Five temperate deciduous woody species of contrasting light requirement, *Corylus avellana* L., *Fagus sylvatica* L., *Fraxinus excelsior* L., *Populus tremula* L. and *Tilia cordata* Mill., were chosen for the analysis. The shade-tolerance of studied trees increases in the order of *P. tremula* < *F. excelsior* < *T. cordata* < *F. sylvatica* (Ellenberg, 1988; Otto, 1994, see Niinemets & Kull, 1998 for the discussion of this qualitative ranking). In central Europe, *C. avellana* is ranked as a species mostly occurring at intermediate irradiances (Ellenberg, 1991). However, in Estonian forests it also grows in deep shade and tolerates irradiances at least as low as in the coppice of *T. cordata* (Niinemets & Kull, 1998).

The details of the study locations are reported in Niinemets & Kull (1998). The major characteristics of the sampled stands are depicted in Table 1.

Foliage collection

Fagus sylvatica was sampled in mid-September 1991, all other species in August 1994. A mobile lift was used for taking foliar samples along the canopy light gradient at two to seven heights per tree. The average highest relative sampling height (height in the tree per total tree height) ranged from 0.88 ± 0.02 in *F. sylvatica* to 1.0 in *C. avellana* and *T. cordata* (the uppermost leaves could always be sampled in these species). Four (*P. tremula*) to 10 trees (*F. excelsior*) were included in the analysis. Foliar samples (5–12 leaves per sampling location) were taken at 1500–1600 hours on cloudy days from south canopy aspect in *F. sylvatica*, and at 0900–1100 hours without any special regard to weather conditions and compass direction in four other species. A detailed sampling scheme is given in Niinemets & Kull (1998).

Estimations of light

Hemispherical photographs (Anderson, 1964; Rich *et al.*, 1993 with modifications of Nilson & Ross, 1979) were used to estimate long-term light levels in the canopy as described in Niinemets and Kull

Table 1. *Parameters of the sampled stands*

Stand	Location	Elevation above the sea level (m)	Stand height (m)	Sampled species (average ± SE height of sampled trees, m)	Co-dominants	Soil* A horizon		
						pH	Base saturation (%)	C:N ratio
Oberwarmensteinach	49°59′N, 11°47′E	700–750	8–12	*Fagus sylvatica* (7.8 ± 1.0)	*Picea abies* (L.) Karst.	3.2–3.8†	4–8	18.7
Tartu	58°15′N, 26°45′E	50–60	14–19	*Tilia cordata* (15 ± 2)	*P. abies*	6.0–6.5‡	91–98	18.3
Ülenurme	58°18′N, 26°42′E	60–65	15–18	*Corylus avellana* (6.0 ± 0.7), *Fraxinus excelsior* (7.2 ± 1.1), *Populus tremula* (16.3 ± 0.6)	*Betula pendula* Roth., *Padus avium* Miller, *Sorbus aucuparia* L.	3.9–4.6‡	42–60	9.4–9.7

*The stands were on following soils: podsols and brown pseudopodsols formed on phyllite (Oberwarmensteinach), a brown pseudopodsol formed on a sandy clay moraine (Tartu), and a sandy loam pseudopodsol formed on a reddish-brown sandy clay moraine (Ülenurme). †pH was determined in 0.01 M solution of $CaCl_2$ (Kaupenjohann *et al.*, 1989) or ‡in 1 M solution of KCl.

(1998). Basically an index, I_{sum} (relative irradiance), was calculated from hemispherical photos by weighting long-term potentially penetrating diffuse and direct irradiance in photosynthetically active spectral region. The I_{sum} varies from 0 to 1, a value of 0.0 corresponds to a situation with no penetrating canopy gaps, and I_{sum} = 1.0 in completely open locations above the canopy.

Chemical composition of foliage and leaf structure

Concentrations of foliar carbon (C_m), nitrogen (N_m), non-structural carbohydrates (NSC, starch plus ethanol-soluble carbohydrates), total minerals (M), lignin (L_m) and structural polysaccharides (cellulose and hemicellulose) were determined as outlined previously (Niinemets & Kull, 1998).

Projected leaf area was measured with a video area-meter (DIAS, Delta-T Devices, Cambridge, UK) in *F. sylvatica*, or with a computer digitizer (QD-1212, QTronix, Taiwan) using self-developed computer software in the four other species. Dry mass of the leaves was determined after oven-drying to a constant mass at 70°C.

