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Leaf traits and associated ecosystem characteristics across subtropical and timberline forests in the Gongga Mountains, Eastern Tibetan Plateau

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Abstract Knowledge of how leaf characteristics might be used to deduce information on ecosystem functioning and how this scaling task could be done is limited. In this study, we present field data for leaf lifespan, specific leaf area (SLA) and mass and area-based leaf nitrogen concentrations (N_{mass}, N_{area}) of dominant tree species and the associated stand foliage N-pool, leaf area index (LAI), root biomass, aboveground biomass, net primary productivity (NPP) and soil available-N content in six undisturbed forest plots along subtropical to timberline gradients on the eastern slope of the Gongga Mountains. We developed a methodology to calculate the whole-canopy mean leaf traits to include all tree species (groups) in each of the six plots through a series of weighted averages scaled up from leaf-level measurements. These defined whole-canopy mean leaf traits were equivalent to the traits of a leaf in regard to their interrelationships and altitudinal trends, but were more useful for large-scale pattern analysis of ecosystem structure and function. The whole-canopy mean leaf lifespan and leaf N_{mass} mainly showed significant relationships with stand foliage N-pool, NPP, LAI and root biomass. In general, as elevation increased, the whole-canopy mean leaf lifespan and leaf Narea and stand LAI and foliage N-pool increased to their maximum, whereas the whole-canopy mean SLA and leaf N_{mass} and stand NPP and root biomass decreased from their maximum. The whole-canopy mean leaf lifespan and stand foliage N-pool both converged towards

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Northern Global Change Research Program, USDA Forest Service, PA 19073, USA threshold-like logistic relationships with annual mean temperature and soil available-N variables. Our results are further supported by additional literature data in the Americas and eastern China.

Keywords Altitudinal patterns · Leaves · Tree canopies · Communities · Scaling-up

Introduction

Leaf lifespan, specific leaf area (SLA, a measure of leaf surface area per unit mass), and mass- and area-based leaf nitrogen concentrations (N_{mass}, N_{area}) are fundamental plant traits (Reich et al. 1991; Körner 1991). Leaf traits interact to determine plant behavior and production and provide a useful conceptual link between processes at short-term leaf scales and long-term whole plant and stand-level scales (Chabot and Hicks 1982; Field 1983: Reich et al. 1992: Schulze et al. 1994; Meir et al. 2002). However, it is unknown to what extent the altitudinal/latitudinal trends in the traits of a leaf reflect geographical variations in ecosystem characteristics of structure and function. The available measurements of the leaf traits associated with altitude and latitude are almost limited to fully sunlit, fully expanded current leaves (e.g., Körner et al. 1986; Körner 1989; Niinemets 2001) in which little information on whole plant and stand-level characteristics is available. These studies indicate that SLA and related structural features appear to be controlled by temperature because they show similar altitudinal changes under different light and moisture gradients. However, leaf lifespan varies substantially among species (Ewers and Schmid 1981; Chabot and Hicks 1982; Reich et al. 1996), and associated leaf traits within species vary with leaf age as well (Field and Mooney 1983; Reich et al. 1991). It is common that different plant species with different leaf traits coexist in a plant community (e.g., Reich et al. 1991, 1999). We need a new integrated approach to associate the traits of

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Whole-canopy mean leaf lifespan and associated leaf traits that include different age-group leaves from all tree species in a plot might be useful for indicating adaptations of natural forests to climatic gradients. Abundant evidence illustrates that needle longevity of evergreen conifers, such as pine, spruce and fir, increases with elevation and latitude (Ewers and Schmid 1981; Reich et al. 1995). In general, leaf photosynthetic capacity and maintenance cost decrease (Reich et al. 1997, 1999), whereas leaf construction cost increases with increasing leaf lifespan (Gulmon and Mooney 1986). Under given environmental constraints, such as low temperatures, length of growing season or light and nutrient availability, the trade-off between leaf carbon costs and benefits for maximizing carbon gain (Chabot and Hicks 1982; Chapin et al. 1987; Pearcy et al. 1987; Kikuzawa 1991; Sobrado 1991; Cordell et al. 2001) might result in the optimal whole-canopy mean leaf lifespan and associated leaf traits. In closed-canopy forest stands, foliage mass increases with increasing mean leaf lifespan (Tadaki 1977; Reich et al. 1992, 1995). The foliage mass reaches an essentially steady state early in succession. with a maximum leaf area index (LAI) in the nearly mature or mature stages (Mooney 1972; Grier and Running 1977; Tadaki 1977). Inside a plant canopy, the total leaf area is controlled in a way that leaf N content is optimal for the given light, temperature and soil nutrient regimes (Field 1983; Körner et al. 1986; Pearcy et al. 1987; Hirose et al. 1997). The seasonal increase in total foliage N is almost proportional to the increase in total LAI. Hence the ratio of total foliage N to LAI changes little during the season (Kull and Jarvis 1995; Kull et al. 1998). Based on published data from different ecological studies of forests across North America, the synthesis by Yin (1993) reveals that stand-level average leaf N_{mass} is strongly correlated with climatic factors. More recently, Smith et al. (2002) found a highly predictive relationship between whole-canopy mean leaf N_{mass} and aboveground forest productivity in diverse forested stands of varying age and species composition.

