

ESTIMATED BIOMASS AND PRODUCTIVITY OF NATURAL VEGETATION ON THE TIBETAN PLATEAU

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Abstract. We developed a methodology for linking together data from forest and grassland inventories and ecological research sites, and provided a comprehensive report about live biomass and net primary productivity (NPP) on the Tibetan Plateau, the “Third Pole” of the earth where little information about plant biomass and production had been available outside China. Results were as follows. (1) The total live biomass of the natural vegetation in the Xizang (Tibet) Autonomous Region and Qinghai Province was estimated as 2.17 Gg dry mass, of which 72.9% was stored in forests where spruce–fir accounted for 65.1%. (2) The total annual NPP of the natural vegetation in these two administrative regions was estimated as 0.57 Gg dry mass, of which grasslands and forests accounted for 69.5% and 18.1%, respectively. (3) The alpine spruce–fir forests of the Tibetan Plateau had the highest maximum live biomass of the spruce–fir forests globally, with values up to 500–1600 Mg DM/ha (including both aboveground and belowground biomass). (4) The QZNPP model generally predicted NPP well for most of the biomes on the plateau, and simulated the various Chinese vegetation divisions. Model results showed a positive reinforcing effect of monsoon climate in China where the warmest season coincides with the wettest season. (5) The live biomass map for 117 counties of Xizang (Tibet) and Qinghai and the potential NPP map for the whole plateau both showed the same decreasing trend from southeast to northwest.

Key words: biomass; net primary productivity (NPP); Qinghai Province; Tibetan Plateau; vegetation; Xizang (Tibet) Autonomous Region.

INTRODUCTION

It is recognized that the increasing atmospheric CO₂ concentration is most likely affecting the climate. More recently, the Kyoto Protocol acknowledged the role of terrestrial ecosystems as carbon sinks and sources, and provided a basis for developing future emission trading credits that involve carbon sequestration in forests and potentially in other ecosystems (IGBP Terrestrial Carbon Working Group 1998). In general, information on the global distribution of terrestrial carbon sinks and sources is essential for policy and scientific purposes in four areas: reporting for multilateral environmental agreements; understanding of the carbon cycle; assessment of global change trends and impacts; and the management of ecosystem resources at local to regional levels (Cihlar et al. 2000). Therefore, it is a big challenge to obtain accurate, objective information about the state and changes in various parts of the terrestrial carbon cycle at all scales from landscape to global. Estimates of biomass and net primary productivity (NPP) are fundamental to understanding carbon storage

and the biogeochemical dynamics of terrestrial ecosystems.

As a result of rapid uplift in the past several million years, the Tibetan Plateau has a mean elevation of >4000 m, which is above almost half of the troposphere, and this plateau has been dubbed the “Third Pole” of the earth (Li 1993, Zheng 1996). The plateau covers 12 degrees of latitude, 28 degrees of longitude, and has an extreme altitudinal range from 1000 m to 8846 m. The area is ~2 500 000 km², almost one-sixth of the area of China. Uplifting of the plateau created and then strengthened the South Asian monsoon, and has had tremendous impact on the evolution and the development of species and ecosystems of the plateau itself and neighboring regions. The Tibetan Plateau is a differentiation center for new species and a refuge for ancient species (Hou and Chang 1992, Li 1993). In this region, interactions between terrestrial ecosystems and the atmosphere have contributed to the development of diverse biomes and unique altitudinal distribution patterns of vegetation from tropical rain forests to boreal forests and tundra (Fig. 1). The tropical rain and monsoon forests extend northward to ~29° N, which is the extreme northern limitation of these forests in the world. Almost 40% of the timber volume of forests in China occurs on the southeastern Tibetan Plateau (Li 1985). The Tibetan Plateau is an ideal place to study and model the responses of natural ecosystems to global climate change.

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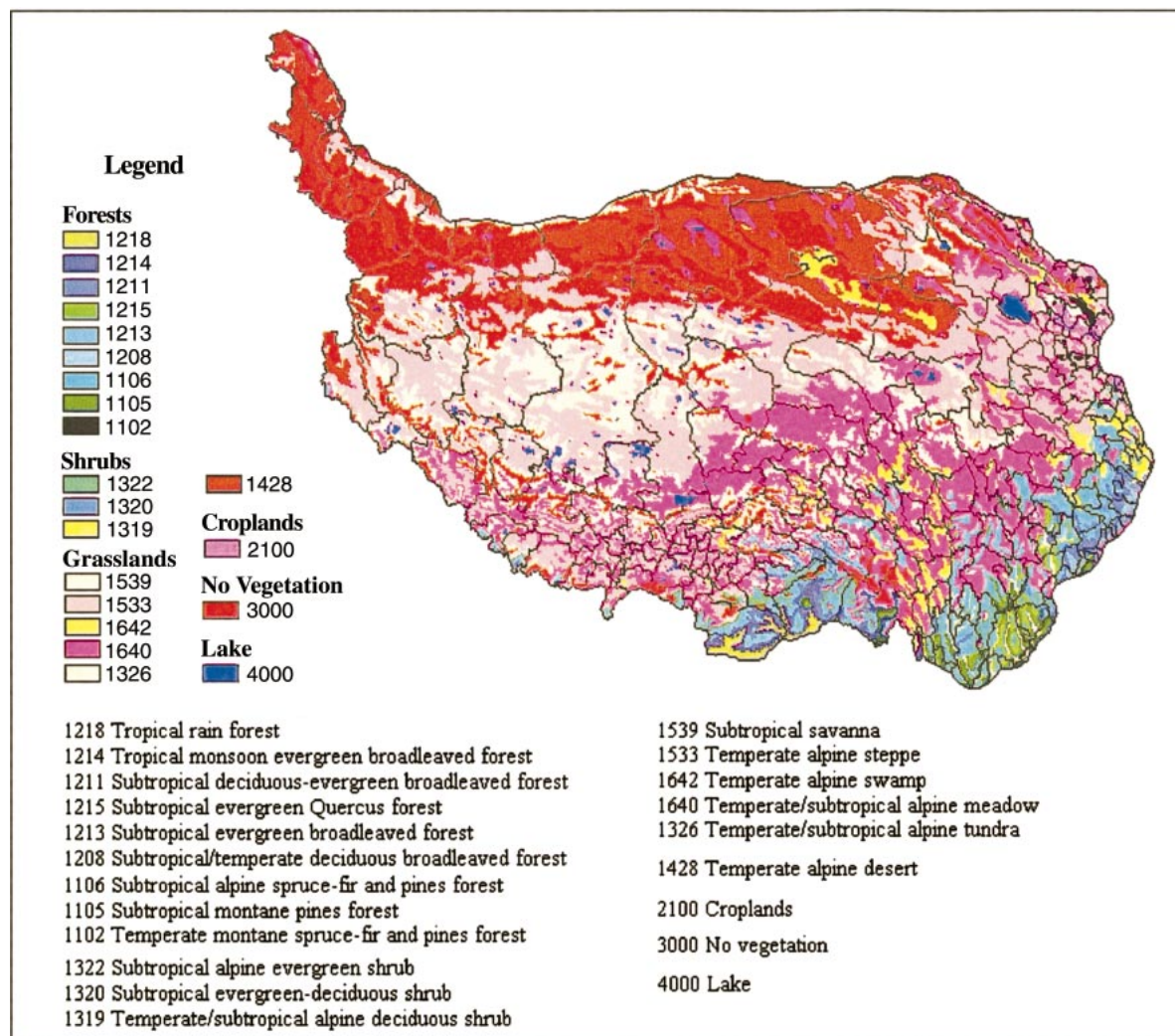


FIG. 1. A real vegetation map of the Tibetan Plateau selected from the Vegetation Map of China (Hou 1979).

