



## Leaf area index and net primary productivity along subtropical to alpine gradients in the Tibetan Plateau

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### ABSTRACT

**Aim** Our aims were to quantify climatic and soil controls on net primary productivity (NPP) and leaf area index (LAI) along subtropical to alpine gradients where the vegetation remains relatively undisturbed, and investigate whether NPP and LAI converge towards threshold-like logistic patterns associated with climatic and soil variables that would help us to verify and parameterize process models for predicting future ecosystem behaviour under global environmental change.

**Location** Field data were collected from 22 sites along the Tibetan Alpine Vegetation Transects (TAVT) during 1999–2000. The TAVT included the altitudinal transect on the eastern slope of the Gongga Mountains in the Eastern Tibetan Plateau, with altitudes from 1900 m to 3700 m, and the longitudinal-latitude transect in the Central Tibetan Plateau, of approximately 1000 km length and 40 km width.

**Methods** LAI was measured as the product of foliage biomass multiplied by the ratio of specific leaf area. NPP in forests and shrub communities was estimated as the sum of increases in standing crops of live vegetation using recent stem growth rate and leaf lifespan. NPP in grasslands was estimated from the above-ground maximum live biomass. We measured the soil organic carbon (C) and total and available nitrogen (N) contents and their pool sizes by conventional methods. Mean temperatures for the year, January and July and annual precipitation were estimated from available meteorological stations by interpolation or simulation. The threshold-like logistic function was used to model the relationships of LAI and NPP with climatic and soil variables.

**Results** Geographically, NPP and LAI both significantly decreased with increasing latitude ( $P < 0.02$ ), but increased with increasing longitude ( $P < 0.01$ ). Altitudinal trends in NPP and LAI showed different patterns. NPP generally decreased with increasing altitude in a linear relationship ( $r^2 = 0.73$ ,  $P < 0.001$ ), whereas LAI showed a negative quadratic relationship with altitude ( $r^2 = 0.58$ ,  $P < 0.001$ ). Temperature and precipitation, singly or in combination, explained 60–68% of the NPP variation with logistic relationships, while the soil organic C and total N variables explained only 21–46% of the variation with simple linear regressions of log-transformed data. LAI showed significant logistic relationships with both climatic and soil variables, but the data from alpine spruce-fir sites diverged greatly from the modelled patterns associated with temperature and precipitation. Soil organic C storage had the strongest correlation with LAI ( $r^2 = 0.68$ ,  $P < 0.001$ ).

**Main conclusions** In response to climatic gradients along the TAVT, LAI and NPP across diverse vegetation types converged towards threshold-like logistic patterns consistent with the general distribution patterns of live biomass both above-ground and below-ground found in our earlier studies. Our analysis further revealed that climatic factors strongly limited the NPP variations along the TAVT because the precipitation gradient characterized not only the vegetation distribution but also the soil N conditions of the natural ecosystems. LAI generally increased with increasing precipitation and was well correlated with soil organic C and total N variables. The

interaction between LAI growth and soil N availability would appear to have important implications for ecosystem structure and function of alpine spruce-fir forests. Convergence towards logistic patterns in dry matter production of plants in the TAVT suggests that alpine plant growth would increase in a nonlinear response to global warming.

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### Keywords

Alpine plants, climate, leaf area index, logistic function, net primary productivity, soil nutrients, Tibetan Plateau, transect.

## INTRODUCTION

Regional and global patterns of net primary productivity (NPP) and their determinants have long interested ecologists (Rosenzweig, 1968; Lieth, 1975; Webb *et al.*, 1978; Knapp & Smith, 2001). At a continental scale, NPP is strongly correlated with climate variables (Rosenzweig, 1968; Lieth, 1975; Sims & Singh, 1978; Webb *et al.*, 1978; Sala *et al.*, 1988; Knapp & Smith, 2001). Weber's Law (Duvigneaud, 1987) indicates that a well-balanced natural plant community, regardless of species composition, should have a similar dry matter production, NPP, and biomass accumulation under the same environmental conditions. It is similar to the Law of Constant Yield derived from the Two-Thirds Thinning Law in population ecology, but further suggests the threshold-like logistic relationship of plant production to natural resource limits. Lieth (1975) has described the relationship between climatic factors (annual mean temperature, annual precipitation, and annual evapotranspiration) and NPP in logistic functions at a global scale. However, it is unclear if regional NPP across biomes also follows such a logistic pattern (Rosenzweig, 1968; Sims & Singh, 1978; Webb *et al.*, 1978; Sala *et al.*, 1988; Luo, 1996; Clark *et al.*, 2001), and the limiting factors vary regionally (Raich *et al.*, 1997; Schuur & Matson, 2001) and interannually (Burke *et al.*, 1997; Knapp & Smith, 2001; Knapp *et al.*, 2002). Both biomass and NPP generally increase asymptotically through time during forest succession (Kira & Shidei, 1967; Odum, 1969; Bormann & Likens, 1979). Physiologically, there is an upper limit for plant growth determined by the balance of assimilation and respiration because growth, with its associated respiration, cannot exceed the cost of maintenance (Schulze, 2000). Exploring the general logistic relationship between NPP and limited climatic factors across an undisturbed vegetation gradient would help us to verify and parameterize process models for predicting future ecosystem behaviour under global environmental change (Canadell, 2000). Two serious problems in developing a dynamic biosphere model is our poor understanding of how to scale up and the inability to validate such a model (Tian *et al.*, 1998).

Leaf area index (LAI) has been widely used as an important variable in relation to carbon, water and energy fluxes (Woodward, 1987; Neilson, 1995; Nemani *et al.*, 2003). Geographically, it has been shown that maximum LAI is well correlated with available soil water (Grier & Running, 1977; Woodward, 1987; Neilson, 1995; Luo *et al.*, 2002a), or long-term climatic variables such as annual mean temperature, annual

precipitation, warmth index and moisture index, singly or in combination (Luo, 1996; Luo *et al.*, 2002a). Inside a plant canopy, the total leaf area is controlled in such 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). Because NPP is positively related to maximum LAI or peak foliar biomass (Webb *et al.*, 1983; Waring & Schlesinger, 1985; Luo, 1996), we hypothesize that LAI across biomes will also show the threshold-like logistic pattern in response to climatic and soil gradients. Resolving this question would be helpful in improving understanding of the mechanisms underlying NPP variation and in examining the generality of Weber's Law.

The Tibetan Plateau is an ideal place to study interactions between natural ecosystems and climate change because the vegetation remains relatively undisturbed by humans and the South Asian Monsoon characterizes wide ranges of temperature and moisture gradients (Li & Zhou, 1998). The uplift of the plateau created and then strengthened the South Asian Monsoon and has had tremendous impacts on the evolution and development of species and ecosystems of the plateau itself and of neighbouring regions (Sun & Zheng, 1998). On the plateau, interactions between terrestrial ecosystems and the atmosphere have contributed to the development of diverse biomes with an altitudinal vegetation range from tropical rain forests to alpine vegetation (Zheng, 1996). We have applied Weber's Law and threshold-like logistic functions 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 sites recorded during the 1970s and 1980s across the plateau (Luo *et al.*, 2002b). Model results show a positive reinforcing effect of the monsoon climate in China where the warmest season coincides with the wettest (Luo, 1996). 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 live biomass, both above-ground and below-ground, have threshold-like logistic relationships with temperature and precipitation (Luo *et al.*, 2002c). In this report, we provide additional field data quantifying climatic and soil controls on NPP and LAI along the TAVT. The TAVT data for above- and below-ground biomass and forest LAI and leaf traits are reported elsewhere (Luo *et al.*, 2002a,c). Previously unpublished data for NPP and soil nutrients from the TAVT sites, as well as other LAI measurements in shrublands and grasslands, are presented herein.