Foliar construction cost

An estimate of leaf construction cost [G, kg glucose (kg dry mass)$^{-1}$] was calculated from mineral-free carbon concentration [$C_m^a = C_m/(1-M)$, kg kg^{-1}] and N_m (kg kg^{-1}) as (Vertregt & Penning de Vries, 1987; Poorter, 1994; Niinemets, 1997b):

$$G = G'(1-M) + \left(\frac{4 \times 180.25 \times 0.0833 P_n N_m}{14.0067}\right), \quad (1)$$

where P_n is the proportion of leaf nitrogen which is reduced at the expense of extra metabolic energy, and G', the construction cost of mineral-free biomass if ammonium is the only source of nitrogen, is equal to $5.077 C_m^a - 1.041$ (Poorter, 1994). The second term of eqn (1) adds additional costs required for nitrate reduction in non-assimilative tissues. Implicit in eqn (1) are the assumptions that nitrate assimilation costs 4 mole reductive equivalents per 1 mole of nitrate, and that 1 mole of NAD(P)H costs 0.0833 mole of glucose. The P_n depends on inorganic nitrogen source and on where inorganic nitrogen is being reduced. Nitrogen assimilation in autotrophic plant cells might proceed with no glucose cost (Raven, 1985; Poorter, 1994), because the reductive equivalents generated by chloroplasts in the light might be used directly for nitrogen assimilation. This is not only because chloroplast electron transport has a capacity beyond that required for CO_2 fixation (Bloom *et al.*, 1989), but also because nitrate photoassimilation does not compete with CO_2 fixation at low irradiance as well (Robinson, 1988). Assuming that nitrate reduction in leaves proceeds with no glucose cost (Raven, 1985; Poorter, 1994),

Table 2. *Foliage carbon concentration* (C_m, *kg kg*$^{-1}$) *and construction cost* (G, *kg kg*$^{-1}$) *in relation to leaf dry mass per area* (*LMA*, *kg m*$^{-2}$) *: linear regression analysis*

Species	C_m vs LMA	r^2	P	G vs LMA	r^2	P	$G_{NSC\text{-}free}$ vs LMA^c	r^2	P
Populus tremula	$y = 0.465 + 0.0854x$	0.04	ns	$y = 1.40 + 0.245x$	0.02	ns	$y = 1.33 + 2.06x$	0.18	ns
Fraxinus excelsior	$y = 0.437 + 0.148x$	0.31	<0.01	$y = 1.25 + 0.630x$	0.23	<0.05	$y = 1.27 + 0.808x$	0.22	<0.05
Corylus avellana	$y = 0.455 + 0.277x$	0.37	<0.001	$y = 1.34 + 1.21x$	0.32	<0.01	$y = 1.34 + 3.00x$	0.51	<0.001
Tilia cordata	$y = 0.425 + 0.649x$	0.78	<0.001	$y = 1.20 + 3.04x$	0.76	<0.001	$y = 1.20 + 5.74x$	0.66	<0.001
Fagus sylvatica	$y = 0.484 + 0.111x$	0.05	ns	$y = 1.48 - 0.155x$	0.01	ns	$y = 1.54 + 1.18x$	0.14	ns

Leaf non-structural carbohydrate (NSC) free dry mass per area (LMA^c, kg m^{-2}) was used in the regressions with glucose cost of NSC-free dry mass ($G_{NSC\text{-}free}$, kg kg^{-1}). Only *P*-values for the statistical significance of the slopes are depicted, since the intercepts were significantly different from zero ($P<0.001$) in all cases.

only the proportion of nitrogen in leaves originating from nitrate reduced in non-assimilative organs adds to foliage construction cost. Thus, P_n is given as (Niinemets, 1997b):

$$P_n = \frac{1}{R}(R - \alpha U_l - \beta S_n U_r)[S_n(1-\beta)], \quad (2)$$

where R is the nitrogen requirement for foliage growth per nitrogen demand for annual tree growth, U_l and U_r are the proportions of annual nitrogen uptake by leaves and roots, respectively, α is the fraction of aerial nitrogen uptake incorporated into leaf tissues, β is the proportion of nitrate absorbed by roots and reduced in leaves, and S_n is the fraction of nitrate of total nitrogen absorbed by roots (all parameters are in kg kg^{-1}). The first part of eqn (2) gives the fraction of leaf nitrogen that is acquired by roots minus the nitrate reduced in leaves; the part in square brackets is the nitrate fraction of total root nitrogen uptake reduced in non-assimilative plant compartments. Both NO_2 and NO_3^- from aerial uptake, which are incorporated into leaf tissues, are assumed to be reduced there. The detailed information on the physiology of plant nitrogen nutrition and site nitrogen balance required for P_n calculations was available only for *F. sylvatica*, where P_n was fixed at 0.12 (see Appendix). Nevertheless, existing data for other species suggested that ammonium was a more important source of foliar nitrogen in all species (except for *T. cordata*, see the discussion in the Appendix), and a value of 0.12 for P_n was used throughout the current study except where noted.

To calculate foliar construction cost per unit NSC-free dry mass ($G_{NSC\text{-}free}$), both the mineral-free carbon and nitrogen concentrations expressed on a NSC-free dry mass (see Niinemets, 1995, 1997a) entered into the eqn 1.