Weber's Law given in Duvigneaud (1987) indicates that a well-balanced natural plant community, regardless of species composition, should have a similar dry matter production, such as net primary productivity (NPP) and biomass accumulation, under the same environmental conditions. Lieth (1975) describes the relationship between climatic factors (annual mean temperature, annual precipitation, and annual evapotranspiration) and NPP by a logistic function at a global scale. We applied Weber's Law and a threshold-like logistic function to establish a climate-based statistical model of NPP of natural vegetation on the Tibetan Plateau, in which the product of annual mean temperature and annual precipitation could explain 70% of the NPP variation for the 180 vegetation site data derived from 1970-1980s inventory plots over the plateau (Luo et al. 2002a). More recently, our independent data

sets from 22 sites along the Tibetan Alpine Vegetation Transects (TAVT) (1999–2000) also indicate that the general distribution patterns of stand aboveground biomass, root biomass, LAI and NPP have thresholdlike logistic relationships with climatic factors of temperature and precipitation (Luo et al. 2002b, 2004; T. Luo et al., submitted manuscript). We hypothesize that whole-canopy mean leaf traits across biomes also show the threshold-like logistic pattern in response to the climatic and soil gradients. If proved, this would be helpful to understanding the mechanisms underlying the NPP, LAI and biomass variations and for further tests of the generality of Weber's Law.

In this report, we explore how leaf characteristics might be used to deduct ecosystem functioning information and how this scaling task could be done based on our field data of leaf traits and associated stand variables in undisturbed forests along the eastern slope of the Gongga Mountains within the TAVT. Our tasks are to: (1) calculate the whole-canopy mean leaf lifespan, SLA, leaf N_{mass} and N_{area} to include different age-group leaves from all tree species (groups) for each forest site, (2) compare relationships among leaf traits at leaf-level and stand-level scales, (3) compare altitudinal trends in leaf traits at leaf-level and stand-level scales, (4) analyze relationships of the whole-canopy mean leaf traits to stand variables, climatic factors and soil available-N content to understand the mechanisms underlying the general geographical distribution patterns in stand LAI and NPP (Luo et al. 2004), aboveground biomass (Luo et al. 2002b) and root biomass (T. Luo et al., submitted manuscript) along the TAVT.

Study sites and methods

Transect study sites in the Gongga Mountains

This study was conducted in the Hailuogou Natural Reserve at the eastern slope of the Gongga Mountains. Six field plots of undisturbed forests (0.1–0.5 ha) were selected along the altitudinal transect, which includes a subtropical evergreen broadleaf forest (EBLF) at 1,900 m. a subtropical evergreen-deciduous broadleaf forest (EDBLF) at 2,200 m, an alpine needle-shaped leaf and broadleaf mixed forest (ANBMF) at 2,850 m, alpine needle-shaped leaf forests (ANLF) at 3,000 m and 3,050 m, and a timberline needle-shaped leaf forest (TNLF) at 3,700 m (Table 1). The altitudinal transect covered latitudes from N29°32' to N29°37' and longitudes from E101°58' to E102°03'. During July and August 1999, we measured leaf traits for lifespan, SLA, leaf N_{mass} and N_{area} across dominant tree species along the transect, and associated stand characteristics for aboveground biomass, root biomass, LAI and NPP, as well as soil available-N content. The data for stand biomass, LAI, and NPP are reported in other works (Luo et al. 2002b, 2004; T. Luo et al., submitted manuscript).

Table 1 Stand variables of diameter at breast height (DBH), shoot height, stem basal area, and foliage biomass and leaf area index (LAI) among dominant tree species (groups) in the six forest plots along the eastern slope of the Gongga Mountains. *EBLF* Subtropical evergreen broadleaf forest, *EDBLF* subtropical evergreen-deciduous broadleaf forest, *ANBMF* alpine needle-shaped leaf and

broadleaf mixed forest, ANLF alpine needle-shaped leaf forests, TNLF timberline needle-shaped leaf forest, AF Abies fabri, A+BAcer sp. + Betula sp., A+P Acer sp. + Populus sp., CO Cyclobalanopsis oxyodon, LC Lithocarpus cleistocarpus, LP Lindera pulcherrina, PC Phoebe chinensis, PB Picea brachytyla, P+B Populus sp. + Betula sp., Rh Rhododendron sp., TC Tsuga chinensis

Forest type	Dominant species (groups)	Mean DBH (minimum–maximum) (cm)	Mean height (minimum–maximum) (m)	Basal area (m ² ha ⁻¹)	Leaf mass (Mg ha ⁻¹)	Trees LAI (ha ha ⁻¹)
EBLF (1,900 m)	СО	18.5 (5-32)	9.9 (6-15)	11.09	1.015	0.61
	LC	16.0 (6-25)	9.5 (5–12)	9.38	0.979	0.60
	PC	19.0 (11–26)	11.6 (8-14)	7.80	0.612	0.44
	LP	10.2 (6-12)	8.7 (6-12)	0.67	0.108	0.09
	A + P	28.2 (6-49)	13.3 (7–18)	22.39	1.503	2.36
EDBLF (2,200 m)	CO	52.0 (17-127)	12.3 (8-18)	25.15	0.941	0.60
	TC	67.4 (44–75)	25.3 (24-27)	18.12	0.801	0.60
	PC	52.4 (25-72)	15.5 (9-26)	14.63	0.616	0.63
	LC	17.2 (6–29)	9.0 (5-16)	3.14	0.296	0.17
	LP	13.5 (8-21)	8.0 (4-12)	2.68	0.307	0.25
	A + P	39.7 (4–92)	11.3 (4-20)	56.46	2.580	2.90
ANBMF (2,850 m)	AF	92.5 (19–154)	46.0 (15-72)	29.23	3.145	1.41
	PB	76.1 (34–133)	39.1 (21-63)	9.88	5.538	4.14
	TC	109.0 (95-122)	52.9 (47-58)	8.11	0.676	0.51
	Rh	11.6 (3-21)	8.4 (3-13)	2.30	0.254	0.20
	A + B	15.4 (4-87)	10.2 (5-21)	12.20	1.201	2.25
ANLF (3,050 m)	AF	15.1 (4-30)	12.7 (9–20)	43.50	10.696	4.52
	Rh	8.4 (5-12)	5.6 (4-8)	0.26	0.043	0.03
	P + B	11.9 (4-26)	7.7 (3-13)	11.21	1.264	2.12
ANLF (3,000 m)	AF	49.9 (6–92)	25.7 (9-46)	58.64	15.727	7.24
	Rh	7.1 (5-10)	4.5 (5-10)	0.09	0.018	0.01
	P + B	9.5 (4-25)	6.3 (3–13)	1.17	0.172	0.28
TNLF (3,700 m)	AF	39.4 (16-60)	14.2 (10-25)	54.83	18.155	7.64
ו• /	Rh		3.0 (2–5)		2.806	1.60