Our aims are to investigate whether NPP and LAI converge towards threshold-like logistic patterns in relation to climatic and soil variables, to test if temperature and/or precipitation gradients also characterize soil nutrient conditions across diverse vegetation types along the TAVT and to determine if soil nutrient variables are also likely limiting factors for large-scale distribution patterns of NPP and LAI.

## DATA AND METHODS

### Study sites along the Tibetan alpine vegetation transects (TAVT)

The TAVT includes the altitudinal transect at the eastern slope of the Gongga Mountains in the Eastern Tibetan Plateau and the longitudinal-latitude transect in the Central Tibetan Plateau (Fig. 1). The altitudinal transect runs from the subtropical evergreen broad-leaved forest at 1900 m to the timberline at 3700 m (Table 1, sites 17–22). The longitudinal-latitude transect covers latitudes from N 29°32' to 35°13' N and longitudes from 91°08' E to 94°43' E, and is approximately 1000 km in length and 40 km in width. The TAVT starts from the forest zone of the Sergyemla Mountains (3000–4800 m) in the south-east Tibetan Plateau, extends westward to the alpine shrub-meadow zone in Lhasa (3700 m), then continues northward to the alpine meadow zone in Nagqu (4700 m), and finally ends in the alpine steppe zone of Wudaoliang (4800 m) (Table 1, sites 1–16 and 23). During July and September of 1999 and 2000, we located 22 sites along the TAVT using a global positioning system (GPS) (Table 1). We measured stand LAI, biomass and NPP both above-ground and

below-ground, and associated leaf traits for lifespan and specific leaf area across dominant woody plant species, as well as soil organic carbon (C) and total and available nitrogen (N) contents and their pool sizes.

### LAI measurements in the TAVT sites

In each forest plot, tree height and diameter at breast height (d.b.h) were measured for all trees of > 3 cm d.b.h. Foliage biomass of trees in the forest plots (Table 1, sites 9–22) was calculated from the measurements of d.b.h. and/or tree height using allometric regressions, while those of the undergrowth were measured by harvesting in 2 × 2 m<sup>2</sup> quadrats (Luo *et al.*, 2002c). We measured specific leaf area (SLA, the ratio of fresh leaf area to dry mass) of dominant tree species and undergrowth shrubs in different leaf age classes. The one-side leaf area for broad-leaved trees was measured using a CI-203 Portable Laser Area Meter (CID, Inc.). 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 a vernier caliper. In total, we collected 186 samples of age-grouped leaves from different woody plant species and forest sites. For each leaf sample, leaf areas of 30–50 fresh leaves were measured, and the leaves were then dried to a constant weight at 70 °C. Then, we converted the foliage biomass of trees and shrubs to LAI values using the biomass-weighted mean SLA ratios. For the undergrowth herbs and mosses, the LAI estimates were based on the cover degrees because of difficulty in measurements of their SLA ratios.

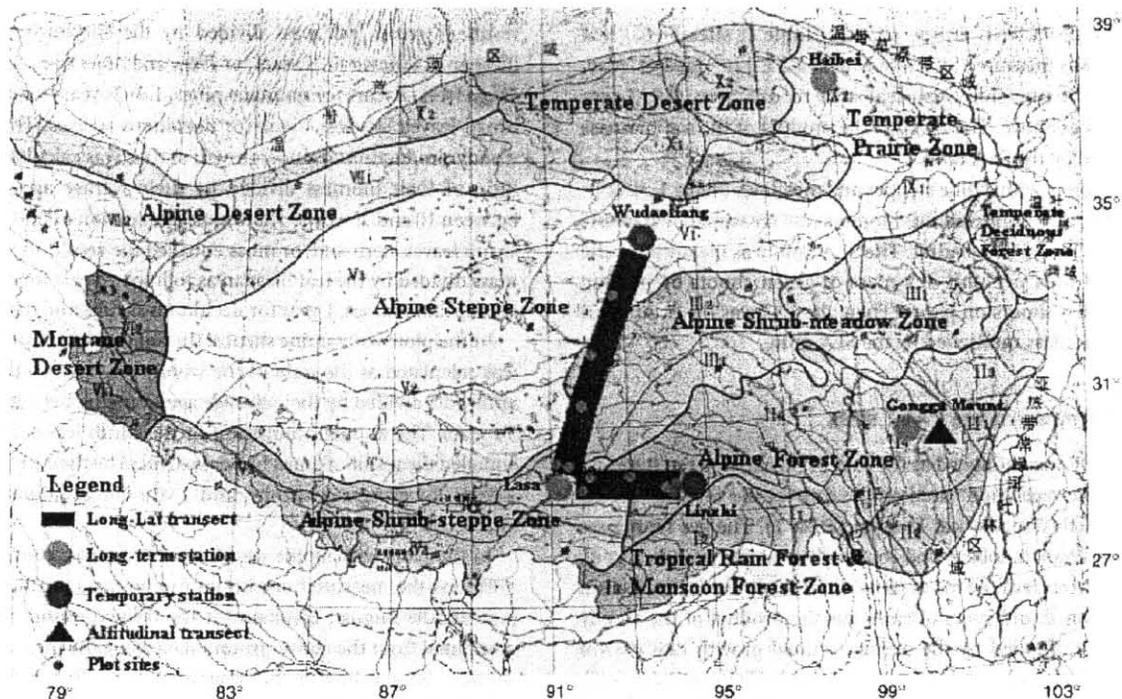


Figure 1 Map of the Tibetan Alpine Vegetation Transects (TAVT). The vegetation zonation was adapted from Zheng (1996).

Table 1 Leaf area index (LAI), net primary productivity (NPP, in dry matter), soil organic C (SOC) and soil total N (STN) storage for 22 sites along the Tibetan Alpine Vegetation Transects (TAVT)

Site no.	Vegetation type and location	Mean age of dominant stems	GPS position	SOC (t C ha <sup>-1</sup> )	STN (t C ha <sup>-1</sup> )	NPP (t ha <sup>-1</sup> year <sup>-1</sup> )	LAI (ha ha <sup>-1</sup> )
1	Alpine <i>Stipa</i> ; steppe	annual	(4626 m, E93 04 05, N35 12 56)	28.92	3.53	1.19	0.63
2	Alpine <i>Stipa</i> ; steppe	annual	(4582 m, E92 32 52, N34 18 51)	22.04	3.43	1.54	0.82
3	Alpine <i>Stipa</i> ; steppe	annual	(4871 m, E91 48 19, N32 27 33)	16.99	3.16	2.25	1.19
23	Alpine <i>Kobresia</i> ; meadow	annual	(4636 m, E91 55 34, N31 33 59)	96.73	6.02	3.15	1.66
4	Alpine <i>Kobresia</i> ; meadow	annual	(4288 m, E91 08 44, N30 29 50)	71.46	5.12	1.53	0.81
5	Alpine <i>Kobresia</i> ; meadow	annual	(4100 m, E91 29 12, N29 45 11)	42.75	3.41	3.12	1.64
6	Alpine <i>Rhododendron</i> - <i>Kobresia</i> ; shrub-meadow	25 yr., annual	(4652 m, E92 18 53, N29 45 14)	127.48	8.56	3.10	3.60
7	Alpine <i>Rhododendron</i> ; shrub	24 year	(4560 m, E94 39 07, N29 36 38)	69.13	4.39	5.36	1.85
8	Alpine <i>Lonicera</i> - <i>Artemisia</i> ; dry shrub	29 year	(3780 m, E91 38 03, N29 47 50)	69.53	8.88	2.38	3.83
9	<i>Betula</i> ; deciduous forest	45 year	(3620 m, E93 30 00, N30 00 00)	28.20	2.55	6.82	5.69
10	<i>Quercus</i> ; evergreen forest	60 year	(3080 m, E94 01 19, N29 45 35)	88.67	3.93	10.83	6.81
11	<i>Pinus densata</i> and <i>Quercus</i> ; mixed forest of evergreen trees	60 year	(3100 m, E94 14 32, N29 45 13)	72.03	4.18	8.41	6.71
13	Alpine <i>Abies georget</i> var. <i>smithii</i> ; fir forest	208 year	(3780 m, E94 33 27, N29 33 32)	359.93	21.07	15.17	12.41
14	<i>Abies georget</i> var. <i>smithii</i> ; timberline forest	168 year	(4073 m, E94 35 31, N29 34 52)	216.24	10.66	3.64	8.86
15	<i>Sabina saltuaria</i> and <i>Rhododendron</i> ; timberline woodland	175 year	(4450 m, E94 37 22, N29 36 55)	222.62	13.26	4.48	4.54
16	Alpine <i>Abies georget</i> var. <i>smithii</i> ; fir forest	200 year	(3800 m, E94 42 51, N29 39 04)	242.73	8.76	11.84	10.18
17	Evergreen broadleaved forest	80 year	(1900 m, E102 03 26, N29 36 16)	71.32	7.18	17.74	4.55
18	Evergreen-deciduous broadleaved forest	140 year	(2200 m, E102 01 28, N29 35 13)	109.75	8.62	17.09	6.23
19	Mixed forest of spruce-fir and deciduous broadleaved trees	270 year	(2850 m, E102 01 20, N29 35 10)	296.66	14.58	10.37	10.31
20	Alpine <i>Abies fabri</i> ; fir forest	75 year	(3050 m, E101 59 55, N29 34 34)	159.95	11.70	12.24	7.78
21	Alpine <i>Abies fabri</i> ; fir forest	180 year	(3000 m, E101 59 55, N29 34 34)	181.93	9.15	10.69	10.17
22	<i>Abies fabri</i> ; timberline forest	145 year	(3700 m, E101 58 05, N29 32 44)	359.51	24.48	7.68	10.21