Data analysis

Regression analyses were carried out to test the influence of irradiance on foliage construction cost. Linear techniques were used where possible, but owing to non-linearity, several relationships were fitted by second-order polynomial regressions. Interspecific differences in G were separated by covariation analysis (species as the main effect, irradiance as the covariate) followed by the Bonferroni test. Owing to species differences in light requirement as well as canopy architecture and life form, the sampled light ranges were different (e.g. *P. tremula* possessed no leaves below a I_{sum} of 0.19, and *C. avellana* did not reach relative irradiances higher than 0.79). Therefore, only the data covering the I_{sum} range of 0.19–0.79 were included in the covariation analysis. This routine also eliminated the problem of non-linear effects of light on foliar variables, because the relationships were effectively linear over the

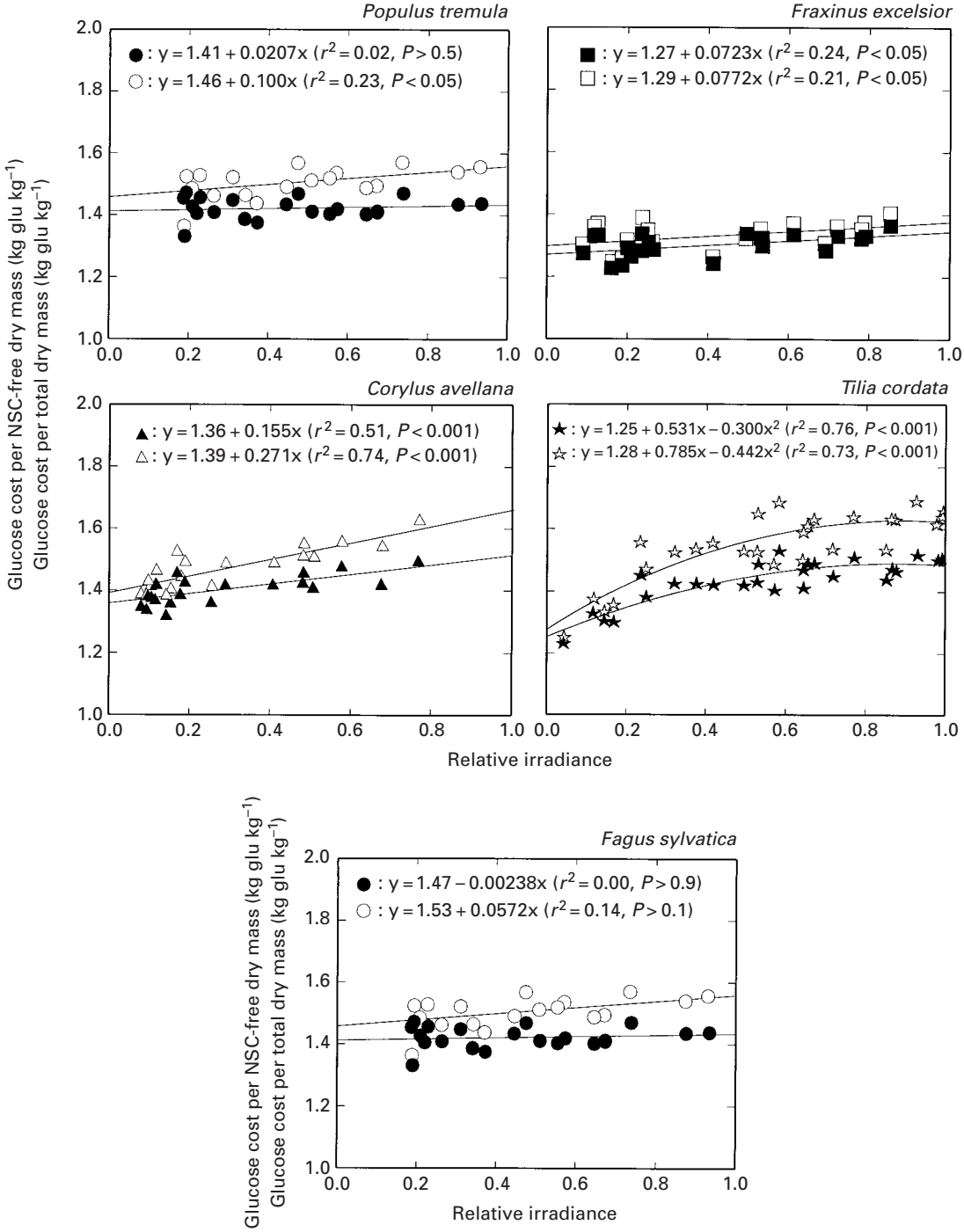

Figure 1. Total foliage glucose cost (G, filled symbols), and G of non-structural-carbohydrate-free dry mass (open symbols) as a function of relative irradiance.

truncated light range (Tsutakawa & Hewett, 1978). The slopes did not differ significantly between the species (detected as the interaction term), and a common-slope ANCOVA model was appropriate. Throughout the study, the term 'at common irradiance' denotes intercept differences as detected by ANCOVA. Covariation analyses were also carried out to compare the parameters between the species at common leaf dry mass per area (LMA); all sampled values were used in these comparisons. However, these comparisons should be interpreted with caution, because the ranges in LMA were inherently different between the species (Niinemets & Kull, 1998). All statistical tests were considered significant at $P < 0.05$ (SAS Institute Inc., 1990).