In the past forty years (1950–1990), especially between 1973 and 1976, there were many integrated surveys of forest and grassland resources on the plateau. Most of the work focused on vegetation distribution, plant and animal communities, and wood volume and grass yield (Li 1985, 1993, Chinese Academy of Sciences 1988, 1992, Land Managing Bureau and Livestock Service of Xizang (Tibet) Autonomous Region 1994). During the 1990s, long-term research on ecosystem structure and function has been carried out in the major vegetation types of the Tibetan Plateau. More recently, field data and inventory records have been collected and can now be synthesized (Li and Zhou 1998). Knowledge about biomass and net primary productivity (NPP) of the natural vegetation of the Tibetan Plateau would contribute to better estimates of carbon storage and cycling for this large region of the world. Unfortunately, because of language and other con-

straints, very little information has been made available outside China.

The objective of our study is to assemble all available sources of data to provide valuable information on live biomass and NPP at scales from point level to the whole plateau. The tasks are: (1) to review and summarize the literature, (2) to collect the inventory plots and county-specific statistics, (3) to estimate live biomass of stem, branch, leaf, and root in the inventory plots and county-specific statistics, (4) to estimate NPP from plot sites to the whole plateau, (5) to analyze biomass allocations to leaf and root, and variations in live biomass and NPP among different vegetation types, and (6) to map live biomass density and potential NPP of natural vegetation on the plateau.

METHODOLOGY

A diagram illustrating our methodology is presented in Fig. 2. We collected five kinds of data from the

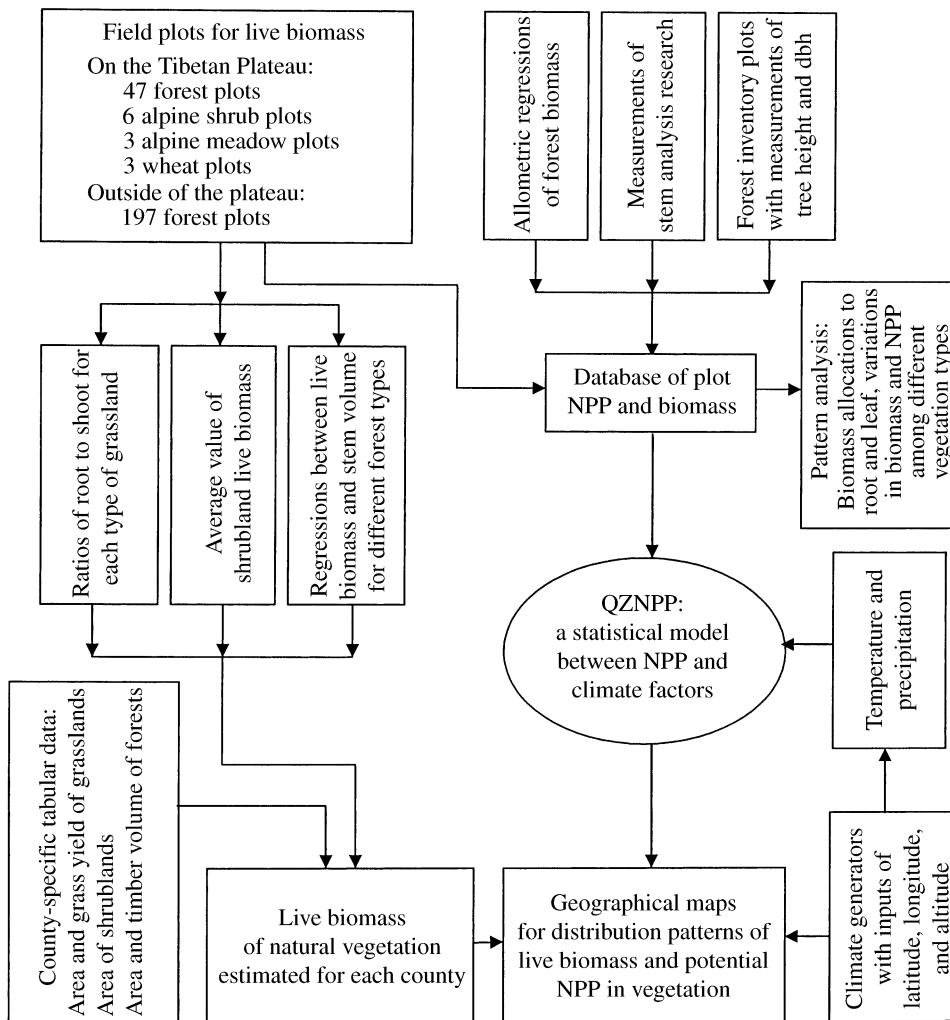


FIG. 2. The flow chart for the research.

literature and county-specific inventories: (1) field plots of grasslands, shrublands, and forests; (2) empirical allometric equations for forest biomass; (3) measurements of stem analysis research; (4) forest inventory plots with measurements of tree height and diameter at breast height (dbh); and (5) tabular data of wood volume, grass yield, and area of forests, woodlands, shrublands, and grasslands in 117 counties of Qinghai Province and the Xizang (Tibet) Autonomous Region.

We set up a database of NPP and live biomass at the site level, including data from both field plots and inventory plots. The field data for live biomass were obtained from the literature. Live biomass from the inventory plots was estimated from measurements of tree height and dbh using empirical allometric regressions. Plot NPP data were estimated from the plot live biomass based on the growth rates derived from stem analysis research and leaf life span. Using this database, we analyzed biomass allocations to leaf and root,

and variations in live biomass and NPP among different vegetation types. Combined with mean annual temperature estimated from latitude, longitude, and altitude, as well as precipitation from a previously published map, the plot NPP data were used to build and calibrate a statistical model (QZNPP, NPP modeling for Qinghai-Xizang Plateau). The QZNPP model was then used to simulate potential NPP for the plateau.

County-specific estimates of live biomass (including aboveground and belowground, and undergrowth) of forests and woodlands were derived from the county-specific tabular data on species-specific timber volume and area using the regression equations derived from the field plot data across China. County-specific estimates of aboveground live biomass of various grasslands were derived from county-specific inventory data of grass yield and area for each type of grassland. The belowground data were estimated from the aboveground data based on root:shoot ratios available from

field measurements. Estimates of aboveground and belowground live biomass of shrublands were the product of county-specific shrubland area multiplied by the mean biomass density that was obtained from available field data. Live biomass for each of 117 counties in the Xizang (Tibet) Autonomous Region and Qinghai Province was the sum of the estimates of forests, woodlands, shrublands, and grasslands. The area-weighted biomass density for vegetation area in each county was used to develop a map for the two administrative regions. Detailed discussion follows.