In the plots with alpine shrubs (Table 1, sites 6–8), leaf biomass was measured by harvesting in a 2 × 2 m<sup>2</sup> quadrat. Also, the ratio of one-side fresh leaf area to dry mass (SLA) was measured as above. The LAI was the product of the leaf biomass multiplied by the SLA ratio.

In the plots with alpine steppes and meadows (Table 1, sites 1–5 and 23), above-ground live biomass was measured by harvesting in a 0.5 × 0.5 m<sup>2</sup> quadrat. The SLA ratio was measured as the projected area per unit dry mass of green shoots by pasting the sampled shoots on paper. Then, the LAI was the product of the live biomass multiplied by the SLA ratio.

#### NPP estimates in the TAVT sites

Forest NPP was estimated as the sum of increases in the standing crop of live vegetation based on the data for live biomass, recent stem growth rate and leaf lifespan (Table 1). The live biomasses for stem, branch, foliage and root were available from Luo *et al.* (2002c). In each of the forest plots, 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 measured over 2 or 5 years. The species-specific equations of annual stem growth rate were developed by Luo *et al.* (2002b). The annual production of leaves equalled the

result of green leaf mass divided by the species-specific leaf lifespan as follows: 6–8 years for *Picea* and *Abies* trees, 3 years for *Tsuga* trees, 2 years for montane pines, 1.5 (2) years for evergreen broad-leaved species, 1 year for deciduous species. 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 equalled 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.

In the plots with alpine shrubs, the annual woody production was calculated as the ratio of the woody biomass (stem, branch and root) divided by their average ages: ranging between 20 and 30 years. The annual production of the shrub leaves and herbs equalled the result of green biomass divided by their leaf lifespan: 2 years for evergreen shrubs, and 1 year for deciduous shrubs and herbs.

In the plots with alpine steppes and meadows, above-ground NPP was the measured maximum live biomass during late July and middle August. Estimates of the below-ground NPP were computed from the above-ground data using the measured NPP root-to-shoot ratios in this region: 2.18 ± 0.20 for the alpine meadow in the Haibei station (Yang *et al.*, 1988), and 1.03 ± 0.20 for the alpine steppe in the Bange station (unpublished observations).

We attempted to reduce the underestimates of NPP, the result of missing litterfall data, using the stem growth rate and leaf lifespan in forests and shrubs, and estimating from above-ground maximum live biomass in grasslands. Losses to herbivores were not considered because we lacked information.

#### Soil organic C and N contents within the maximum rooting depth

We collected soil samples and measured soil bulk densities by layer (A<sub>0</sub>, A<sub>1</sub> and/or B horizons) from the soil pits (0.5 × 0.5 m<sup>2</sup> quadrats) to the depth of the deepest visible root. One soil pit was dug in each grassland and shrub plot, while 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 analysed for organic C and total and available N contents by layer. The total N content was determined by HClO<sub>4</sub> + H<sub>2</sub>SO<sub>4</sub> digestion and NaOH distilling neutralization analysis. The FeSO<sub>4</sub> + Zn + NaOH distilled water extraction analysis determined the available soil N content. The organic C content was determined by the K<sub>2</sub>Cr<sub>2</sub>O<sub>7</sub> method. The soil bulk density was measured with the cutting ring method in most plots, or by weighing soil mass in some forest plots with rocky soils. The storage of organic C and total and available N in soils was calculated from the soil-mass-weighted averages for organic C content, total and available N contents and soil bulk density, and the maximum plant rooting depth average (Table 1).

#### Estimates of climatic factors in the TAVT sites

Climatic data included mean temperatures for the year, January, and July, and annual precipitation. Because few meteorological stations exist in the Central Tibetan Plateau (approximately 50 stations), the climatic data of the sites along the longitudinal-latitude transect were obtained from Chinese temperature and precipitation databases at a resolution of 2.5' × 2.5' (c. 4–5 km), simulated by PRISM (Parameter-elevation Regressions on Independent Slopes Model, Daly *et al.*, 1994, 2000a) according to GPS locations (latitude, longitude and altitude). The PRISM's database is developed on the averages of 30-year (1961–90) observation data of monthly minimum and maximum mean temperatures and monthly precipitation from approximately 2450 temperature stations and 2600 precipitation stations in China and neighbouring countries (Daly *et al.*, 2000b). On the other hand, the climatic data of the sites along the altitudinal transect were estimated from 10 years' of meteorological observations measured at 1600 m and 3000 m, by the Alpine Ecosystem Observation and Experiment Station, Chinese Academy of Sciences (Zhong *et al.*, 1997). The site temperatures were calculated using a lapse rate of 0.6 °C per 100 m of altitude. Annual precipitation below 2500 m in elevation was estimated from the meteorological observatory at 1600 m in increments of 120 mm per 100 m (from 1600 to 2500 m). Annual precipitation above 2500 m was estimated from the meteorological observatory at 3000 m in decrements (between 2500 m and 3000 m) or increments (above 3000 m) of 74 mm per 100 m. The climatic condi-

tions across the sites along the transects showed a broad range of temperature and precipitation, with annual mean temperature from -4.2–10.4 °C and annual precipitation from 27 to 240 cm.

#### Modelling relationships of NPP and LAI with climatic and soil variables

We hypothesized that NPP and LAI both follow Weber's Law and have logistic relationships with climatic and soil variables:

$$y = k/(1 + \exp(a + bx)), \quad \text{or} \quad y = k/(1 + \exp(a + bx + cx^2))$$

where,  $y$  is for dependent variables of NPP and LAI, and  $x$  is for independent climatic and soil variables, including mean temperatures for the year, January, and July, and annual precipitation (singly or the products of temperature and precipitation), as well as soil organic C and total and available N contents and their pool sizes.  $k$  is the maximum NPP and LAI, estimated as 20 t ha<sup>-1</sup> year<sup>-1</sup> (Luo *et al.*, 2002b) and 13 ha/ha in this study, respectively.  $\exp$  is the base of the natural logarithm, and the other parameters of  $a$ ,  $b$ , and  $c$  are equation coefficients. The site-specific data were used to determine the equation coefficients by least squares regression method. When there was a nonrobust logistic relationship ( $P > 0.01$ ), we tested the data with other models, such as linear, power, log and exponential functions.