RESULTS

G *in relation to irradiance and foliage structure*

There was a positive correlation between leaf carbon concentration (C_m) and irradiance in *C. avellana*

Table 3. *Interspecific differences in foliar structural and morphological variables at common irradiance : results of one-way ANCOVA**

Species	Carbon concentration (C_m, kg kg^{-1})	Glucose cost of total dry mass (G, kg kg^{-1})	Glucose cost of NSC-free dry mass ($G_{NSC\text{-}free}$, kg kg^{-1})
Populus tremula	47.42 ± 0.16a	1.421 ± 0.008a	1.501 ± 0.011a
Fraxinus excelsior	44.85 ± 0.17b	1.300 ± 0.008b	1.330 ± 0.010b
Corylus avellana	46.99 ± 0.22a	1.403 ± 0.011a	1.472 ± 0.015a
Tilia cordata	47.60 ± 0.30a	1.427 ± 0.015a	1.533 ± 0.022a
Fagus sylvatica	48.71 ± 0.11c	1.473 ± 0.005c	1.540 ± 0.007c

*Species as the main effect, irradiance as the covariate. Parameter averages (±SE) with the same letter are not significantly different (Bonferroni test, $P > 0.05$).

($r^2 = 0.56$, $P < 0.001$), *F. excelsior* ($r^2 = 0.28$, $P < 0.05$), and *T. cordata* ($r^2 = 0.66$, $P < 0.001$), but not in *F. sylvatica* ($r^2 = 0.04$, $P > 0.4$) or in *P. tremula* ($r^2 = 0.03$, $P > 0.4$). The relationships with C_m were qualitatively identical with LMA (Table 2). Given that leaf nitrogen concentration (N_m) was relatively constant along the light gradients in all species (Niinemets & Kull, 1998), the variability in glucose requirements for formation of a unit foliar biomass (G), dependent on both N_m and C_m (eqn (2)), was dominated by changes in C_m. With increasing irradiance (Fig. 1) and LMA (Table 2) G increased in *C. avellana*, *F. excelsior* and *T. cordata*, but was independent of light and leaf morphology in *P. tremula* and *F. sylvatica*.

At common irradiance, *F. sylvatica* had the highest and *F. excelsior* the lowest G (Table 3), and at common LMA, species ranked as *F. sylvatica* > *T. cordata* = *C. avellana* > *P. tremula* > *F. excelsior* and ranked identically on the basis of their carbon concentration (Table 3). Assuming that root nitrate assimilation is the major source of reduced nitrogen in the foliage of *T. cordata* ($P_n = 0.8$, cf. Appendix), G in this species was larger than that in *C. avellana*, and equal to that in *F. sylvatica*.

If the values for all species were combined, G was positively related to both LMA ($r^2 = 0.25$, $P < 0.001$) and I_{sum} ($r^2 = 0.26$, $P < 0.001$). However, when the positive relationship between LMA and I_{sum} (Niinemets & Kull, 1998) was accounted for by a multiple linear regression analysis, G was negatively related to LMA ($P < 0.001$), indicating that at common light the species with greater G had lower LMA.

Glucose cost of non-structural-carbohydrate-free dry mass ($G_{NSC\text{-}free}$)

Non-structural carbohydrates (NSC), which contain less carbon (40% in ethanol-soluble carbohydrates such as glucose and 44.4% in starch) than the whole leaf on average, increased significantly with increasing irradiance in all species except *F. excelsior* (Niinemets & Kull, 1998), and therefore $G_{NSC\text{-}free}$ was generally more strongly related to irradiance (Fig. 1) and LMA (Table 2) than was the cost of total biomass. There was a positive relationship of $G_{NSC\text{-}free}$ with I_{sum} and LMA also in *P. tremula*. Thus, light-related changes in NSC (see Niinemets & Kull, 1998), diluting carbon-rich leaf compounds, outweighed the positive effects of irradiance on lignin and protein concentrations in this species. Although carbon concentration of NSC-free dry mass was positively correlated with irradiance in *F. sylvatica* ($r^2 = 0.21$, $P < 0.05$), a negative relationship between leaf nitrogen and light (Niinemets & Kull, 1998, eqn (1)) was responsible for the constant $G_{NSC\text{-}free}$ along the canopy light gradient (Fig. 1).