Data sources

Field plots for live biomass.—We collected data from 59 field plots for live biomass from the literature in this region (Bao and Zuo 1982, Yang et al. 1982, 1988, Li 1984, Jiang et al. 1985, Jiang and Zhu 1986, Zhu et al. 1988, 1993, Ma 1989, Fang et al. 1991, Wang et al. 1991, Yan et al. 1991, Zhou and Huang 1991, Liu 1992, Guan and Liu 1993, Tang and Xu 1993, Li and Zhou 1998, Luo et al. 1998, Yu et al. 1998). Among the 59 plots, there were 47 forest plots, six alpine shrub plots, three alpine meadow plots, and three winter and spring wheat plots. Some of the plots were limited to aboveground biomass, but most of the plots contained measurements of both aboveground and belowground biomass. Nineteen of the 59 plots that had the most comprehensive information about live biomass allocations in different components, including biomass of stem, branch, leaf, and root in forests and shrubs, and aboveground and belowground biomass in grasslands and croplands, were selected (Appendix A). The data were used to analyze biomass allocations to leaf and root and to verify the NPP estimates by climate-based modeling. The other 39 forest plots and one alpine shrub plot that had incomplete information about measurements of stem, leaf, branch, and root, combined with the following forest inventory plots, were used in modeling NPP distributions.

Aboveground and belowground live biomass in the forest plots was measured based on harvesting trees and dimensional analysis. Aboveground live biomass of grasslands and croplands was measured every 2–5 yr by seasonal harvesting in 0.5×0.5 m² quadrats and the mean of seasonal maximum live biomass was used in the analysis. Shrublands were measured once in autumn by harvesting in 2×2 m² quadrats. The belowground live biomass was harvested by excavating whole root systems in 0.5×0.5 m² quadrats to a depth where all root tips were contained in the sample. Litter and biomass losses to herbivores were not considered due to the lack of information.

Inventory plots with measurements of tree height and dbh.—Field plot biomass data available from the literature did not provide enough information for analyzing variations in live biomass and NPP among different vegetation types or for modeling NPP distribution patterns because of limited coverage. Therefore

we collected data on forest inventory plots with measurements of tree height and dbh as well. These unpublished plot data were obtained from various investigators: (1) 376 plots from the Forest Team of Scientific Survey on the Tibetan Plateau, Chinese Academy of Sciences, between 1973 and 1976; (2) 497 plots from the Sichuan Academy of Forestry Surveying and Engineering between 1980 and 1983; and (3) 140 plots from the Yunnan Academy of Forestry Surveying and Engineering between 1980 and 1983. Trees >4 cm dbh within a plot were recorded. The plot area was from 0.0667 to 0.1000 ha. The plots were set up by a systematic sampling method with an 8-km square grid in Sichuan and Yunnan Provinces, and by a typical sampling method along altitudinal transects in the Xizang (Tibet) Autonomous Region.

County-specific tabular data of wood volume, grass yield, and area.—Inventory data from forests and grasslands were useful for estimating live biomass at regional scales. County-specific tabular data of area and timber volume of forests, woodlands, and shrublands in Xizang (Tibet) and Qinghai were obtained from the following sources: (1) Tabular Data of Forest Resources in 30 Forestry Counties of the Xizang (Tibet) Autonomous Region by Aerial Survey, Zhongnan Monitoring Center of Forest Resources and Zhongnan Academy of Forestry Surveying and Engineering (1992, unpublished data); and (2) Tabular Data of Forest Resources of Qinghai Province, Qinghai Academy of Forestry Surveying and Engineering (1978, unpublished data). We obtained tabular data for area and grass yield (fresh mass per unit area) for 39 counties from Tabular Data of Qinghai Grasslands, Qinghai Grassland Station (1988, unpublished data), and a series of survey reports of grassland resources for 78 counties of the Xizang (Tibet) Autonomous Region collected in Li and Zhou (1998). Timber volume measurements followed the technical standards of Forest Survey I of the Forestry Ministry of China (1983) prescribing that the relative error in the total volume estimate for a province (autonomous region) should be <10%, regardless of inventory methods. County-specific forest resource statistics for Xizang (Tibet) were compiled from aerial surveys combined with temporary plot data, while the data compiled from systematic sampling plots with a 2-km square grid were used for Qinghai Province. Grass yield measurements were based on the technical standards of China's First Grassland Resources Survey (Livestock Service of Agricultural Ministry of China 1994). The county-specific grass yield statistics of Qinghai (1980–1986) and Xizang (Tibet) (1987–1990) were compiled from 18 796 and 34 250 temporary plots, respectively, while the type-specific grassland area was measured by combination of remote sensing (Landsat TM images or aerial photos) and ground surveys (Land Managing Bureau and Livestock Service of the Xizang (Tibet) Autonomous Region 1994).

TABLE 1. Regressions between forest live biomass (y ; Mg DM/ha) and stem volume (x ; m³/ha) for major forest types on the Tibetan Plateau based on field biomass data over China collected by Li and Luo (1996) and Luo (1996).

Forest types	Equations	1 SE (Mg DM/ha)	Correlation coefficients (r value)	Plots sampled (n)	Biomass range (Mg DM/ha)
<i>Larix</i> forest	$y = 1.6481x^{0.84788}$	24.00	0.9530***	34	17–285
<i>Picea</i> – <i>Abies</i> forest	$y = 50.8634 + 0.5406x$	31.26	0.9330***	26	52–512
Montane pine forest	$y = 23.9124 + 0.5232x$	17.72	0.9646***	23	28–365
<i>Cupressus</i> forest	$y = -2.8232 + 0.9268x$	8.80	0.9915***	20	24–305
Evergreen broad-leaved forest	$y = -1.5306 + 1.1595x$	51.14	0.9255***	50	46–727
<i>Quercus</i> forest	$y = 1.8409x^{0.89262}$	31.79	0.9469***	49	34–516
<i>Populus</i> – <i>Betula</i> forest	$y = 2.3727x^{0.79024}$	24.81	0.8976***	42	14–207

*** $P < 0.001$.

Regression equations

Live biomass from tree height and dbh.—Allometric regressions for calculating live biomass of stem, branch, leaf, and root of trees had been developed by various investigators (Appendix B); for evergreen broad-leaved trees by Qiu et al. (1984) and Dang and Wu (1992); for montane *Populus*–*Betula* trees by Zhu et al. (1988) and Chen and Zhu (1989); for *Pinus armandii* trees by Chen (1984); for *Pinus yunnanensis* trees by Jiang et al. (1985); for *Pinus tabulaeformis* trees by Ma (1989); for *Larix* trees by Zhou et al. (1991); and for *Picea*, *Abies*, and *Pinus densata* from our early field study.

Live biomass from wood volume.—Due to the lack of sufficient information for each vegetation type from the field plots on the plateau, we used the data collected in Li and Luo (1996) and Luo (1996) from 197 forest plots outside of the plateau. These plot data, combined with the data from the 47 forest plots on the plateau, were used to develop a series of regressions between forest live biomass (total aboveground and belowground live biomass for trees and undergrowth) and stem volume (Table 1). Fang et al. (1998) reported that the relationship between stand biomass and volume could be used for regionally estimating forest live biomass density based on national forest inventory data. We assumed the regression equations in Table 1 could be used for the same forest types on the plateau.

Growth rates of stem volume.—Luo (1996) collected data for 1616 sample trees from 180 tree species across China from various investigators. Data from 704 trees in this region and the neighboring provinces were used

in this study to simulate the mean annual growth rate (%) of stem volume at 5–10-yr intervals for 15 dominant tree-species groups on the plateau (Appendix C).

Climate.—Mean annual temperature was estimated with a multiple regression functions using plot latitude, longitude, and altitude (Table 2). Mean annual precipitation was estimated from the 1:6000000 “Map of annual mean precipitation in China,” based on the latitude and longitude of the plots (Institute of Geography, Chinese Academy of Sciences 1985).