## RESULTS

#### Variations in NPP and LAI among vegetation types and their geographical patterns

NPP (Mg ha<sup>-1</sup> year<sup>-1</sup>) along the TAVT varied by over an order of magnitude across vegetation types: 1.2–2.3 for alpine steppes, 1.5–3.2 for alpine meadows, 2.4–5.4 for alpine shrubs, 3.6–7.7 timberline, 8.4–10.8 for dry valley forests, 10.4–15.2 for alpine spruce-fir forests, and 17.1–17.7 for subtropical forests (Table 1). The LAI values showed a similar trend among vegetation types, except subtropical forests: 0.6–1.2 for alpine steppes, 0.8–1.7 for alpine meadows, 1.9–3.8 for alpine shrubs, 4.5–10.2 at timberline, 6.7–6.8 for dry valley forests, 7.8–12.4 for alpine spruce-fir forests, and 4.6–6.2 for subtropical forests (Table 1). The subtropical forests had the highest NPP but a lower LAI. Simple linear regressions of log-transformed data with an equation of  $y = ax^b$  indicated that the LAI explained about 70% of the NPP variation ( $P < 0.001$ ) among most vegetation types, except the subtropical broadleaved evergreen forests and some timberline fir forests (Fig. 2).

Geographically, NPP and LAI both significantly decreased with increasing latitude (Fig. 3a,b) ( $P < 0.02$ ) but increased with increasing longitude (Fig. 3c,d) ( $P < 0.01$ ). Altitudinal trends in NPP (Fig. 3e) and LAI (Fig. 3f) showed different patterns. NPP generally decreased with increasing altitude in a linear relationship ( $\text{NPP} = -0.0054\text{Alt} + 27.714$ ,  $r^2 = 0.73$ ,  $P < 0.001$ ), whereas LAI showed a negative quadratic relationship with altitude ( $\text{LAI} = -3\text{E-}06\text{Alt}^2 + 0.0175\text{Alt} - 18.229$ ,  $r^2 = 0.58$ ,  $P < 0.001$ ). As altitude increased, LAI increased among forests but decreased at the timberline and in shrublands and grasslands.

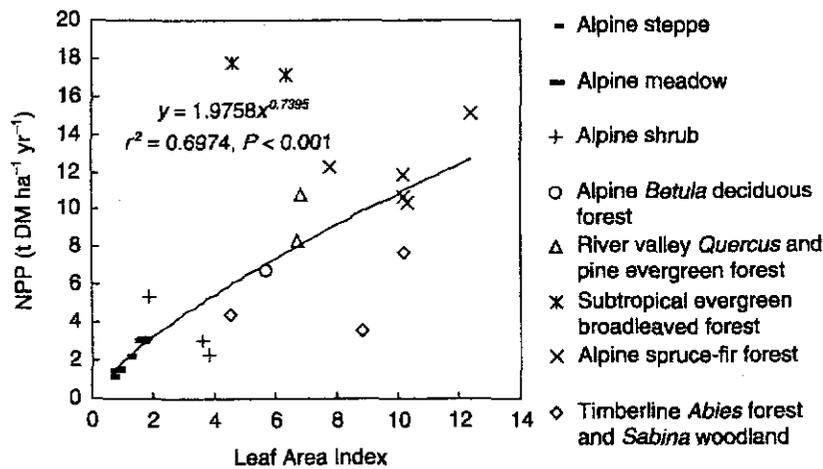


Figure 2 Relationship between leaf area index (LAI) and net primary productivity (NPP) for 22 sites along the Tibetan Alpine Vegetation Transects (TAVT).

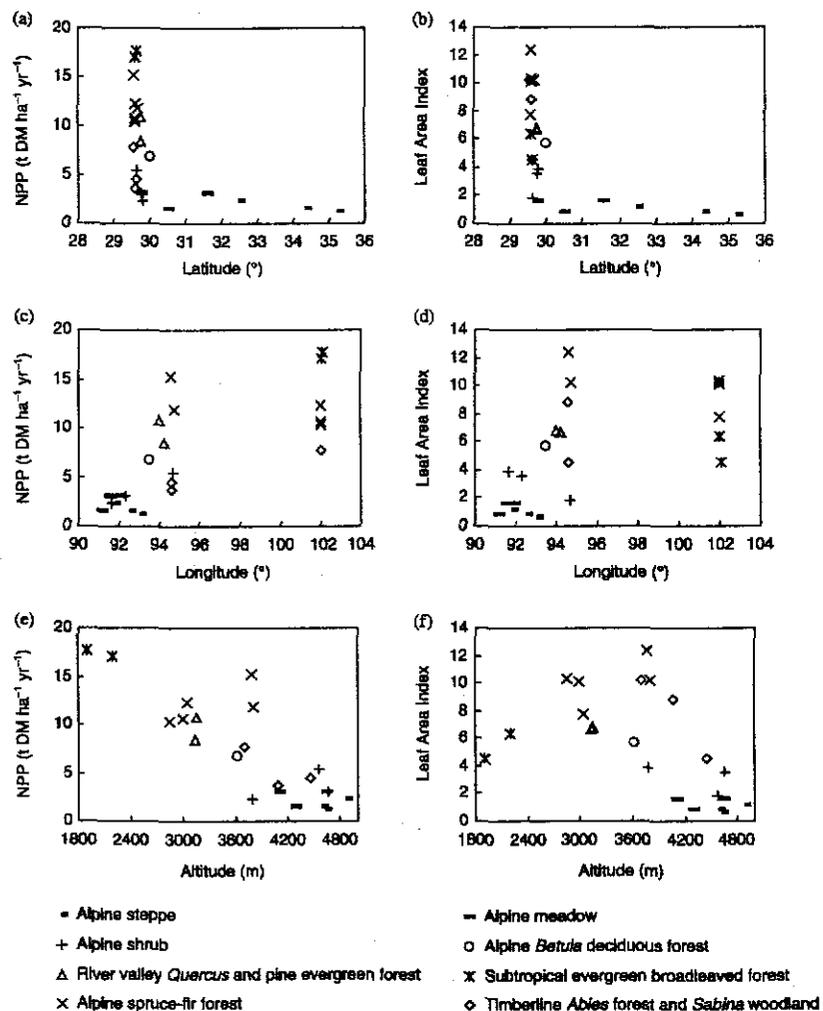


Figure 3 Geographical variations in leaf area index (LAI) and net primary productivity (NPP) for 22 sites along the Tibetan Alpine Vegetation Transects (TAVT). NPP and LAI were related to latitude (a, b), longitude (c, d) and altitude (e, f), respectively.