Associated stand variables in a forest plot

Table 1 summarized general stand variables of diameter at breast height (DBH), shoot height, stem basal area, and foliage mass (biomass and LAI) according to dominant tree species (groups). Tree height and DBH of each forest plot were measured for all trees > 3 cm DBH. The species-specific stem basal area was calculated from measurements of tree DBH. The species-specific foliage biomass was calculated from measurements of DBH and tree height using speciesspecific allometric regressions that were developed in our earlier study (Luo et al. 2002b). The species-specific LAI was the product of the species-specific foliage biomass multiplied by the species-specific SLA from Table 2.

Stand foliage N-pool was the sum of products of the species-mean leaf N_{mass} (Table 2) multiplied by the species-specific foliage biomass (Table 1). Stand LAI was the sum of the tree LAI (Table 1) plus the undergrowth LAI (Luo et al. 2004). The total root biomass of trees and undergrowth was measured by digging up all the roots in $0.5\times0.5\text{-m}^2$ quadrats to the depth of the deepest visible root (50–100 cm), which included live medium and coarse roots and live and dead fine roots. Aboveground live-biomass of trees in the six forest plots was estimated by species-specific allometric regressions on measured tree height and DBH, and undergrowth biomass was measured by harvesting quadrats (2×2 m²). NPP was estimated as the sum of increases in standing

crops of live vegetation based on the data for live-biomass, recent stem growth rate and leaf lifespan. The annual woody production (stem, branch and root) of trees was the product of the woody biomass multiplied by the average annual growth rate (%) of stem volume during the past 2 or 5 years. The annual production of leaves equaled the result of green leaf mass divided by the species-specific leaf lifespan. The annual woody production of undergrowth shrubs was calculated as the ratio of their biomass divided by their average ages ranging between 10 and 25 years. The annual production of undergrowth shrub leaves, herb and/or moss equaled the result of green biomass divided by the leaf lifespan as follows: 2 years for evergreen shrubs and mosses, 1 year for deciduous shrubs and herbs. More information about field methods of live-biomass both aboveground and belowground and the NPP estimates is found in Luo et al. (2002b, 2004; T. Luo et al., submitted manuscript).

Leaf samples at leaf and shoot levels

We selected three to five standard trees with average tree height and quadratic mean DBH calculated from the average per-tree basal area according to dominant tree species (groups). For each tree, three sample shoots with twigs and leaves were cut from the upper, middle and lower canopy positions by climbing access. In total, we collected 90 sample shoots from 30 standard trees for 20

Forest type	Dominant species	Species-mean lifespan (years) $(m \pm SD)$	Species-mean SLA $(cm^2 g^{-1})(range)$	Species-mean leaf N_{mass} (mg g ⁻¹) (range)	Species-mean leaf N_{area} (g m ⁻²) (range)
EBLF (1,900 m)	CO	2.0 ± 0.0	60 (49–67)	13.8 (10.1–16.2)	2.3 (2.0-2.4)
	LC	2.0 ± 0.0	61 (53-65)	15.6 (13.1–16.4)	2.6 (2.5-2.6)
	PC	2.0 ± 0.0	72 (53–113)	13.5 (11.6–17.2)	2.0 (1.5-2.2)
	LP	2.0 ± 0.0	82 (73–90)	19.8 (17.4–22.3)	2.4 (2.4–2.5)
	A. + P.	0.5 (6 months)	157 (131–188)	20.6 (17.1–22.0)	1.3 (1.2–1.4)
EDBLF (2,200 m)	CO	2.0 ± 0.0	64 (50-67)	14.3 (11.0–17.2)	2.2 (1.9–2.5)
	TC	2.7 ± 0.6^{a}	75 (57–96) ^a	17.5 (15.8–17.9) ^a	$2.4 (1.9-2.9)^{a}$
	PC	2.0 ± 0.0	103 (78–119)	14.3 (11.9–15.5)	1.4 (1.3–1.6)
	LC	2.0 ± 0.0	59 (44-74)	14.5 (11.5–16.2)	2.5 (2.2–2.9)
	LP	2.0 ± 0.0^{b}	82 (73–90) ^b	19.8 (17.4–22.3) ^b	2.4 (2.4–2.5) ^b
	A. + P.	0.5 (6 months)	112 (94–131)	20.2 (18.6–21.8)	1.9 (1.4–2.3)
ANBMF (2,850 m)	AF	6.7 ± 0.6	45 (32–61)	13.1 (11.2–14.6)	3.0 (2.4–3.5)
	PB	6.0 ± 0.0	75 (63–95)	12.5 (8.5–14.9)	1.7 (1.3–1.8)
	TC	2.7 ± 0.6	75 (57–96)	17.5 (15.8–17.9)	2.4 (1.9–2.9)
	Rh	1.0 ± 0.0	77 (51–98)	14.5 (10.9–17.3)	1.9 (1.6–2.1)
	A. + B.	0.4 (5 months)	196 (169-230)	20.9 (17.1–26.7)	1.1 (0.7 - 1.4)
ANLF (3,050 m)	AF	7.1 ± 1.7	42 (31-60)	13.6 (8.8–17.1)	3.3 (2.9–3.5)
(/ /	Rh	2.0 ± 0.0	68 (55-94)	13.9 (11.4–16.9)	2.0 (1.7–2.1)
	P. + B.	0.3 (4 months)	180 (131-230)	22.0 (18.6-25.4)	1.2 (1.1–1.4)
ANLF (3,000 m)	AF	6.9 ± 1.3	42 (34–53)	13.4 (10.6–16.3)	3.2 (3.1–3.6)
	Rh	$2.0\pm0.0^{ m c}$	68 (55–94) ^c	13.9 (11.4–16.9) ^c	$2.0 (1.7-2.1)^{c}$
	P. + B.	0.3 (4 months)	200 (169-230)	25.8 (25.4-26.2)	1.3 (1.1–1.5)
TNLF (3,700 m)	AF	7.5 ± 0.6	42 (32–71)	13.2 (10.5–18.2)	3.0 (2.6–3.5)
	Rh	2.0 ± 0.0	57 (47–93)	15.9 (8.5–21.4)	2.4 (2.0–2.9)