Methods for estimating live biomass from forest inventory plot data

Live biomass of an average tree with mean height and dbh in a forest inventory plot was calculated using species-specific allometric regressions (Appendix B). The live biomass of all trees in a forest inventory plot equaled the product of the mean tree biomass multiplied by the stand density. The biomass of undergrowth (shrub and herb) was estimated using ratios to the biomass of trees as reported in the literature with ranges from 0.44% to 6.09% for shrub and from 0.25% to 2.64% for herb (Luo 1996). Litter and biomass losses to herbivores were not considered due to the lack of information.

Methods for estimating live biomass from county-specific tabular data

Forest and woodlands.—Live biomass of forests and woodlands from the 117 counties was estimated from the county-specific tabular data of area and timber volume using the regressions from Table 1.

TABLE 2. Geographical models of mean annual air temperature in the provinces of Sichuan, Yunnan, Qinghai, and the Xizang (Tibet) Autonomous Region based on 20 years of weather records for 351 meteorological stations.

Region or province	Equations†	Correlation coefficient (r value)	1 SE (°C)	Stations (n)
Tibet and Qinghai	$T = 54.839 - 0.8337(\text{Lat.}) - 0.0689(\text{Lon.}) - 0.0052(\text{Alt.})$	0.9187***	1.33	55
Sichuan	$T = 59.210 - 0.6710(\text{Lat.}) - 0.1892(\text{Lon.}) - 0.0042(\text{Alt.})$	0.9314***	1.12	179
Yunnan	$T = 55.634 - 0.4930(\text{Lat.}) - 0.2001(\text{Lon.}) - 0.0044(\text{Alt.})$	0.8309***	1.05	117

*** $P < 0.001$.† Variables and units: T = mean annual air temperature (°C); Lat. = latitude (°); Lon. = longitude (°); Alt. = altitude (m).

Shrublands.—According to available field data (Yang et al. 1982, Wang et al. 1991, Zhu et al. 1993, Li and Zhou 1998), the range of live biomass of major shrublands on the Tibetan Plateau was 13–62 Mg DM/ha, with a mean of 35.166 ± 16.865 Mg DM/ha. Because of the lack of detailed information about shrubland biomass on the plateau, we considered the shrubland live biomass of each county as the product of the shrub area from the above tabular data multiplied by the mean value of 35.166 Mg DM/ha.

Grasslands.—The aboveground live biomass was calculated from dry mass ratios of various grassland types presented in Livestock Service of Agricultural Ministry of China (1994). The belowground live biomass was estimated from the aboveground using root : shoot ratios reported in the literature: 4.325 ± 1.150 for typical temperate steppe (Jiang et al. 1985, Huang et al. 1987); 7.917 ± 0.211 for alpine meadow (Yang et al. 1988); 4.420 ± 1.179 for other steppe (Zhu and Jia 1991a, b, 1992); and 7.893 ± 0.009 for deserts (Webb et al. 1983). Live biomass of various grasslands for each county was calculated as the product of their dry mass per unit area multiplied by the area.

Methods for estimating NPP from point level to large scale

Plot NPP estimates of forests.—Based on biomass data from 1013 inventory plots and 47 field plots on the plateau, the annual woody production was obtained by multiplying the woody biomass by the mean annual growth rate of stem volume during the recent five or 10 yr calculated from species-specific equations (Appendix C). The annual production of leaves equaled the result of green leaf mass divided by the species-specific leaf life span as follows: five years for *Picea* and *Abies* trees, two years for montane pines, one and one-half years for evergreen broad-leaved species, and one year for deciduous species (Luo 1996, Li and Luo 1996, 1997, Li and Zhou 1998). The annual production of undergrowth (shrub and herb) was calculated as the ratio of their biomass divided by their average ages (Luo 1996). We attempted to reduce the underestimates of NPP due to missing litterfall data, using the recent growth rate and leaf life span.

Plot NPP estimates of alpine meadows.—Mean field data of the aboveground NPP (maximum live biomass) of *Kobresia* meadow for 35 counties of Qinghai and corresponding climate data were obtained from the “Report of Qinghai Grasslands” (Qinghai Grassland Station 1987, *personal communication*) and “Agricultural Resources and Divisions in Qinghai” (Qinghai Agricultural Division Group 1987). Estimates of the belowground NPP were computed from the aboveground data using a root : shoot ratio of 2.182 ± 0.204 reported for *Kobresia humilis* meadows of this region (Yang et al. 1988).

A model for NPP distribution on the plateau.—On a large scale, it was difficult to make NPP estimates

directly from the tabular data due to the lack of detailed information such as stand age, leaf production, and turnover rate of root biomass. Here we used a climate-based model to map the potential NPP of natural vegetation on the plateau. For this purpose, we developed a simple statistical model for the relationship between NPP and climate factors (annual mean temperature and precipitation), using the plot NPP data and corresponding climate factors.

According to Weber's law (Duvigneaud 1987), a well-adapted plant community regardless of species composition should have a similar dry matter production under the same environmental conditions. Duvigneaud (1987) reported that Weber's law was generally correct. We assumed that temperature and precipitation were the limiting factors for NPP distribution patterns of natural vegetation on the plateau. We used a logistic equation to express the relation of NPP to temperature and precipitation as follows:

$$\text{NPP} = k/(1 + \exp[a + bX]).$$

In the formula, exp is the base of natural logarithm, NPP is net primary productivity (Mg DM·ha⁻¹·yr⁻¹), X is the product of mean annual temperature (°C) and precipitation (mm), k is maximum NPP, other parameters of a and b are for equation constants.

Mean NPP for 160 forest areas was calculated from 1013 forest inventory plots and 39 forest field plots. Combined with the other NPP data of 35 alpine meadow areas, a plot NPP data set of forests and grasslands on the plateau was created and used to determine the equation constants of k , a , and b by the least squares method. Then a statistical regression equation, called the QZNPP model, was established as follows:

$$\text{NPP} = 20/(1 + \exp[1.57716 - 0.0003026(T \times \text{PR})]).$$

($F = 416.1356$, $r = 0.8369$, $n = 180$, $P < 0.0001$), where, T is mean annual air temperature (°C), PR is mean annual precipitation (mm), F is the statistical value of F distribution, r is the correlation coefficient, n is the number of sample points, and P is the significance level.

RESULTS

Variations in live biomass and NPP among different vegetation types

Based on the field plot data (Table 3), live biomass of alpine spruce–fir forests varied from 195 to 515 Mg DM/ha, with a maximum of 1600 Mg DM/ha. Net primary productivity for these sites varied from 8 Mg DM·ha⁻¹·yr⁻¹ to 16 Mg DM·ha⁻¹·yr⁻¹ (Sites 3 to 7). Biomass of alpine shrubs varied between 13 Mg DM/ha and 62 Mg DM/ha, with an NPP of 4–7 Mg DM·ha⁻¹·yr⁻¹ (Sites 9 to 13; and from Yang et al. 1982, Wang et al. 1991). Biomass of alpine meadows varied between 20 Mg DM/ha and 60 Mg DM/ha, but was >100 Mg DM/ha in swamp meadows, where NPP var-

TABLE 3. Measurements of live biomass and NPP (dry mass) in selected field plots on the Tibetan Plateau.