**Correlations between independent variables**

Table 2 summarizes correlation coefficients among independent variables. Mean temperatures for the year, January, and July, were highly correlated but had low or nonrobust correlations

with other independent variables. Mutually correlated soil organic C and total N variables showed significant correlations with annual precipitation but had nonrobust correlations with all the mean temperatures. The soil available N variables were significantly correlated with the soil organic C and total N

Table 2 Correlation matrix for independent variables for 22 sites along the Tibetan Alpine Vegetation Transects (TAVT)

Independent variables	Data range	Correlation of variables†											
		1	2	3	4	5	6	7	8	9	10		
1 Annual mean temperature (°C)	-4.2–10.4	1											
2 Annual precipitation (cm)	27–238	0.37	1										
3 January mean temperature (°C)	-15.5–1.6	0.99**	0.44*	1									
4 July mean temperature (°C)	6.6–18.2	0.98**	0.37	0.95**	1								
5 Soil total N storage (t N ha <sup>-1</sup> )	2.6–24.5	0.10	0.64**	0.19	0.02	1							
6 Soil total N content (mg N g <sup>-1</sup> )	0.5–9.8	0.20	0.66**	0.26	0.15	0.84**	1						
7 Soil available N storage (t N ha <sup>-1</sup> )	0.2–1.5	0.01	0.11	0.06	-0.11	0.76**	0.55**	1					
8 Soil available N content (mg N 100 g <sup>-1</sup> )	2.8–51.7	-0.04	0.09	0.01	-0.15	0.61**	0.67**	0.82**	1				
9 Soil organic C storage (t C ha <sup>-1</sup> )	17–370	0.11	0.60**	0.20	0.02	0.93**	0.84**	0.72**	0.63**	1			
10 Soil organic C content (mg C g <sup>-1</sup> )	3–197	0.20	0.70**	0.27	0.14	0.81**	0.90**	0.51*	0.60**	0.82**	1		

The correlation coefficients (*r*) with asterisks were statistically significant at \**P* < 0.05 and \*\**P* < 0.01. Those without asterisks were not statistically significant at *P* < 0.05. †See column 1 for definition of variables.

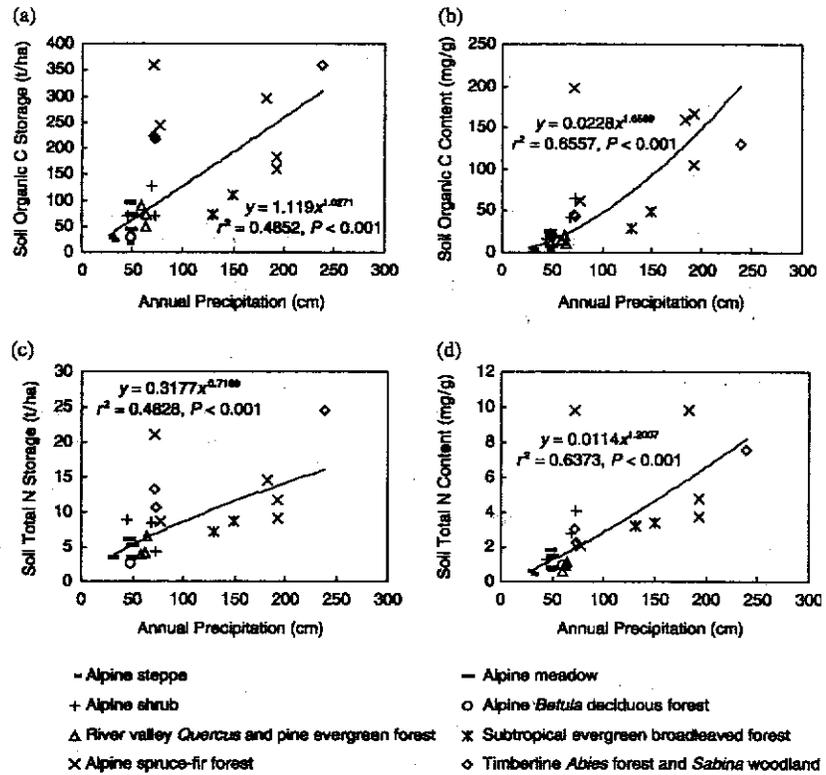


Figure 4 Relationships between annual precipitation and soil variables for 22 sites along the Tibetan Alpine Vegetation Transects (TAVT). Soil organic C storage (a) and content (b) and soil total N storage (c) and content (d) were correlated with annual precipitation, respectively.

variables but had no relationships with any of the climatic variables. Simple linear regressions of log-transformed data with an equation of  $y = ax^b$  indicated that annual precipitation explained 64–66% ( $P < 0.001$ ) of the variation in soil organic C and total N contents (Fig. 4b,d) and 48–49% ( $P < 0.001$ ) of those in both pool sizes (Fig. 4a,c) across diverse vegetation types.

**Relationships of NPP and LAI with climatic factors**

As expected, NPP and LAI along the TAVT both fitted significantly with the threshold-like logistic patterns associated with

temperature and precipitation (Figs 5 and 6). The NPP showed much higher correlations (Fig. 5,  $r^2 = 0.60$ – $0.68$ ,  $P < 0.001$ ) than the LAI (Fig. 6,  $r^2 = 0.35$ – $0.65$ ,  $P = 0.01$ – $0.001$ ). In general, NPP increased with increasing mean temperature (Fig. 5a–c) and increasing temperature and precipitation combinations (Fig. 5e,f). Moreover, the NPP increased with increasing precipitation when annual precipitation was lower than the threshold level of 149 cm but decreased when the annual precipitation was higher than the threshold level (Fig. 5d).

LAI generally increased with increasing precipitation (Fig. 6d) and showed negative quadratic relationships with mean

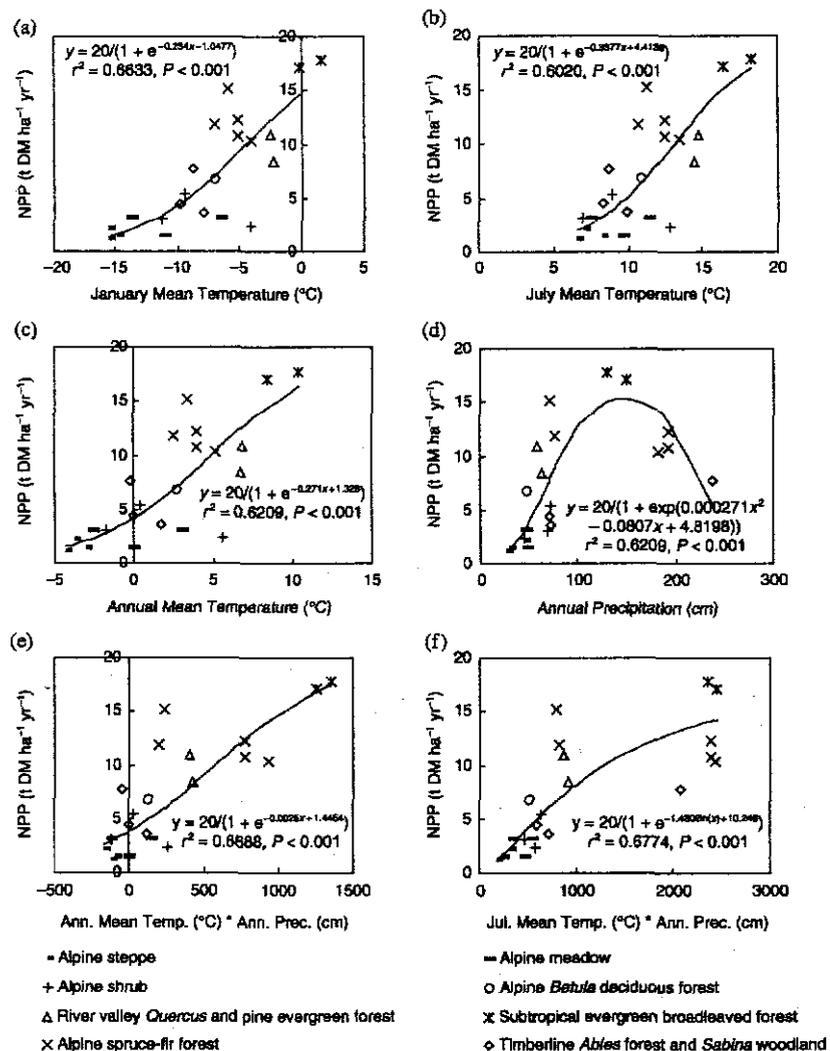


Figure 5 Relationships between net primary productivity (NPP) and climatic variables for 22 sites along the Tibetan Alpine Vegetation Transects (TAVT). NPP was correlated with mean temperatures for (a) January, (b) July and (c) the year, (d) annual precipitation, and (e, f) combinations of annual/July mean temperatures and annual precipitation, respectively.

temperature (Fig. 6a–c) and temperature and precipitation combinations (Fig. 6e,f). However, the field data from spruce-fir sites diverged greatly from the modelled patterns, where the measured LAI tended to be higher than the modelled values.