Table 2 Species-mean leaf traits of lifespan, specific leaf area (*SLA*), mass-based leaf nitrogen concentrations (N_{mass}) and area-based leaf nitrogen concentrations (N_{area}) among dominant tree species (groups) in the six forest plots along the east slope of the Gongga Mountains. For other abbreviations, see Table 1

^aUsing the measurements at 2,850 m

^bUsing the measurements at 1,900 m

^cUsing the measurements at 3,050 m

woody plant species along the altitudinal transect. We separated leaf age classes and measured the dry mass of different age-group leaves for each sampled shoot. In evergreen conifers, the apex of a long shoot produces a yearly growth increment that bears a single age class of needles (Ewers and Schmid 1981). We counted back leaf age classes from shoot tips, which were validated by counting tree-rings at the base of the shoots. In broadleaved evergreen trees, leaf age classes were determined by counting back the internodes from the shoot tips (Wang et al. 2000). The leaf age of current leaves of deciduous and evergreen trees was determined as the duration between leaf onset and sampled date. The leaf lifespan of evergreen trees was determined by the maximum leaf age in each sampled shoot. The leaf lifespan of deciduous trees were determined as the duration between leaf onset and leaf fall according to local phenological observations.

We collected 146 samples of age-group leaves from the 90 sample shoots according to different tree species and forest sites. We measured leaf N_{mass} and N_{area} concentrations and SLA. The leaf N_{mass} was analyzed with a micro-Kjeldahl assay. The leaf N_{area} was calculated from the leaf N_{mass} and associated SLA (the ratio of fresh leaf area to dry mass). The one-side leaf area for broadleaved trees was measured using a CI-203 portable laser area meter (CID). The curve surface leaf area exposed to sunlight for coniferous trees was determined according to the needle shapes: single rectangular area for *Abies* and *Tsuga* trees and double rectangular area for *Picea* trees, where side length and width (mm) of a single needle were measured using Vernier callipers. For each of the 146 leaf samples, leaf areas of 30-50 fresh leaves were measured, and the leaves were then dried to a constant weight at 70° C.

Species-mean leaf traits among dominant tree species (groups) in a forest plot

Based on leaf sample measurements of the leaf and shoot levels given above, we calculated species-mean leaf lifespan, SLA, leaf N_{mass} and N_{area} concentrations according to dominant tree species (groups) in the six forest plots (Table 2). The species-mean leaf lifespan was the arithmetic average of maximum leaf ages from each sampled shoot in different canopy positions of a tree. Other species-mean leaf traits were the shoot-level weighted-average leaf traits from different canopy positions of the tree based on weighted dry mass or area of leaves in different age classes.

Whole-canopy mean leaf traits in a forest plot

The whole-canopy mean leaf traits (W) to include all tree species (groups) in a forest plot were defined as the weighted averages of leaf traits using the species-mean leaf traits (Si) (Table 2) and the species-specific stem basal area or foliage mass (Ki) (Table 1): $W = \sum (Si \times Ki) / \sum (Ki)$. The whole-canopy mean leaf lifespan was based on the species-mean leaf lifespan and the species-specific stem basal area. The whole-canopy mean SLA and leaf N_{mass} were based on the species-mean SLA and leaf N_{mass} and the species-specific foliage biomass. The whole-canopy mean leaf N_{area} was based on the speciesmean leaf N_{area} and the species-specific LAI.

Soil available-N content

We collected soil samples and measured soil bulk densities by layer (A₀, A₁ and/or B horizons) from the soil pits (0.5×0.5 -m² quadrats) to the depth of the deepest visible root. Four soil pits were dug under an average tree in each forest plot where the layer-specific soil samples were from different soil pits. The soil samples were chemically analyzed for available-N content by layer. The FeSO₄+Zn+NaOH distilled water extraction analysis determined the soil available-N content. The soil bulk density was measured with the cutting ring method in most plots, or by weighting soil mass in some forest plots with rocky soils. The storage of available-N in soils was calculated from the soil-mass-weighted averages for available-N content and soil bulk density and the maximum plant root depth average (Table 3).

Estimates of climatic factors along the transect

The climatic data of the six forest sites along the altitudinal transect were estimated from 10 years of meteorological observations measured at 1,600 and 3,000 m by the Alpine Ecosystem Observation and Experiment Station, Chinese Academy of Sciences (Table 3). Annual mean temperature was calculated using a lapse rate of 0.6° C per 100 m of altitude. Annual precipitation at below 2,500 m in elevation was estimated from the meteorological observatory at 1,600 m in increments of 120 mm per 100 m (1,600–2,500 m). Annual precipitation above 2,500 m was estimated from the meteorological observatory at 3,000 m in decrements (2,500–3,000 m) or increments (above 3,000 m) of 74 mm per 100 m (Zhong et al. 1997).