Interplay between foliar carbon, nitrogen and carbon investment in structural compounds

Given that carbon is a major determinant of leaf construction cost (eqn (1)), it is important to examine which leaf compounds are responsible for the change in C_m along the light gradients. Carbohydrates containing less carbon than leaves on average diminish C_m. However, there was a qualitative difference between the relationships of structural and non-structural carbohydrates vs C_m. A single negative dependence between structural polysaccharides and C_m was appropriate (Fig. 2a), but the correlation of NSC with C_m was species-dependent, and slightly positive for the whole material (Fig. 2b). Since both C_m and NSC tend to increase with increasing irradiance and LMA (Niinemets & Kull, 1998, Table 2), a positive relationship between these variables is attributable to a covariation of C_m and NSC with irradiance. Nevertheless, non-structural carbohydrate contribution to total leaf carbohydrates was much smaller than that of structural polysaccharides. When all data were pooled, the ratio of structural to total carbohydrates was negatively related to both I_{sum} ($r^2 = 0.27$, $P < 0.001$) and to C_m ($r^2 = 0.58$, $P < 0.001$).

As expected, the concentration of carbon-rich lignin was positively related to C_m in all species (r^2-s ranged from 0.22 to 0.86, $P < 0.05$). However,

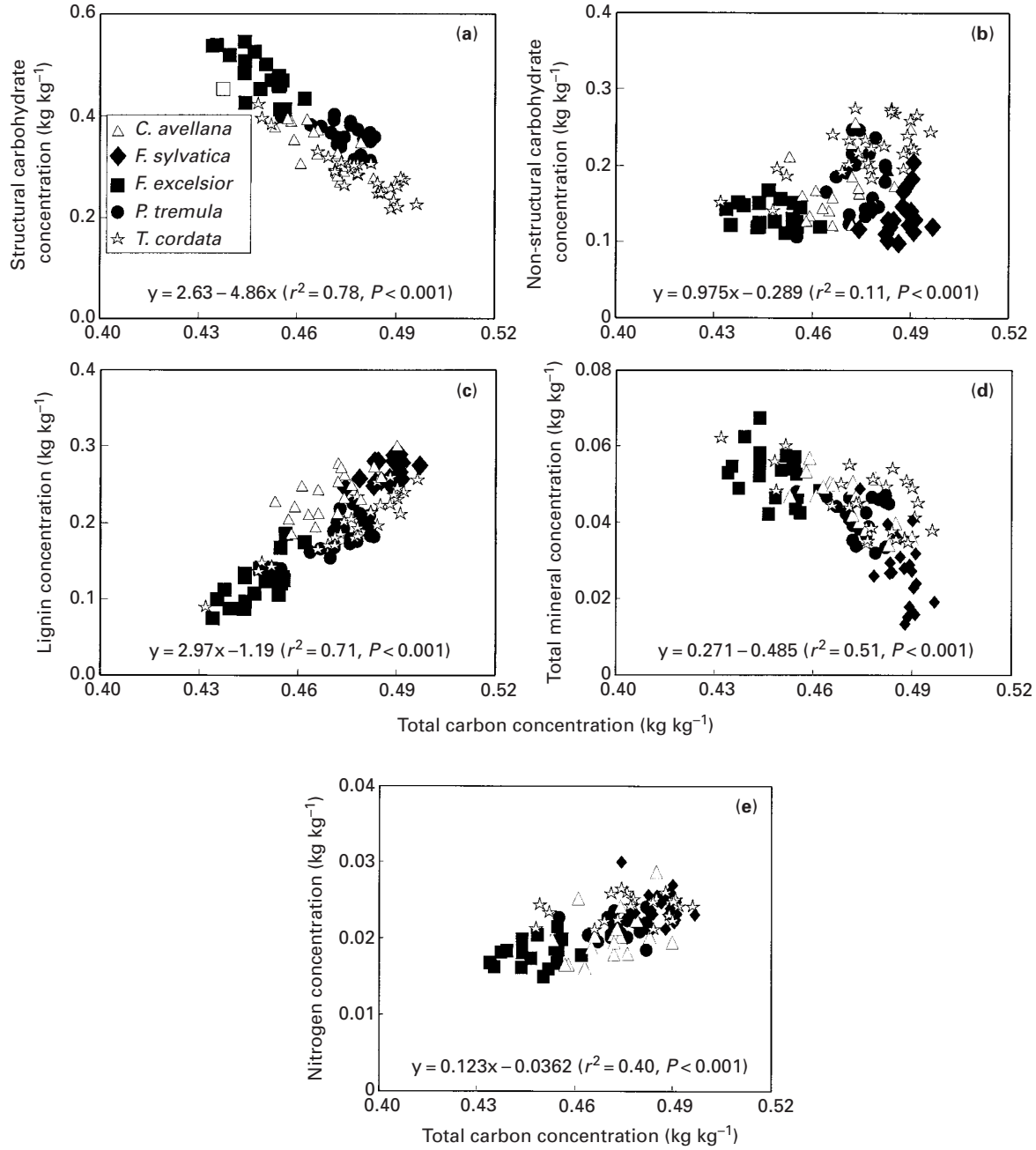

Figure 2. Foliar total carbon concentration in relation to concentrations of (a) cell-wall polysaccharide, (b) non-structural carbohydrate, (c) lignin, (d) total mineral, (e) nitrogen. *Fagus sylvatica* was not analysed for structural polysaccharides.

N_m, an estimate of carbon-rich protein content (53.5% carbon, see Vertregt & Penning de Vries, 1987) was independent of C_m in four species, and decreased with increasing C_m in *F. sylvatica* (r^2 = 0.36, P < 0.05). Though N_m varied little with irradiance, the variability within and between species was about twofold (0.015–0.0299 kg kg^{-1}, Niinemets & Kull, 1998), and for the whole material both lignin (Fig. 2c) and N_m (Fig. 2e) positively influenced C_m. There was also a negative correlation between C_m and total minerals (Fig. 2d), signifying that total minerals diluted organic leaf constituents containing carbon.

DISCUSSION

Variability of glucose requirement for formation of a unit foliar biomass (G) *with irradiance*

Studies of temperate deciduous woody species *Acer platanoides*, *Aesculus hippocastanum*, *Betula pendula* (Dadykin & Kononenko, 1975), *Fagus sylvatica* (Runge, 1986), temperate evergreen conifer *Picea abies* (Frey & Ivask, 1983), tropical liana *Boquila trifoliata* (Steubing *et al.*, 1979), and of several evergreen Mediterranean species (Larcher & Thomaser-Thin, 1988) have yielded a consistent

positive relationship between the heat of combustion (ΔH) and irradiance. Yet, ΔH is not necessarily an estimate of construction cost, because the latter also depends on mineral concentration, N_m and the reduction state of inorganic nitrogen substrate (eqn (1), see also Niinemets, 1997b). Nevertheless, N_m varies relatively little along light gradients (Walters & Field, 1987; Ellsworth & Reich, 1993; Niinemets, 1997c; Niinemets & Kull, 1998), suggesting that the light-related variability in ΔH may be compatible with a positive effect of irradiance on G as also found in the current study (Fig. 1). In contrast, across a data set including seven tropical rain-forest species, G was positively correlated with irradiance in only two (Williams *et al.