**Relationships of NPP and LAI with soil nutrient factors**

Along the TAVT, NPP showed nonrobust logistic relationships with soil organic C and total N contents ( $r^2 = 0.25–0.27$ ,  $P < 0.02$ ) and their pool sizes ( $r^2 = 0.14–0.17$ ,  $P < 0.10$ ) and had no relationship with soil available N variables ( $r^2 = 0.03–0.05$ , not statistically significant at  $P < 0.10$ ) (data not shown). We further tested the data with other models. Simple linear regressions of log-transformed data with an equation of  $y = ax^b$  better fitted the relationships between NPP and soil organic C and total N variables ( $r^2 = 0.21–0.46$ ,  $P < 0.05$ ) (Fig. 7).

In contrast, the logistic function ( $y = k/(1 + \exp(a + bx))$ ) fitted well the relationships between LAI and soil organic C and total N variables, with similar patterns ( $r^2 = 0.50–0.68$ ,  $P < 0.001$ ) (Fig. 8a–d). However, the LAI showed weak logistic relationships with soil available N content and its storage ( $r^2 = 0.21–0.27$ ,

$P < 0.05$ ) (Fig. 8e,f). Regressions with other kinds of models also indicated weak relationships between LAI and soil available N variables ( $r^2 = 0.14–0.26$ ,  $P = 0.02–0.10$ ). The soil organic C storage had the highest predictive value for LAI (Fig. 8a).

**DISCUSSION**

**Climatic gradients characterizing soil nutrients along the TAVT**

The precipitation gradient along the TAVT characterizes not only the vegetation distribution but also the soil nutrients in the natural ecosystems (Fig. 4). In general, higher precipitation tends to have higher foliage mass (Fig. 6d). Figure 8 provides evidence that LAI is closely related to the soil organic C and N contents and their pool sizes within the maximum rooting depths of plants. Because LAI and NPP are closely correlated (Fig. 2), the soil organic C and N might come into equilibrium between NPP-based inputs and climate-based outputs (such as soil organic matter decomposition and the leaf-lifespan-related strategy as follows). The C and N cycles are coupled closely in terrestrial

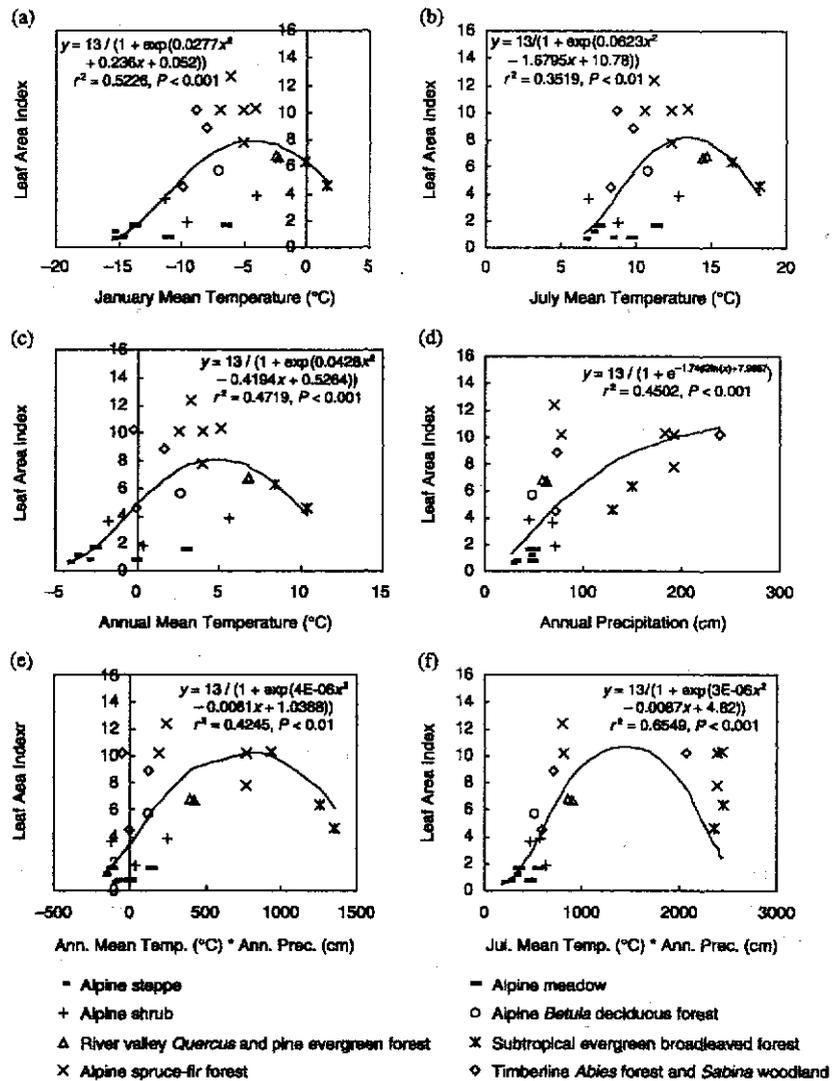


Figure 6 Relationships between leaf area index (LAI) and climatic variables for 22 sites along the Tibetan Alpine Vegetation Transects (TAVT). LAI was correlated with mean temperatures for (a) January, (b) July and (c) the year; (d) annual precipitation and (e, f) combinations of annual/July mean temperatures and annual precipitation, respectively.

ecosystems (McGuire *et al.*, 1995; Schuur & Matson, 2001). An important trend in the successional development is the closing of the biogeochemical cycling of major nutrients such as nitrogen, phosphorus and calcium (Odum, 1969). Biophysical and biogeochemical (nutrients) limitations to productivity and carbon storage may come into equilibrium as ecosystems develop over time (Burke *et al.*, 1997; Schimel *et al.*, 1997). Such a mechanism may generally exist over the Tibetan Plateau because the vegetation remains relatively undisturbed by humans and the South Asian Monsoon characterizes the temperature and moisture gradients (Li & Zhou, 1998).

**Explanations for high LAI measurements in forests**

Along the TAVT, alpine spruce-fir forests had the highest LAI, ranging from 7.8 to 12.4 (Table 1) based on the biomass allometric regressions with harvested trees ranging from 10 to 74 cm in d.b.h. Our previous literature synthesis indicates that temperate/alpine evergreen conifers and subtropical evergreen broadleaved forests have the highest LAI in China, ranging from 6 to 14 on

average among different forest types (Luo, 1996), although there is uncertainty in LAI data because of the use of different methods. Water balance simulations further suggest that available soil water is enough to support such a high forest LAI (Luo *et al.*, 2002a). High measurements of forest LAI have been questioned in respect of the methodology used since Marshall & 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 unreliable. However, Ren & 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 LAI of a 200-year-old stand of monsoon evergreen broadleaved forest in the reserve was measured by four methods: 17.76 by empirical allometric regressions, 17.60 by inclined point quadrats, 16.99 from light interception, and 6.57 from litterfall. Here, the first three methods have the same estimates. According to the analysis of Ren & Peng (1997), the serious underestimate from litterfall is because of the influences of frequent typhoons and storms in the region. The measurements from the mixed forest of