Modeling relationships between whole-canopy mean leaf traits and climatic and soil variables

We hypothesized that the relationships between the whole-canopy mean leaf traits and climatic and soil variables follow Weber's Law with simple logistic equations:

$$y = k/[1 + \exp(a + bx)],$$
 or
 $y = k/[1 + \exp(a + bx + cx^2)]$

where, v is dependent variables of the whole-canopy mean leaf traits, and x independent climatic and soil variables, including annual mean temperature and soil available-N content. Temperature was considered the limiting factor for the vegetation distribution in the Gongga Mountains because actual evapotranspiration is generally low and accounts for only 27% of the annual precipitation at 3,000m (Zhong et al. 1997). Only annual mean temperature was used in the modeling because the estimated mean temperatures for January, July and the year and annual precipitation along the altitudinal transect were highly correlated ($r^2 = 0.99$, P < 0.001). k is the maximum leaf trait measurements estimated from Table 2: eight for leaf lifespan (year), 30 for leaf N_{mass} concentration (mg/g DM), four for leaf N_{area} concentration (g/m² leaf area) and 250 for SLA (cm²/g DM). exp is the base of the natural logarithm, and the

Table 3 Whole-canopy mean leaf traits^a in relation to stand foliage N-pool, LAI, net primary productivity (*NPP*), root biomass, aboveground biomass, soil available-N content and storage, and climatic factors of annual mean temperature and annual precipitation. DM Dry mass; for other abbreviations, see Table 1

Leaf traits and associated ecosystem variables	EBLF (1,900 m)	EDBLF (2,200 m)	ANBMF (2,850 m)	ANLF (3,000 m)	ANLF (3,050 m)	TNLF (3,700 m)
Whole-canopy mean leaf lifespan (year)	1.35	1.40	4.59	6.76	5.68	7.50
Whole-canopy mean leaf N_{mass} (mg g ⁻¹ DM)	16.8	17.8	14.0	13.5	14.5	13.6
Whole-canopy mean leaf N_{area} (g m ⁻² leaf area)	1.73	1.96	1.78	3.13	2.60	3.07
Whole-canopy mean SLA ($cm^2 g^{-1} DM$)	97	93	81	44	56	44
Foliage N-pool (Kg ha ⁻¹ land)	70.6	98.8	151.0	215.6	173.9	284.3
Stand LAI (ha ha ⁻¹ land)	4.6	6.3	10.3	10.2	7.8	10.2
NPP (Mg $\dot{D}M$ ha ⁻¹ year ⁻¹)	17.7	17.1	10.4	10.7	12.2	7.7
Root biomass (Mg DM ha ⁻¹ land)	67.5	95.1	35.6	23.8	35.5	7.0
Aboveground biomass (Mg DM ha ⁻¹ land)	165.2	348.6	481.6	369.4	162.9	242.2
Soil available-N content (mg per 100g soil)	9.2	9.4	18.9	13.0	9.8	16.7
Soil available-N storage (kg ha ⁻¹ land)	358.0	368.7	529.3	407.0	430.9	820.6
Annual mean temperature (°C)	10.4	8.4	5.1	4.0^{b}	4.0^{b}	-0.2
Annual precipitation (cm)	130.1	149.3	182.4	192.6 ^b	192.6 ^b	238.5

^aThe whole-canopy mean leaf traits (W) to include all tree species (groups) in a forest plot were defined as the weighted averages of leaf traits using the species-mean leaf traits (Si) (Table 2) and the

species-specific stem basal area or foliage mass (*Ki*) (Table 1): $W = \sum (Si \times Ki) / \sum Ki$

^bStation observations at 3,000 m

other parameters of a, b and c are equation coefficients. The site-specific data in Table 3 were used to determine the equation coefficients by the least squares regression method. When there was a non-robust logistic relationship (P > 0.05), we further tested the data with other models such as linear, power, log and expon ential functions.

Results

Comparisons of relationships among leaf traits at leaf and whole-canopy scales

At a leaf scale, the leaf N_{mass} and SLA both exponentially decreased with increasing leaf age $(r^2=0.50-0.53, P<0.001)$ (Fig. 1a, c). However, the leaf N_{area} showed a distinct pattern in relation to leaf age (Fig. 1b), which logarithmically increased with age $(r^2=0.23, P<0.001)$. The leaf N_{mass} logarithmically increased with increasing SLA $(r^2=0.55, P<0.001)$ (Fig 1d) because both were strongly correlated with leaf age. The results indicated that as a leaf aged, the leaf N_{mass} and SLA sharply decreased, while the leaf N_{area} slightly increased

across tree species groups. Accounting for the age effects is the basis for scaling up the traits of a leaf to whole plant and stand-level scales. At a stand-level scale, the analysis of simple linear relationships among the scaledup leaf traits indicated similar trends (from Table 3): the whole-canopy mean leaf N_{mass} and SLA both deceased $(r^2=0.88-0.93, P<0.01)$, whereas the whole-canopy mean leaf N_{area} increased $(r^2=0.75, P<0.05)$ with increasing whole-canopy mean leaf lifespan. The wholecanopy mean leaf N_{mass} and SLA were significantly correlated $(r^2=0.71, P<0.05)$.

Comparisons of altitudinal trends in leaf traits at leaf and whole-canopy scales

Figure 2 presents altitudinal trends of the within-age leaf trait measurements in 1-year-old leaves across evergreen tree species groups. As elevation increased, the leaf N_{mass} was generally stable ($r^2=0.03$, not statistically significant at P < 0.10) (Fig. 2c), but the leaf N_{area} increased ($r^2=0.16$, P < 0.10) (Fig. 2a), and the SLA decreased ($r^2=0.16$, P < 0.10) (Fig. 2b). At a stand-level scale, the percentage of stem basal area of evergreen

Fig. 1a-d Relationships among the traits of a leaf across tree species groups along the eastern slope of the Gongga Mountains. Because leaf massbased nitrogen concentrations (N_{mass}) (a), area-based leaf nitrogen concentrations (N_{area}) (b) and specific leaf area (SLA)(c) were closely related to leaf age, both SLA and leaf N_{mass} were well correlated (d). yr Year



trees significantly increased with increasing altitude $(r^2 = 0.73, P < 0.05)$ (Fig. 2d) where the whole-canopy mean leaf lifespan also significantly increased $(r^2 = 0.91, P < 0.01)$ (from Table 1). As elevation increased, the whole-canopy mean SLA significantly deceased $(r^2 = 0.80, P < 0.02)$ and the leaf N_{area} slightly increased $(r^2 = 0.63, P < 0.10)$ with similar patterns in the traits of a leaf. However, the whole-canopy mean leaf N_{mass} significantly decreased with altitude $(r^2 = 0.74, P < 0.05)$ in contrast to the leaf-level variation. Although the traits of a leaf varied greatly with plant species groups, the whole-canopy mean leaf traits indicated more significant altitudinal patterns consistent with the change in relative percentages of evergreen versus deciduous canopy.