*, 1989), and was independent of growth light environment in the other five species. During leaf growth G was also independent of irradiance in the herb *Alocasia macrorrhiza* (Sims & Pearcy, 1991, 1994), and tree *Picea abies* (Niinemets, 1997b). These contrasting response patterns suggest that it is not irradiance *per se*, but other environmental factors co-varying with light availability which could be responsible for the correlations between light and G. Data indicate that a positive correlation between evaporative demand, compatible with greater leaf water stress, and irradiance in the canopy (e.g. Myers *et al.*, 1987) is responsible for changing chemical composition of leaf cell walls (Niinemets & Kull, 1998). Acclimation to long-term differences in availability of water includes increases in cell-wall lignin content and the proportion of supporting structures in the foliage (Myers *et al.*, 1987; Rascio *et al.*, 1990; Fredeen *et al.*, 1991).

Foliage construction cost as an integrated estimate of leaf chemical composition

In the current study, greater G at high irradiance was mostly attributable to enhanced lignification. The paramount importance of lignin as determinant of foliage construction cost is also seen in the study of Miller and Stoner (1979), where the foliage of the evergreen Mediterranean shrubs *Adenostoma fasciculatum* and *Arctostaphylus glauca* had higher construction costs (1.71 and 1.72 kg glu kg^{-1}, respectively) than that of Arctic grass species *Dupontia fischerii* (1.31 kg glu kg^{-1}), leaves of which had a considerably lower lignin concentration than those of the evergreen species. This relationship between lignin concentration and G is likely to be more general, since lignin is rich in carbon and present in high concentrations in foliar tissues. There is a strong positive correlation between lignin and carbon concentrations in the cell walls (Van Soest, 1963). Though the recovery of leaf biomass from the analyses of foliar biochemical fractions was only 49–91%, it is also possible to calculate that lignin (L_m) and C_m were positively related in 23 tropical rain-forest species ($r^2 = 0.63$, $P < 0.001$; Steubing *et al.*, 1979) and in 46 tropical trees ($r^2 = 0.21$, $P < 0.001$; Coley, 1983). By contrast, the carbon cost of several tundra plants was not related to L_m (Chapin, 1989), because there was a negative relationship between lignin and proteins, which both are energetically expensive (Chapin, 1989). In the conifer *Picea abies*, N_m was also negatively correlated with L_m, but L_m and C_m were positively related in this species (Niinemets, 1997b). In a previous study (Niinemets & Kull, 1998), an inverse relationship between total investment in foliar structural compounds and N_m, serving as a proxy for protein concentration, was observed. Recalculation of the data of Loveless (1961) highlighted a similar dependence in 51 species ($r^2 = 0.12$, $P < 0.02$). Thus, studies suggest that a basic trade-off exists between investments in structural (lignin, cell wall polysaccharides) and assimilative (proteins) leaf components.