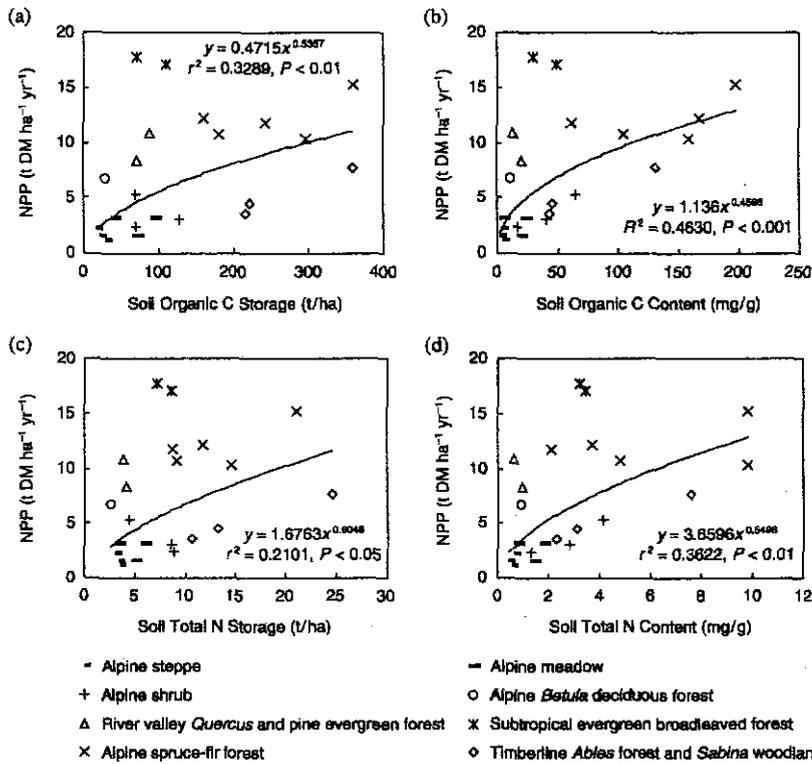


Figure 7 Relationships between net primary productivity (NPP) and soil variables for 22 sites along the Tibetan Alpine Vegetation Transects (TAVT). NPP was correlated with soil organic C storage (a) and content (b) and soil total N storage (c) and content (d), respectively.

pine and broadleaved trees and the pure pine forest in the reserve indicate similar differences among the four methods.

Generally, when the stand LAI is greater than 6 or 7, forest growth efficiency decreases and total above-ground NPP reaches a maximum and keeps constant (Waring & Schlesinger, 1985). However, it is still unclear why some forest types, such as temperate/alpine evergreen conifers and subtropical evergreen broadleaved forests, maintain such high LAI values of more than 6 or 7 and what their biological function is. The LAI of alpine spruce-fir forests at high altitudes seems to be controlled by additional climatic factors (Fig. 6) such as low soil temperatures and the interaction between foliage production and soil N availability (Fig. 8). Geographically, seasonality and distribution of forest LAI is controlled not only by soil water balance (Grier & Running, 1977; Woodward, 1987; Neilson, 1995) but also by other physiological constraints such as the lifespan-related strategy for maximizing carbon gain, mineral conservation mechanisms and nutrient-use efficiency (Chabot & Hicks, 1982; Luo *et al.*, 2002a). In this study, forest ecosystems at higher altitudes tend to have higher foliage mass and higher soil N pools (Table 1 and Fig. 3f). The data from the altitudinal transect in the Gongga Mountains indicate that stand canopy-mean leaf longevity increased with altitude ( $r^2 = 0.88$ ,  $P < 0.01$ ) and was positively correlated with LAI ( $r^2 = 0.73$ ,  $P < 0.05$ ) and foliage N stock ( $r^2 = 0.91$ ,  $P < 0.01$ ) (Luo *et al.* unpublished observation). There is evidence that needle longevity of evergreen conifers increases with increased elevation and latitude (Ewers & Schmid, 1981; Reich *et al.*, 1995) and that foliage mass (biomass and LAI) generally increases with increased mean leaf lifespan (Tadaki, 1977; Reich *et al.*, 1992, 1995). Low temperature and consequen-

tial low growth rates favour plant longevity (Fig. 9, Grime, 1977; Schulze, 1982; 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 low soil temperature, which impairs root activity (Körner, 1998). Consequently, carbon costs for nitrogen absorption by roots in alpine plants become more expensive and extending leaf lifespan is more economic. Since rates of leaching increase in a latitudinal gradient from the poles to the equator, the role of the biotic community in nutrient retention is especially important in the high-rainfall areas of the subtropical and tropical latitudes (Odum, 1969). For tropical or subtropical evergreen broadleaved forests, evergreen canopy leaves with relatively shorter mean leaf lifespan (generally about 1–3 years) would favour mineral conservation and maintain optimal growth rates by reducing nutrient leaching losses from leaves and soil as a result of high rainfall and temperatures (Monk, 1966; Chabot & Hicks, 1982; Chapin *et al.*, 1987; Austin & Vitousek, 1998; Cordell *et al.*, 2001; Schuur & Matson, 2001).

#### Limited factors for NPP distribution patterns

Our field data indicate that temperature and precipitation, singly or in combination, explained 60–68% of the NPP variation along the TAVT (Fig. 5), while the soil organic C and total N variables explained only 21–46% of the variation (Fig. 7). Although we have no data to show how NPP keeps unchanged after it reaches

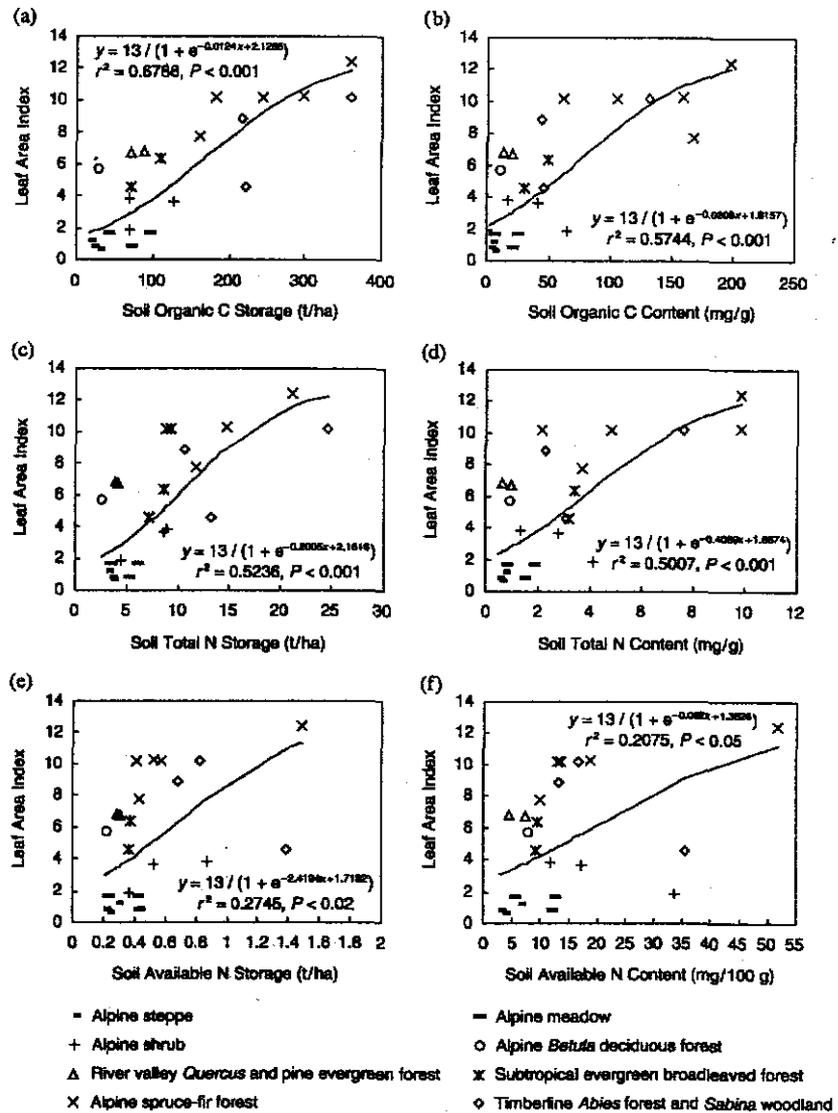


Figure 8 Relationships between leaf area index (LAI) and soil variables for 22 sites along the Tibetan Alpine Vegetation Transects (TAVT). LAI was correlated with soil organic C storage (a) and content (b) and soil total N storage (c) and content (d), and soil available N storage (e) and content (f), respectively.

the maximum ( $20 \text{ t ha}^{-1} \text{ year}^{-1}$ ) while the temperature further increases, the TAVT site data confirm our earlier climate-based NPP model for the whole Tibetan Plateau (Luo *et al.*, 2002b) (Fig. 10). This indicates that the combination of temperature and precipitation constitutes the major limiting factor of NPP in natural vegetation on the plateau.