Relationships between whole-canopy mean leaf traits and stand characteristics

We did a correlation analysis between whole-canopy mean leaf traits and stand characteristic variables for the

six forest plots of the Gongga Mountains (Table 4). Stand foliage N-pool increased with increasing wholecanopy mean leaf lifespan (P < 0.01) and leaf N_{area} (P < 0.05), but decreased with increasing SLA (P < 0.01)and leaf N_{mass} (P < 0.05). Stand LAI had a significant positive relationship with the whole-canopy mean leaf lifespan (P < 0.05) and a negative relationship with the leaf N_{mass} (P < 0.05). However, the LAI showed weak relationships with the whole-canopy mean leaf Narea and SLA (not statistically significant at P < 0.05). Stand root biomass and NPP, in contrast, both had a negative relationship with the whole-canopy mean leaf lifespan (P < 0.01) and a positive relationship with the leaf N_{mass} (P < 0.01) and SLA (P < 0.05). All four whole-canopy mean leaf traits had no linear relationship with stand aboveground biomass (data not shown). The results indicated that the whole-canopy mean leaf traits had significant implications for the structure and function of forest ecosystems.

Fig. 2 Altitudinal trends in leaflevel N_{area} (a), SLA (b) and N_{mass} (c) of 1-year-old leaves across evergreen tree species groups were compared with the change in percentages of stem basal area of evergreen versus deciduous trees (d) along the eastern slope of the Gongga Mountains. For abbreviations, see Fig. 1



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Whole-canopy mean leaf traits in relation to climatic and soil factors

The logistic function $\{v = k/[1 + \exp(a + b \cdot x)]\}$ fitted the relationship between whole-canopy mean leaf lifespan and annual mean temperature significantly $(r^2 = 0.94,$ P < 0.01) (Fig 3a), while another logistic function $\{y = k/k\}$ $[1 + \exp(a + b \cdot x + c \cdot x^2)]$ fitted the relationship between the leaf lifespan and soil available-N content well $(r^2 = 0.82, P < 0.02)$ (Fig. 3b). Because whole-canopy mean SLA, N_{mass} and N_{area} were closely correlated with the leaf lifespan (as indicated above), they also showed similar logistic relationships with annual mean temperature $(r^2 = 0.64 - 0.78)$ and soil available-N content $(r^2 = 0.76 - 0.92)$ (data not shown). Because the wholecanopy mean leaf lifespan was closely related to the altitudinal distribution of evergreen forest trees (from Fig. 2d, Table 3), it would be an integrated indicator for ecological adaptations of natural forests to the climate gradients in the Gongga Mountains.

Discussion

Approach to scaling up the traits of a leaf to the stand-level scale

Leaf mass-based photosynthetic capacity and leaf N concentration are usually positively correlated. Both are

positively correlated with SLA, and all three traits decline with increasing leaf lifespan (see Reich et al. 1997, 1999). Generality in the relationships among leaf traits across diverse communities and ecosystems has significant implications for global-scale modeling of vegetation-atmosphere CO_2 exchange (Schulze et al. 1994; Reich et al. 1999). However, limited knowledge exists about their relationships with ecosystem characteristics of structure and function (Reich et al. 1992).

Taking into account age effects and species variations is the basis for scaling up the traits of a leaf to a standlevel scale. In this study, we developed a methodology to calculate the whole-canopy mean leaf traits to include all tree species (groups) in a forest plot through a series of weighted averages scaled up from leaf-level measurements. Such defined whole-canopy mean leaf traits were well correlated and consistent with the general relationships among the traits of a leaf in this study (Fig. 1) and many previous studies of diverse taxonomic groups and biomes (e.g., Field and Mooney 1986; Reich et al. 1999). Much evidence from altitudinal transect studies on within-age leaf traits indicates consistent trends that as elevation increases, SLA decreases, whereas leaf N_{area} increases (Woodward 1986; Körner et al. 1986; Körner 1989) or remains unchanged in evergreen conifers (Hultine and Marshall 2000). Furthermore, leaf N_{mass} increases with altitude in herbaceous and deciduous woody plants (Woodward 1986; Körner 1989; Weih and Karlsson 1999) but is

Table 4 Correlation coefficients for linear relationships between whole-canopy mean leaf traits and stand variables among the six forest sites in the Gongga Mountains. For abbreviations, see Tables 1, 2 and 3

Independent variables	Foliage N-pool	LAI	Root biomass	NPP
Whole-canopy mean leaf lifespan	0.9542**	0.8567*	-0.9477^{**}	-0.9454^{**}
Whole-canopy mean leaf N_{area}	0.8819*	0.6050	-0.7281	-0.6911
Whole-canopy mean leaf N_{mass}	-0.8313*	-0.8848*	0.9662^{**}	0.9383^{**}
Whole-canopy mean SLA	-0.9298**	-0.7450	0.8648^{*}	0.8344^{*}

P* < 0.05, *P* < 0.01

Fig. 3 Whole-canopy mean leaf lifespan showed logistic relationships with annual mean temperature (a) and soil available-N content (b) across the six forest sites in the Gongga Mountains



remarkably stable in evergreen woody plants (Körner 1989) or decreases in evergreen conifers (Hultine and Marshall 2000). Our field data for the within-age leaf traits and their whole-canopy weighted averages along the east slope of Gongga Mountains generally confirm previous conclusions. Moreover, the scaled-up wholecanopy mean leaf traits indicated more significant altitudinal patterns consistent with the change in relative percentages of evergreen versus deciduous canopy.