As previously observed among herbaceous species (Poorter & Bergkotte, 1992), there was a negative correlation between total minerals and C_m (Fig. 2d) which has been suggested as a major factor stabilizing foliar G (Poorter & Bergkotte, 1992). However, in herbs, total mineral concentration varied from 8 to 16%, and lignin concentration from 2 to 5% (Poorter & Bergkotte, 1992). In the woody species studied, the concentration of minerals only varied from 4 to 8% (Fig. 2d), but that of lignin varied between 8 and 30% (Fig. 2c). Thus, in the current study, the dilution of leaf organic components by minerals played a considerable less significant part in altering leaf G than in herbaceous species. Moreover, according to simulation analyses, proportionally equal changes in total mineral concentration alter G much less than changes in lignin concentration (Griffin *et al.*, 1996).

Variability in foliar non-structural carbohydrates might also play an important part in altering foliage construction cost (Griffin *et al.*, 1996; Poorter *et al.*, 1997). In the current study, the increase in NSC with light, and resulting decrease in foliar carbon concentration, compensated for the increase in leaf carbon concentration due to lignin accumulation in *P. tremula*. Though the subtraction of NSC from total biomass also improved the correlations between light and G in the other species, it did not influence their relationships qualitatively, because of the greater increase with increasing light in lignin than in NSC.

Implications of different G vs light relationships for foliage morphological plasticity

Across the whole set of data, G (range 1.23–1.53 kg glu kg^{-1}) varied by *c.* 25% (Fig. 1). The variability of such magnitude in energy requirement for unit biomass construction might be a factor significantly

limiting foliage production. In comparable environments, leaf payback time (the time necessary for a leaf to fix the amount of carbon equivalent to that used for its construction) is directly proportional to G (Poorter, 1994). Even though high G values were found in high light, where higher foliage photosynthesis decreases leaf pay-back time, the extent to which the changes in G can be balanced by alterations in leaf photosynthetic production might be inherently limited. Insofar as G scaled positively with LMA in the current study, the value of LMA attainable at high light might be constrained by G. Thus, it is appropriate to ask whether leaf growth patterns determining LMA are related to metabolic energy requirements for their construction.

LMA was lower at common irradiance, and the relationships between LMA and I_{sum} tended to be more curvilinear in more shade-tolerant species (Niinemets & Kull, 1998), which also had greater fractional biomass investments in lignin and therefore a higher G than the intolerant species (Fig. 1; Table 3). In the shade-tolerant *T. cordata*, the relationship between G and I_{sum} (Fig. 1) was curvilinear, but the relationships between LMA and G were always linear (Table 2). This difference might signify that the upper limit of LMA in the canopy depends on how adequately the energy requirements for growth could be satisfied during foliage expansion. This is directly related to the absolute values of G and to the steepness of the increase of G with LMA and irradiance. In shade-tolerant species, with generally lower potential photosynthetic rates (Bazzaz, 1979; Björkman, 1981; Abrams & Mostoller, 1995; Niinemets *et al.*, 1998) and higher G, growth should become more readily limited by carbohydrates than in intolerant species. This might provide an explanation of the tendency of shade-tolerant species to have a lower LMA at common irradiance than intolerant species (Niinemets & Kull K, 1994; Niinemets & Kull O, 1998). Though few data are available, I hypothesize that at common irradiance there is a basic negative relationship between species G and LMA. For a number of tropical *Piper* species, both LMA and G at high light (incident daily integrated average photosynthetically active quantum flux density within 24.7–28.8 mol m^{-2} d^{-1}) and at low light (integrated light within 2–8 mol m^{-2} d^{-1}) were negatively correlated ($r^2 = 0.83$, $P<0.05$ for four species in high light, and $r^2 = 0.74$, $P<0.02$ in seven species in low light; recalculated from Williams *et al.*, 1989). When the data on high light from Williams *et al.* (1989) were pooled with our data at a I_{sum} of 0.8 [LMA calculated from the regression equations in Niinemets & Kull (1998), and G from Fig. 1], a significant negative relationship was also observed ($r^2 = 0.50$, $P<0.05$). Further analysis including more species from different habitats is needed to test this hypothesis. Nevertheless, current study indicates that foliar G varies along light gradients in temperate trees, because of changes in the stoichiometry of foliage carbon constituents, and also suggests that changes in cell wall composition may lead to modifications in leaf growth patterns, because of effects on foliage construction cost.