Along the TAVT, the NPP increased with increasing precipitation when annual precipitation was lower than the threshold level of 149 cm but decreased when the annual precipitation was higher than the threshold level (Fig. 5d). Such a logistic pattern is not consistent with the Miami model that predicts NPP as a logistic increasing function of annual precipitation between 0 and 400 cm at a global scale. Similar to the TAVT data, Clark *et al.* (2001) indicate that tropical forest NPP begins to decrease at approximately 250 cm in annual precipitation. Schuur & Matson (2001) further indicate that increased water availability in excess of plant demand is likely to have decreased the other resources for plant growth where increased nutrient limitation in wetter sites could be the direct cause of the decline in NPP.

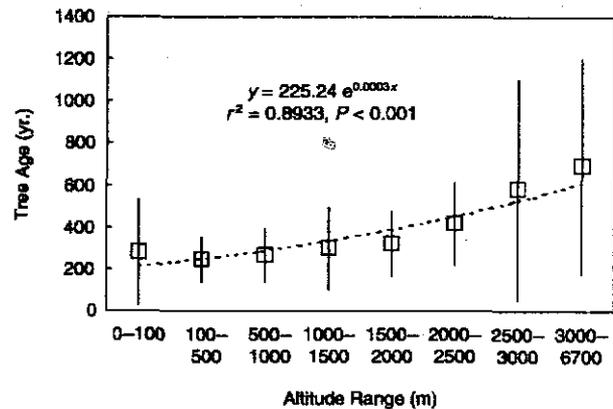


Figure 9 Relationship between average tree age and altitude based on data from the International Tree-ring Data Bank Correlation Statistics (ITRDB Version 4.0) (Numerous ITRDB, 2000).

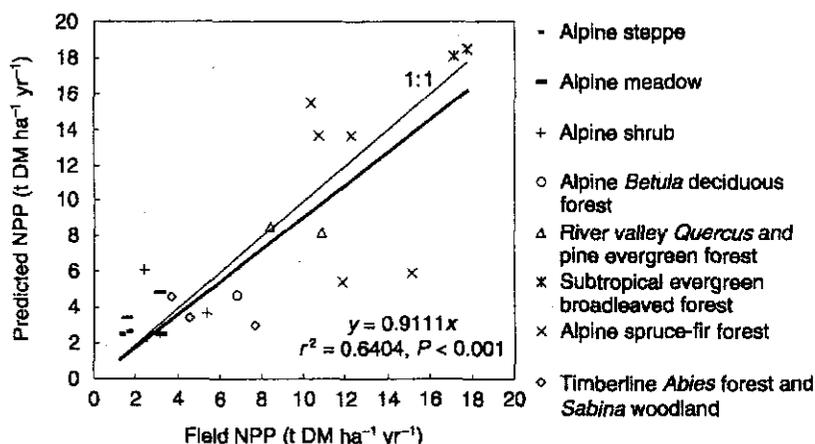


Figure 10 Relationship between the measured net primary productivity (NPP) from the TAVT sites and the predicted NPP by our earlier climate-based NPP model for the whole Tibetan Plateau:  $NPP = 20 / (1 + \exp(1.57716 - 0.0003026(T \times PR)))$  (Luo *et al.*, 2002b).  $T$  is for annual mean temperature ( $^{\circ}\text{C}$ ), and  $PR$  is for annual precipitation (mm).

However, it is unclear that increased nutrient limitation would occur at higher altitudes because the TAVT's forest ecosystems at higher altitudes tend to have higher foliage mass and higher soil N pools. A main cause for lower NPP in the alpine spruce-fir forests and timberline conifers should be lower temperature (Fig. 5c). The NPP at high altitudes varies with the product of July mean temperature and annual precipitation (Fig. 5f), indicating that to a certain extent, the combined effect of temperature and precipitation in this area controls NPP. On the other hand, increase in productivity of a plant canopy may result from increasing LAI, as well as the photosynthetic activity of leaves. Figure 2 indicates that the NPP was significantly related to the LAI across most vegetation types except for the subtropical evergreen broadleaved forests and some timberline conifers ( $r^2 = 0.70$ ,  $P < 0.001$ ). Because the LAI was well correlated with the soil organic C and N variables (Fig. 8), we predict that interactions between LAI growth and soil N availability also affect the NPP of alpine plants at high altitudes.

#### Convergence towards logistic patterns in dry matter production of natural vegetation

In response to climatic gradients along the TAVT, LAI and NPP across diverse vegetation types converged towards threshold-like logistic relationships with temperature and precipitation (Figs 5 and 6). Such threshold-like logistic patterns are also found in live biomass both above-ground and below-ground along the TAVT (Luo *et al.*, 2002c), and the whole-canopy mean leaf traits (leaf lifespan, specific leaf area and leaf N concentrations) across subtropical and timberline forests in the Gongga Mountains within the TAVT (Luo *et al.*, unpublished observation). These results confirm that in plant growth, natural selection favours a high carbon gain, close to the maximum that can be maintained in any given environment (Mooney, 1972; Grime, 1977).

Ecosystems at the low temperature limits of plant life (arctic and alpine environments) are generally considered to be sensitive to climate change (Pounds *et al.*, 1999; Walther *et al.*, 2002). Because of their continuous exposure to extreme environmental conditions, mountain systems have developed well-adapted, but still sensitive, forms of life that respond in characteristic ways to continuous

and/or abrupt environmental changes (Becker & Bugmann, 2001). Convergence towards logistic patterns in dry matter production of plants in the TAVT suggests that alpine plant growth would increase in a nonlinear response to global warming.

#### Future directions

A major challenge for the scientific community today is to explore the dynamic behaviour of the Earth System and its resilience to large-scale perturbations (GAIM Task Force, 2002). In 2000, the International Geosphere-Biosphere Program initiated a new research focus to study biospheric responses to global change that involve rapid nonlinear changes and thresholds (Canadell, 2000). Ecosystem nonlinearity has been recognized as a vital and challenging component of global change science (GAIM Task Force, 2002). We need to identify processes and resource gradients prone to generate nonlinear responses of ecosystems and understand when nonlinear responses are important to scaling issues in time and space (Canadell, 2000). Such knowledge will help us to quantify transfer functions between forcing factors and ecosystem responses and then to verify and parameterize predictive process models (Canadell, 2000). The TAVT data provide evidence that simple functional and structural threshold-like responses to large altitudinal gradients exist across subtropical and alpine vegetation on the Tibetan Plateau. Understanding the mechanisms underlying these relationships will increase our capacity to predict future ecosystem behaviours in response to global climate change.

#### ACKNOWLEDGEMENTS

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#### BIOSKETCH

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