More importantly, the whole-canopy mean leaf lifespan and leaf N_{mass} generally showed significant relationships to stand foliage N-pool, LAI, root biomass and NPP (Table 4). We believe that the whole-canopy mean leaf traits are equivalent to the traits of a leaf but are more useful for large-scale pattern analysis of ecosystem functioning.

Relationships between foliage N-pool and abiotic factors of climate and soil

Stand foliage N-pool has important implications for ecosystem structure and function (Chapin et al. 1990). Because estimates of foliage N-pool were based on the data for leaf N_{mass} and stand foliage biomass, we applied a similar logistic function to the one above to analyze their relationships with annual mean temperature and soil available-N storage. Here, we set the maximum foliage N-pool (k) to equal 300 kg/ha land that was estimated from the data in Table 3. Annual mean temperature and soil available-N storage explain 92 and 78% of the variation in foliage N-pool, respectively (Fig. 4). The soil available-N storage also exponentially increased with increasing altitude $(r^2=0.71, P<0.05)$ (from Table 3). Along the altitudinal transect, foliage Npool was linearly correlated with stand NPP ($r^2 = 0.86$, P < 0.01), root biomass ($r^2 = 0.78$, P < 0.02) and LAI $(r^2 = 0.67, P < 0.05)$ (from Table 3). The results indicate that the climatic gradient characterizes not only the vegetation distribution but also the soil N conditions of the forest ecosystems.

Generality of logistic relationships between whole-canopy mean leaf traits and climatic factors

The estimated annual mean temperature and annual precipitation in the Gongga Mountains are highly correlated, and the temperature in the subtropical forests is low. We need to test for a generality of the logistic relationships between the whole-canopy mean leaf traits and mean temperature found in this study.

We collected more data from Reich et al. (1999) and Wang et al. (2000) and then estimated the whole-canopy mean leaf traits for an additional six forest communities in the Americas and eastern China (Appendix 1). Because of the lack of data for stem basal area and foliage biomass in the literature, the whole-canopy mean leaf traits in the additional forest stands were estimated as the arithmetic average of the leaf trait measurements available for the dominant tree species. Then we mixed the additional plot data from other studies with our plot data and did the same logistic regression analysis for the pooled data sets from 12 plots (Fig. 5). The data sets cover a wide range of forests along tropical/subtropical to temperate/alpine gradients where annual mean temperature and annual precipitation have a low relationship $(r^2 = 0.16, \text{ not statistical significance at } P < 0.10).$ All three whole-canopy mean leaf traits for leaf lifespan, SLA and leaf N_{mass} fit the logistic patterns associated with annual mean temperature ($r^2 = 0.49 - 0.76$, P < 0.02) (Fig. 5a, c, d). The whole-canopy mean leaf lifespan also fits the logistic relationship for annual precipitation across tropical and temperate forests $(r^2=0.92,$ P < 0.001) where annual mean temperature is $> 8^{\circ}C$ (Fig. 5b). However, annual precipitation shows no relationship with the canopy-mean SLA and leaf N_{mass} (data not shown).

Leaf lifespan has highly important implications for the altitudinal distribution of evergreen forest trees (from Fig. 2d). The pooled data from this study and additional literature indicate that the whole-canopy mean leaf lifespan shows higher correlations with temperature and precipitation than the other three leaf

Fig. 4 Stand foliage N-pool showed logistic relationships with annual mean temperature (a) and soil available-N storage (b) across the six forest sites in the Gongga Mountains



traits. It seems that temperature and/or precipitation characterize mainly the size of the whole-canopy mean leaf lifespan that sets the upper limit of stand canopy leaf ages, while the canopy-mean SLA and leaf N_{mass} are according to seasonal changes in canopy leaf-age structure (e.g., leaf mass ratios among different agegroup leaves). The lower relationship between leaf N_{area} and leaf age (Fig. 1b) indicates that more complicated N allocations to leaf areas exist. Inside a plant canopy, evidence shows that the vertical distribution of leaf N_{area} is mainly controlled by photosynthetic photon flux density (Field 1983; Ellsworth and Reich 1993; Meir et al. 2002). In a plant community, canopy leafage structure is generally considered a control on allocating leaf N for maximization of carbon gain (Field 1983; Kull et al. 1998). Given a climate regime, the optimal leaf age structure for resource use should exist. Earlier analyses among genera and species suggest that both phenotypic plasticity and genotypic variation

Fig. 5 Based on the pooled data from this study (Table 3) and the literature (Appendix 1), whole-canopy mean leaf lifespan (a), SLA (c) and leaf N_{mass} (d) fit the logistic patterns associated with annual mean temperature. The whole-canopy mean leaf lifespan also fits the logistic relationship for annual precipitation across tropical and temperate forests where annual mean temperature is >8°C. For abbreviations, see Fig. 1



(a)

contribute to the effects of elevation and latitude on conifer needle longevity (Ewers and Schmid 1981; Chabot and Hicks 1982; Reich et al. 1995). A later report by Reich et al. (1996) provides evidence from garden experiments that longer needle longevity of spruce and pine populations at high elevations and high latitudes is largely an environmentally regulated phenotypic acclimation.

Strategy for nitrogen conservation and maximum carbon gain in natural forests

It is still unclear why some forest types, such as temperate/alpine evergreen conifers, maintain high LAI values of more than six or seven and what their biological function is. In the Gongga Mountains, alpine spruce-fir forests had the highest LAI ranging from 7 to 10 (Table 3) based on the biomass allometric regressions

(b)

with harvested trees ranging from 10 to 74 cm in DBH. Water balance simulations further suggest that available soil water is enough to support such a high forest LAI (Luo et al. 2002c). High measurements of forest LAI have led to questions concerning the methodology used to calculate them since Marshall and Waring (1986) reported that estimates of leaf area based on tree diameter appear to be inaccurate, and therefore the exceedingly high leaf-area indices previously reported for Douglas-fir forests are thought to be unreliable. However, Ren and Peng (1997) present different results in their study on comparisons of different LAI measurement methods in three forest types in the Dinghushan Reserve, south China. The study indicates that three methods, including empirical allometric regressions, inclined point quadrats and light interception, give the same LAI estimates and the serious underestimate from litterfall is because of the influences of frequent typhoons and storms in the region.