Sites	Vegetation type	Altitude (m)	Annual mean temperature (°C)	Annual mean precipitation (mm)	Aboveground		Belowground		Leaf mass (Mg/ha)
					Biomass (Mg/ha)	NPP (Mg · ha ⁻¹ · yr ⁻¹)	Biomass (Mg/ha)	NPP (Mg · ha ⁻¹ · yr ⁻¹)	
1	evergreen broad-leaved forest	2100	13.0	800	249.75	16.843	21.73	0.826	14.07
2	montane pine	2200	12.4	800	329.92	13.093	35.09	0.356	8.02
3	spruce–fir	3500	4.6	800	477.98	8.046	33.64	0.356	14.31
4	spruce–fir	2750	8.5	900	1438.59	15.280	131.33	0.525	38.72
5	spruce–fir	3100	3.9	1900	275.59	9.578	59.31	2.149	7.97
6	spruce–fir	3100	3.9	1900	211.29	14.382	48.02	2.087	11.36
7	spruce–fir	3000	1.5	551	133.83	12.447	21.16	1.058	21.04
8	deciduous broad-leaved forest	2650	2.9	552	65.10	14.369	9.41	1.000	9.40
9	alpine shrub	4200	0.4	800	25.54	3.730	13.43	0.134	3.51
10	alpine shrub	2970	2.0	570	21.89	5.586	12.43	0.731	4.16
11	alpine shrub	3050	2.0	570	29.86	4.832	10.97	0.645	2.76
12	alpine shrub	2733	2.0	570	10.63	6.251	6.03	0.670	5.70
13	alpine shrub	2910	2.0	570	7.50	4.769	5.81	0.447	4.54
14	alpine meadow	3250	-1.7	600	2.51	2.769	19.88	6.036	2.51†
15	alpine meadow	3500	-1.7	600	3.68	3.684	56.05	...	3.68†
16	alpine meadow	3500	-1.7	600	5.18	5.184	111.83	...	5.18†
17	wheat	3700	7.9	425	25.076	25.076	1.642	1.642	12.54†
18	wheat	2900	3.8	175	30.753	30.753	15.56†
19	wheat	2900	3.8	175	12.391	12.391	6.37†

Note: The detailed information on location, dominant species, and reference can be seen in Appendix A.

† Green leaf mass of grasslands and croplands equaled their shoot biomass.

ied from 4 Mg DM·ha⁻¹·yr⁻¹ to 9 Mg DM·ha⁻¹·yr⁻¹ (Sites 14 to 16). The highest annual production of spring and winter wheat on the Tibetan Plateau reached 26–30 Mg DM/ha (Sites 17 to 19). Obviously, forest biomass and NPP were greater than those for shrublands and grasslands. Croplands of winter and spring wheat had the highest annual production under well-irrigated and fertilized conditions.

Table 4 presented maximum stem volume and live biomass for the major forest types on the Tibetan Plateau selected from 1013 forest inventory plots and 47 field biomass plots. The spruce–fir forest of *Picea likiangensis* var. *linzhiensis* in Bomi of eastern Tibet had the highest stem volume and live biomass (2389–3831 m³/ha and 1079–1570 Mg DM/ha). The upper limits of stem volume and live biomass in spruce–fir forests were, respectively, 2.5–3.3 and 1.7–2.8 times greater than that of montane pine forests; 3.9 and 2.5 times greater than that of subtropical evergreen deciduous broad-leaved forests; 4.9 and 2.2 times greater than that of montane sclerophyllous forest; and 6.7–8.5 and 4.4–7.0 times greater than that of deciduous broad-leaved forests. These large values of maximum stem volume and live biomass of the coniferous forests on the plateau were the highest reported in China (Li 1985, 1993).

Fig. 3 presented the comparisons of the annual growth rates of stem volume of seven dominant tree species in eastern Tibet. The maximum age of spruce–fir was >350 yr, much more than montane pines (140–170 yr) and subtropical broad-leaved trees (79–119 yr). Annual growth rates of stem volume generally declined

with age. Before they reached 50 yr of age, the growth rates of the seven species were almost at a same level: 2.9–8.4% for spruces and firs, 2.2–9.9% for montane pines and 2.6–9.0% for subtropical broad-leaved trees. When trees were older than 50 yr, the growth rates of spruce–fir exceeded that of the other species. Between 50 and 120 yr of age, the rate varied between 2.8% and 5.4% for spruces and firs, between 0.9% and 2.3% for montane pines, and between 1.6% and 3.5% for subtropical broad-leaved trees. The spruce–fir ecosystem maintained a slow growth rate of 1.2–3.2% between 130 and 190 yr and 0.4–1.6% after 200 yr of age.

Live biomass allocations to leaf and root among different vegetation types

Generally, forest green leaf biomass on the Tibetan Plateau was >8 Mg DM/ha, with a maximum ~39 Mg DM/ha, and the root : shoot ratio ~0.1–0.2. Alpine shrub leaf biomass varied between 3 Mg DM/ha and 6 Mg DM/ha, with a root : shoot ratio ranging between 0.4 and 0.8. The leaf biomass of alpine meadows varied between 2.5 Mg DM/ha and 5.5 Mg DM/ha, with a root : shoot ratio between 8 and 20. The leaf biomass of high-yield croplands of winter and spring wheat on the plateau varied between 12 Mg DM/ha and 16 Mg DM/ha. This value was comparable to that of the forest, and the root : shoot ratio was ~0.06 (from Table 3).

Differences in leaf biomass and root : shoot ratios among different vegetation types were mostly related to precipitation, soil moisture, and temperature. In Table 3, we presented annual mean temperature and pre-

TABLE 4. Maximum stem volume, mean dbh, mean tree height, live biomass, and NPP for the major forest types on the Tibetan Plateau selected from 1013 forest inventory plots and 47 field biomass plots.

Location	Forest type	Dominant species	Age (yr)	Mean dbh (cm)	Mean height (m)	Stem volume (m ³ /ha)	Live biomass (Mg DM/ha)†	NPP (Mg DM·ha ⁻¹ ·yr ⁻¹)
Bomi, Tibet (29.92° N, 95.88° E, alt. 2750 m)	spruce–fir forest‡	<i>Picea likiangensis</i> var. <i>linzhiensis</i>	250	114.0	65.1	3831	1472.98 (131.33)	15.81
Bomi, Tibet (29.83° N, 95.67° E, alt. 3120 m)	spruce–fir forest	<i>Picea likiangensis</i> var. <i>linzhiensis</i>	250	83.3	55.0	2389	984.36 (95.09)	8.67
Bomi, Tibet (29.83° N, 95.67° E, alt. 3050 m)	montane pine forest	<i>Pinus armandii</i>	80	64.5	49.0	1080	401.71 (181.91)	20.09
Linzhi, Tibet (29.70° N, 94.10° E, alt. 1820 m)	montane pine forest	<i>Pinus yunnanensis</i>	140	81.9	47.3	922	452.04 (30.48)	12.01
Bomi, Tibet (29.80° N, 95.70° E, alt. 2730 m)	montane pine forest	<i>Pinus densata</i>	60	46.9	33.0	889	353.90 (55.20)	18.30
Shangchayu, Tibet (28.70° N, 96.70° E, alt. 2050 m)	evergreen broad-leaved forest	<i>Machilus</i> sp., <i>Toona sinensis</i>	105	58.0	32.0	785	318.17 (134.71)	19.73
Weixi, Yunnan (27.10° N, 99.20° E, alt. 3400 m)	montane sclerophyllous forest	<i>Quercus aquifolioides</i>	108	25.6	15.5	647	365.65 (123.80)	20.96
Bomi, Tibet (30.08° N, 95.00° E, alt. 2300 m)	deciduous broad-leaved forest	<i>Populus</i> sp.	50	33.5	25.0	500	201.27 (87.09)	23.87
Shangchayu, Tibet (29.00° N, 96.67° E, alt. 2470 m)	deciduous broad-leaved forest	<i>Populus</i> sp.	70	44.0	35.5	402	139.81 (57.15)	14.58

† Values without parentheses were for aboveground biomass, and the values with parentheses were for belowground biomass.