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APPENDIX

Calculation of the fraction of foliar nitrogen reduced in non-assimilative organs (P_n, *eqn* (*2*))

Proportion of leaf nitrogen reduced at the expense of extra metabolic energy in Fagus sylvatica

According to the laboratory experiments, this species preferentially uses ammonium rather than nitrate as a source of nitrogen (Finlay *et al.*, 1989; Neitzke, 1990; Paar, 1994). Four times more ammonium than nitrate is taken up at a nitrogen concentration of 0.3 mM and a NH_4^-:NO_3^- molar ratio of 1:1 (Paar, 1994); at a nitrogen concentration of 3 mM and a NH_4^+:NO_3^- molar ratio of 1:3, 2.5 times more ammonium than nitrate is drawn up from the nutrient solution (recalculated from Neitzke, 1990). In the studied stand, annual nitrate input to the mineral soil (litter lysimeter) was 0.64 kmol ha^{-1} yr^{-1} and the annual ammonium flux was 0.84 kmol ha^{-1} yr^{-1} during 1984–1990 (Türk, 1992). Studies with ^{15}N-labelled NH_4^+ and NO_3^- in a *Picea abies* stand in Wülfersreuth (Fichtelgebirge, Germany) in the vicinity of the current experimental plot indicated that the actual ratio of ammonium vs nitrate uptake is *c.* 4:1 (Schmidt *et al.*, 1995). Given that in the same stand in Wülfersreuth the natural nitrogen isotope ratio was the same for the foliage in both *P. abies* and *F. sylvatica* (Gebauer & Dietrich, 1993), the nitrate to ammonium nitrogen ratio (S_n – see eqn (2) for the explanation of symbols) for root uptake was fixed at 0.25. The U_1 (0.09) was calculated from the data of Brumme *et al.* (1992), giving the annual uptake of NH_4^+ and NO_3^- by leaves (1.5 kg ha^{-1} yr^{-1}), and of Eichhorn (1995), giving the proportion of aerial uptake of total nitrogen requirement for annual growth. Further, assuming proportions similar to those in *P. abies* (Schulze, 1994), the obtained value (0.03) was increased by a factor of three to take account also of foliar NH_3 and NO_x uptake. The α was taken as 0.6 (Brumme *et al.*, 1992). Calculating U_r from total above-ground nitrogen uptake (identical source of data), taking β as 0.2 (Gojon, *et al.*, 1994), and considering that *c.* 25% of nitrogen

required for annual biomass increment is used for foliage growth (recalculation of the data of Schulze, 1994; Eichhorn, 1995), P_n was fixed at 0.12.

Proportion of leaf nitrogen reduced at the expense of extra metabolic energy (P_n) *in the other species*

The soil subtype of the Ülenurme site was the same as that at Oberwarmensteinach, and both soils were acidic (Table 1). Generally, ammonium is a more important nitrogen source in acidic soils, though, some nitrification can also occur in these soils (Runge, 1983). There is also a general preference for ammonium over nitrate in many species when both ions are supplied simultaneously (Runge, 1983; Vessey *et al*., 1990). Few tree species have been studied in this respect, but preferability of ammonium uptake has been demonstrated for *Fraxinus excelsior* (Gebauer & Stadler, 1990; Stadler *et al*., 1993). The potential for nitrate reduction in leaves (on average 22% of total nitrate reduction) and the fraction of NO_3^--nitrogen in xylem sap (on average 23%; Stadler *et al*., 1993) in *F. excelsior* are also similar to those reported for other woody species (Gojon *et al*., 1994). Thus, the species at Ülenurme should possess P_n values close to those calculated for *F. sylvatica*, and a P_n of 0.12 was used for these species.

P_n might be different for *Tilia cordata* in the Tartu stand in less acidic soils, where nitrate was probably the dominant form of soil mineral nitrogen (Runge, 1983). When nitrate is the only source of inorganic nitrogen, P_n is equal to 0.8, because in woody species *c*. 20% of foliar nitrogen is reduced in leaves (Smirnoff *et al*., 1984; Gojon *et al*., 1994). To account for these uncertainties, the calculations of foliar construction costs in *T. cordata* were conducted with two P_n values, 0.12 and 0.8. Different values of P_n did not alter G vs irradiance relationships qualitatively, because nitrogen concentration was independent of irradiance in this species (Niinemets & Kull, 1998). However, the problem of attaining exact values of P_n might have altered species comparisons in several instances, and these cases have been outlined in the main text.

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