The LAI of alpine spruce-fir forests at high altitudes seems to be controlled by low soil temperatures and the interaction between foliage production and soil N availability. Approximately 75% of the nitrogen in a plant leaf with C₃ photosynthesis is invested in photosynthetic components, and nitrogen acquisition by roots is a major carbon expense of a plant (Chapin et al. 1987). In the Gongga Mountains, forest ecosystems at higher altitudes tended to have higher foliage N-pool and higher soil N storage where stand canopy had longer leaf longevity and higher foliage mass. We found that root biomass was negatively correlated with whole-canopy mean leaf lifespan and foliage N-pool. Our synthesis in Fig. 5 suggests that the whole-canopy mean leaf lifespan appears to be an integrated indicator for such ecological adaptations of natural forests to temperature and/or precipitation gradients. Many theories explain that variations in leaf lifespan are a strategy for optimizing plant carbon gain (Grime 1977; Chabot and Hicks 1982; Pearcy et al. 1987; Kikuzawa 1991) and/or plant adaptations to specific temperature, moisture and nutrient regimes (Monk 1966; Waring and Franklin 1979; Coley et al. 1985; Chapin et al. 1987). Low temperature and then low growth rates favor plant longevity (Grime 1977; Coley et al. 1985) where leaf and tree lifespan are correlated (Reich et al. 1992). The growth of leaves at high altitude seems to be controlled in a way that leads to comparatively high nutrient contents, which in turn support high metabolic activity (Körner 1989). On the other hand, the closed canopy of trees with high leaf mass and long leaf longevity generally creates a low soil temperature, which impairs root activity (Körner 1998). Then carbon costs for nitrogen absorption by roots in alpine plants become more expensive and extending the leaf lifespan is more economic. For tropical or subtropical evergreen broadleaf forests, evergreen canopy leaves with a relatively shorter mean lifespan (generally approximately 1-3 years) would favor mineral conservation and maintain optimal growth rates by reducing nutrient leaching losses from leaves and soil as a result of high rainfall and temperature (Monk 1966; Chabot and Hicks, 1982; Sobrado 1991; Cordell et al. 2001).

Implications from convergence towards logistic patterns in whole-canopy mean leaf traits and stand characteristics

The community-oriented growth analysis can provide a better basis to predict effects of climate change on plant growth than the species-based analysis (Körner 1991). In response to climatic and soil gradients in the Gongga Mountains, whole-canopy mean leaf lifespan and stand foliage N-pool converged towards threshold-like logistic relationships with annual mean temperature and soil available-N variables (Figs. 3, 4). In general, as elevation increased, the whole-canopy mean leaf lifespan and leaf Narea and stand LAI and foliage N-pool increased to their maximum, whereas the whole-canopy mean SLA and leaf N_{mass} and stand NPP and root biomass decreased from their maximum. Such threshold-like logistic patterns are also found in stand NPP, LAI and live-biomass both aboveground and belowground across subtropical forests to alpine vegetation on the Tibetan Plateau (Luo et al. 2002a, b, 2004; T. Luo et al., submitted manuscript). These results confirm that in plant growth, natural selection favors a high carbon gain, close to the maximum that can be maintained in any given environment (Mooney 1972; Grime 1977). Understanding the mechanisms underlying these relationships will increase our capacity to predict future ecosystem behaviors under global climate change.

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Appendix 1

Estimated whole-canopy mean leaf traits of forests in the Americas and eastern China based on the data in Reich et al. (1999) and Wang et al. (2000). Because of the lack of data for stem basal area and foliage biomass, the whole-canopy mean leaf traits were estimated as the arithmetic average of the leaf trait measurements available for the dominant tree species in each forest stand. *AMT* Annual mean temperature, *AP* annual precipitation, *SLA* specific leaf area, N_{mass} leaf mass-based nitrogen concentrations, *yr*. year, *DM* dry mass

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Locations	Vegetation type	AMT (°C)	AP (cm)	Whole-canopy mean leaf lifespan (yr.)	Whole-canopy mean SLA (cm ² g ⁻¹ DM)	Whole-canopy mean leaf N_{mass} (mg g ⁻¹ DM)	Authors
San Carlos, Amazonas, Venezuela	Tropical rainforest (22 tree species)	26.0	356	2.31±1.46	88±25	14.0±4.7	Reich et al. (1999)
South Wisconsin	Cold temperate forest of pines and deciduous broad leaved trees (25 tree species)	8.0	82	1.02 ± 1.03	98 ± 58	18.1±11.2	Reich et al. (1999)
Coweeta, North Carolina	Montane humid temperate forest of pines and deciduous broadleaved trees (eight tree species)	12.5	183	1.90 ± 1.83	122 ± 72	18.1±5.1	Reich et al. (1999)
Hobcaw, South Carolina	Warm temperate forest of pines and deciduous broadleaved trees (six tree species)	18.3	130	1.42 ± 0.88	67 ± 26	11.9±3.5	Reich et al. (1999)
Niwot Ridge, Colorado	Sub-alpine spruce-fir and pine forest ecotone (three tree species)	-1.2	90	6.17±2.75	33±6	10.6 ± 0.5	Reich et al. (1999)
Tiantong National Forest Park, Zhejiang, China	Subtropical evergreen broadleaf forest(35 tree species)	16.2	138	1.69 ± 0.73		_	Wang et al. (2000)

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