‡ These data were from Xu (1995); other plot data in the table were from the unpublished inventories.

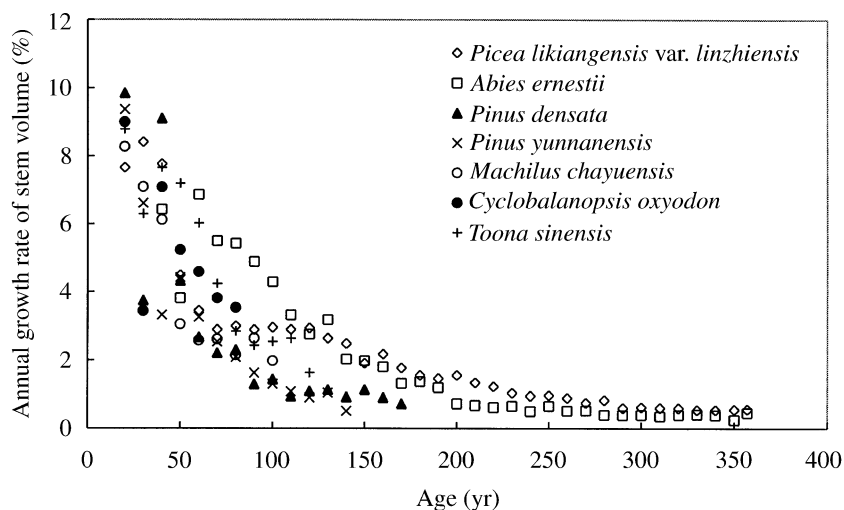


FIG. 3. Comparison of annual growth rates of stem volume of seven dominant tree species. The seven sampled trees with maximum ages were selected from 704 trees for stem analysis research in the southeastern Tibetan Plateau. Ages, dimensions, and sites of the sampled trees are as follows: *Picea likiangensis* var. *linzhiensis*, 357 yr, dbh 100.0 cm, height 64.3 m, located in Zhamu, Bomi of Tibet, altitude 3070 m; *Abies ernestii*, 355 yr, dbh 137.6 cm, height 61.0 m, located in Muzong, Shangchayu of Tibet, altitude 2400 m; *Pinus densata*, 170 yr, dbh 77.6 cm, height 44.8 m, located in Zhamu, Bomi of Tibet, altitude 2700 m; *Pinus yunnanensis*, 140 yr, dbh 69.4 cm, height 52.8 m, located in Jiongdong, Chayu of Tibet, altitude 2000 m; *Machilus chayuenis*, 99 yr, dbh 48.1 cm, height 25.1 m, located in Bentuiqiao, Shangchayu of Tibet, altitude 2100 m; *Cyclobalanopsis oxyodon*, 79 yr, dbh 37.4 cm, height 24.2 m, located in Bentuiqiao, Shangchayu of Tibet, altitude 2100 m; *Toona sinensis*, 119 yr, dbh 51.0 cm, height 25.3 m, located in Bentuiqiao, Shangchayu of Tibet, altitude 2100 m.

TABLE 5. Root biomass distributions by depth for major vegetation types on the Tibetan Plateau (%).

Location	Vegetation type	Altitude (m)	0–10 (cm)	11–20 (cm)	21–30 (cm)	31–40 (cm)	41–60 (cm)	61–80 (cm)
Hongwei Farm, Linzhi of Tibet†	<i>Picea</i> forest	3000	25.78	54.83	7.12	8.01	3.41	0.85
Zhuwagen, Chayu of Tibet†	<i>Abies</i> forest	3500	27.37	52.37	16.57	2.02	1.67	
Jigong, Chayu of Tibet†	<i>Pinus yunnanensis</i> forest	2200	11.51	13.51	39.96	27.61	7.41	
Zhuwagen, Chayu of Tibet†	<i>Rhododendron</i> shrubs	4200	83.84	11.32	3.65	1.19		
Haibei Station, Qinghai‡	<i>Kobresia</i> meadow	3200	82.96	7.84	5.68	3.52		

† From Li (1985).

‡ From Wang et al. (1988).

precipitation for forests (3–13°C and 550–900 mm), shrubs (0.4–2°C and 570–800 mm), and alpine meadows (–1.7°C and 600 mm). Forests and croplands had a higher green leaf biomass and lower root : shoot ratios than alpine shrubs and meadows. Most of live biomass in alpine meadows was stored belowground. Because of irrigation and fertilization in wheat croplands, even though the root : shoot ratio was the smallest, high value of leaf biomass caused high wheat yields in this arid region.

Root distribution also affected leaf growth and root : shoot ratios. More than 70% of forest roots were distributed in soil layers of 11–80 cm, with only 12–27% in the soil surface (0–10 cm) (Table 5). The deepest root depth could exceed 0.8 m. In contrast, >80% of alpine shrub and meadow roots were distributed in the soil surface (0–10 cm). Their deepest root depth was <40 cm. Xu (1995) reported that in a massive long-lived spruce stand, the deepest root distribution

could reach 1.4 m, with 96% of the root biomass in the 0–60 cm soil layer. These analyses further explained that biomass and NPP of forests were greater than those for alpine shrubs and grasslands.

A map for live biomass in the Xizang (Tibet) Autonomous Region and Qinghai Province

Estimated live biomass of natural vegetation types in 78 counties in Xizang (Tibet) and 39 counties in Qinghai is presented in Table 6. The total area covered 114 067 955 ha and accounted for 51% of the total land area of these two administrative regions. Total live biomass was estimated as 2 173 545 339 Mg DM with 88.1% in Xizang (Tibet) and 11.9% Qinghai. For total live biomass, forests, grasslands, shrublands, and woodlands accounted for 72.9%, 19.0%, 7.5%, and 0.6%, respectively. For forest live biomass, spruce–fir forests accounted for 65.1% (47.4% of the total live biomass).

TABLE 6. Live biomass of natural vegetation in the Xizang (Tibet) Autonomous Region and Qinghai Province estimated from inventory tabular data.

Vegetation type	Vegetation area (ha)	Timber volume (m ³)	Live biomass (Mg DM)
Forests			
<i>Larix</i> forest	284	42 890	32 624
<i>Picea-Abies</i> forest	4 520 680	1 480 325 510	1 030 232 213
<i>Pinus</i> forest	1 378 312	325 460 289	203 227 204
<i>Cupressus</i> forest	146 196	9 987 309	8 865 446
<i>Quercus</i> forest	36 016	5 775 836	7 235 227
<i>Populus-Betula</i> forest	271 305	29 989 864	29 024 844
Evergreen broad-leaved forest	1 570 800	336 575 316	303 614 356
Subtotal	7 923 593	2 188 157 014	1 582 231 914
Woodlands	273 891	19 461 142	13 404 012
Shrubs	4 662 778		163 971 249
Grasslands			
Alpine meadow	44 810 416		297 153 211
Montane meadow	1 007 999		9 353 439
Lowland meadow	1 321 606		8 284 489
Wet-temperate steppe	25 558		141 740
Typical temperate steppe	4 238 979		14 285 311
Alpine cold-temperate steppe	42 569 741		66 709 428
Other steppe	130 135		1 746 698
Marsh	7 745		159 570
Others	269 232		2 355 250
Subtotal	94 381 411		400 189 136
Deserts	6 826 282		13 749 028
Total	114 067 955	2 207 618 156	2 173 545 339

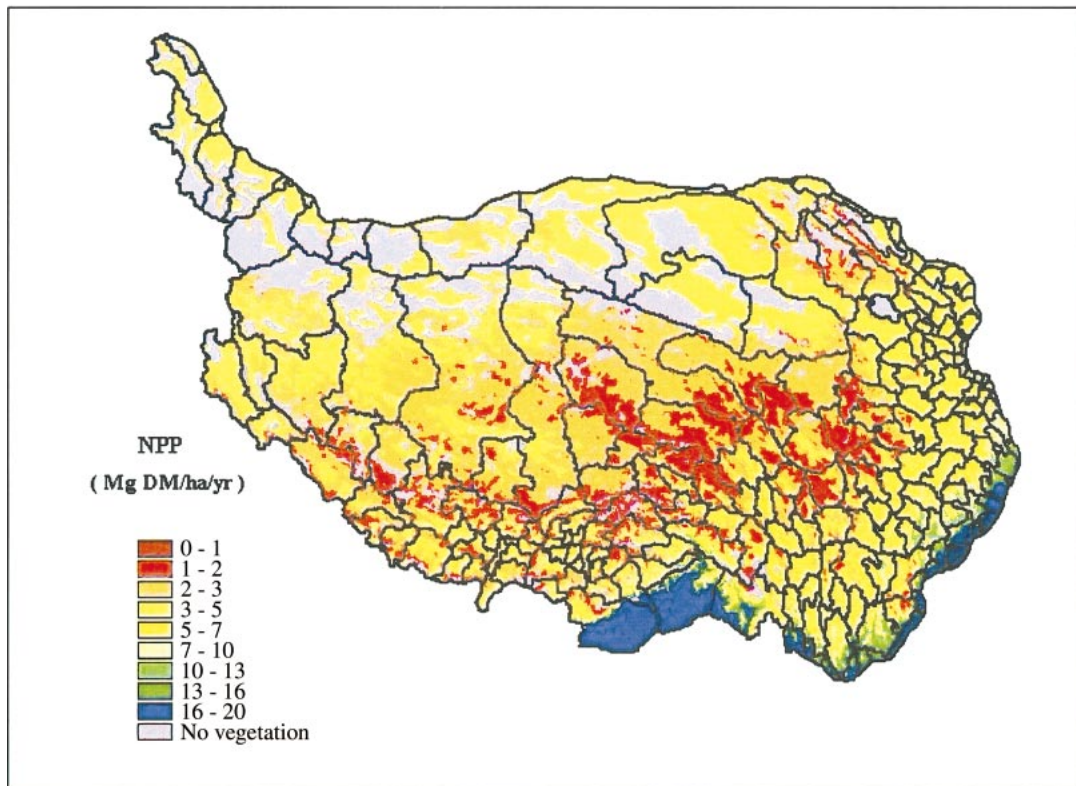
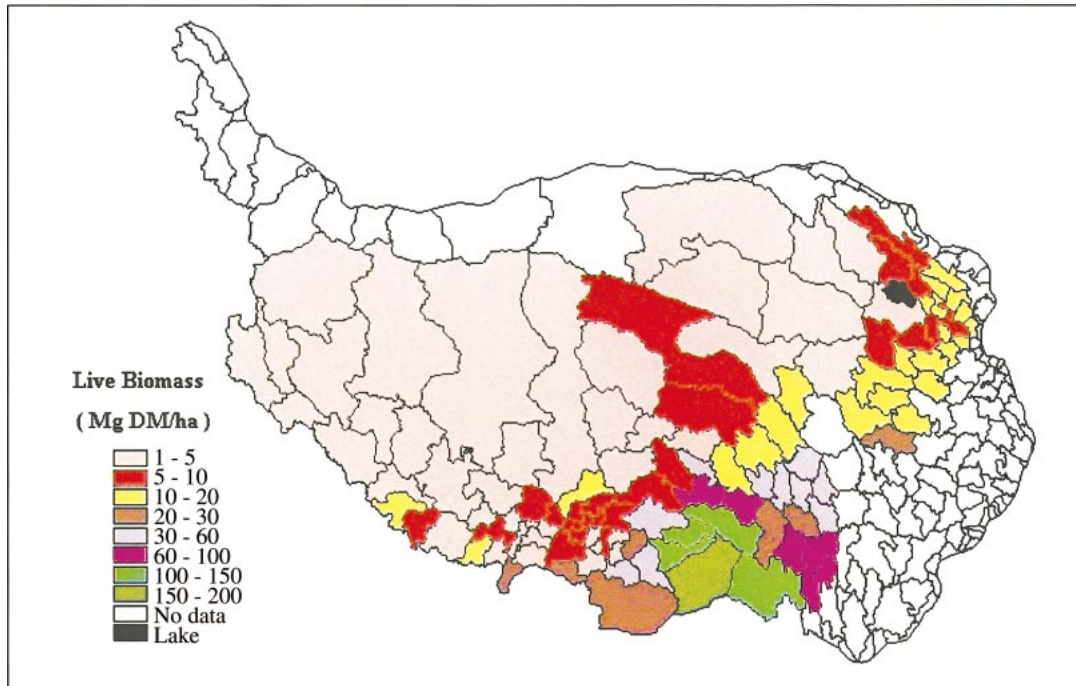


FIG. 4. (Top panel) Live biomass map for natural vegetation in 117 counties of the Xizang (Tibet) Autonomous Region and Qinghai Province.

FIG. 5. (Bottom panel) Potential NPP map for natural vegetation of the Tibetan Plateau.

TABLE 7. Variations in potential NPP among different vegetation types on the Tibetan Plateau simulated by the QZNPP model.

Vegetation type	Area-weighted NPP (Mg DM $\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$)	1 SE (Mg DM $\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$)
Forests		
Subtropical alpine deciduous larch forest	2.522	0.547
Temperate montane spruce–fir and pines forests	3.875	1.291
Subtropical alpine spruce–fir and pines forests	7.735	5.553
Temperate pine and arborvitae forests	11.775	3.726
Subtropical montane pines forests	18.986	2.591
Temperate mixed forest	5.144	0.816
Subtropical/temperate deciduous broad-leaved forests	7.243	4.846
Subtropical deciduous–evergreen broad-leaved forests	18.819	2.945
Subtropical evergreen <i>Quercus</i> forest	9.546	5.594
Subtropical evergreen broad-leaved forests	19.624	1.034
Subtropical bamboo forest	19.859	0.921
Tropical monsoon evergreen broad-leaved forest	19.343	2.598
Tropical monsoon semi-evergreen broad-leaved forest	17.169	5.971
Tropical rain forest	19.965	0.607
Subtotal	12.908	3.413
Woodlands		
Temperate deciduous woodland	4.263	0.850
Shrublands		
Temperate/subtropical alpine deciduous shrubs	9.063	5.445
Subtropical alpine evergreen shrub	9.321	5.759
Subtotal	9.071	5.456
Grasslands		
Subtropical savanna	16.992	4.415
Temperate/subtropical alpine tundra	5.928	2.121
Temperate/subtropical alpine meadows	3.312	1.958
Temperate alpine swamps	4.767	0.746
Temperate alpine steppes	3.947	0.800
Subtotal	4.161	1.659
Desert		
Temperate alpine deserts	3.937	0.451

At large scales the mean area-weighted live biomass density for the vegetation area in the two administrative regions was 19.05 Mg DM/ha, which was much lower than the mean biomass density of global vegetation (122 Mg DM/ha) from Lieth and Whittaker (1975). Biomass density varied with different vegetation types: 50–228 Mg DM/ha for forests and woodlands, and 1.5–21 Mg DM/ha in grasslands and deserts (from Table 6). The values of live biomass density estimated from inventory data were much less than the data from the field plots.

Using the area-weighted mean of live biomass per unit vegetated area for 117 counties, we constructed a map for live biomass density of natural vegetation for the two administrative regions (Fig. 4). County-specific biomass density for vegetated areas ranged from 1.0 Mg DM/ha to 197 Mg DM/ha with higher values in the southern and eastern rims of the plateau and lower values in the center and northwest.

A map of the potential net primary productivity of natural vegetation on the Tibetan Plateau

We used the QZNPP model to map the potential NPP of natural vegetation on the Tibetan Plateau (Fig. 5).

The input data were from a 5×5 km Chinese temperature and precipitation database simulated by PRISM (Parameter-elevation Regressions on Independent Slopes Model; Daly et al. 1994, 1997, 2000) that was recently obtained from the Spatial Climate Analysis Service of Oregon State University, Corvallis, Oregon, USA.

By overlapping of the county boundaries and a real vegetation map compiled from Vegetation Map of China of Hou (1979), mean NPP per unit vegetated area (with exclusion of croplands, land with no vegetation, and water) was calculated for 117 counties in Xizang (Tibet) and Qinghai. The mean NPP was 3.44 ± 1.72 Mg DM $\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ for these two administrative regions, and 7.85 ± 2.70 Mg DM $\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ for the whole plateau, which was consistent with the mean NPP of global vegetation (7.82 Mg DM $\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) from Lieth and Whittaker (1975).

Potential NPP varied in different vegetation types (Table 7): 12.91 ± 3.41 Mg DM $\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ in forests, 4.26 ± 0.85 Mg DM $\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ in woodlands, 9.07 ± 5.46 Mg DM $\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ in shrublands, 4.16 ± 1.66 Mg DM $\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ in grasslands, and 3.94 ± 0.45 Mg DM $\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ in deserts. Using the inventory data of

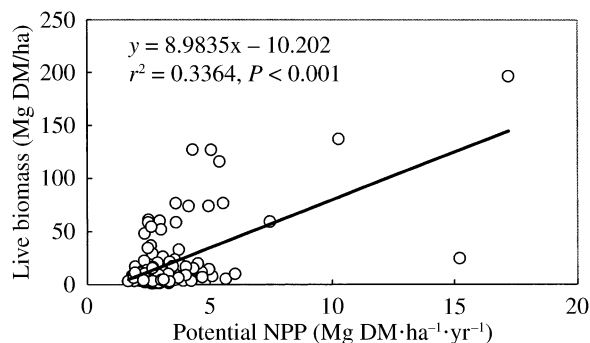


FIG. 6. Relationship between potential NPP and live biomass density of natural vegetation in 117 counties of the Xizang (Tibet) Autonomous Region and Qinghai Province.

natural vegetation area in the Xizang (Tibet) Autonomous Region and Qinghai Province (from Table 6), we estimated total annual NPP of 565 337 517 Mg DM with 69.5%, 18.1%, 7.5%, 4.7%, and 0.2% in grasslands, forests, shrublands, deserts, and woodlands, respectively.

Geographical patterns of potential NPP (Fig. 5) were consistent with those of live biomass presented in Fig. 4, but more fragmented due to elevation variations. Both maps of biomass and NPP showed a decreasing trend from southeast to northwest. Figure 6 showed a close linear relationship between the potential NPP and the area-weighted live biomass density at statistical significance ($P < 0.001$).

DISCUSSION

Comparisons of maximum live biomass from Tibetan forest plots with the data from the world's forest plots

Spruce–fir forests represented a large pool of carbon stocks on the Tibetan Plateau. The total live biomass of the natural vegetation in the Xizang (Tibet) Autonomous Region and Qinghai Province was estimated as 2.17 Gg dry mass, of which 72.9% was stored in forests where the spruce–fir accounted for 65.1%.

Based on the world forest biomass data (Cannell 1982), we selected the first five maximum values of live biomass for different forest types in the world (aboveground live biomass): 500–930 Mg DM/ha for tropical evergreen forests of Papua New Guinea, Thailand, Malaysia, Venezuela, and Guatemala; 350–500 Mg DM/ha for temperate deciduous broad-leaved forests of the former USSR, United States, Bulgaria, Belgium, and Japan; 600–3500 Mg DM/ha for temperate evergreen coniferous forests of the Pacific Northwest; and 400–880 Mg DM/ha for boreal spruce–fir forests of the former USSR, Canada, United States, Romania, and Japan. The highest maximum forest biomass occurred in the temperate evergreen coniferous forests, not in tropical evergreen forests. The maximum biomass of the boreal spruce–fir forests was close to that

of tropical evergreen forests. In contrast, the spruce–fir forests on the plateau had the highest maximum aboveground live biomass (980–1440 Mg DM/ha) compared with montane pine forests (350–450 Mg DM/ha), evergreen broad-leaved forests (320–370 Mg DM/ha), and deciduous broad-leaved forests (140–200 Mg DM/ha) (from Table 4), which were higher than that of the world spruce–fir forests and close to that of the world temperate evergreen coniferous forests. Waring and Franklin (1979) suggested that the combined effects of plant adaptations to temperature, moisture, and nutrient regimes favored the evolution of the massive long-lived evergreen coniferous forests of the Pacific Northwest in contrast to the deciduous hardwood forests in other temperate regions. Geophysical evidence suggests that the Daxiawan (great gorge) in Yarlung Zangbo River of the southeastern Tibetan Plateau should be a hot spot (named Daxiawan Hot Spot, DHS) with high ground temperature and rainfall (Tang et al. 1999). The DHS was located between 92° E and 97° E, south of 30° N, where the maximum biomass forests with deep root distribution occurred (from Table 4). In the south of this region, there was an annual rainfall of 10 000 mm on the south side of Khasi Hills, which was the heaviest rainfall in the world. This implied that the rising mass and energy flow from the DHS maintained luxuriant forest growth.

Spruce–fir forests had the highest leaf biomass in correspondence with the highest stand live biomass (from Table 3). For spruce–fir forests in cold-temperate zones or on alpine mountains where there were long day lengths and low temperatures (Li 1985, 1993), long leaf life span and high canopy leaf mass had three advantages (Chapin 1980, Chabot and Hicks 1982): (1) maximizing the utilization of sunlight available and compensating for low rates of photosynthesis by large leaf area for light interception; (2) moderating the recycling of nutrients through litterfall and decomposition processes and increasing nutrient use efficiency; and (3) serving as storage organs for carbohydrates and mineral nutrients in avoiding problems with translocation through frozen soils to support early season growth. The massive leaf mass needed a strong and high stem volume to transport the required water and nutrients from soil.

Net primary productivity estimates at large scales

In Fig. 7, predicted NPP by the QZNPP model was compared with field NPP from 16 natural vegetation plots of forests, alpine shrubs, and alpine meadows (Table 3, Site 1 to Site 16). Their correlation coefficient (r^2) was 0.6484 ($P < 0.001$). The analysis of model accuracy was as follows: >90% in three plots, 80–90% in eight plots, 70–80% in one plot, 60–70% in two plots, and <60% in two plots. This indicated that the QZNPP model generally predicted NPP well for most of the biomes on the plateau. However, we should note that the simulated NPP for deserts (3.937 ± 0.451 Mg

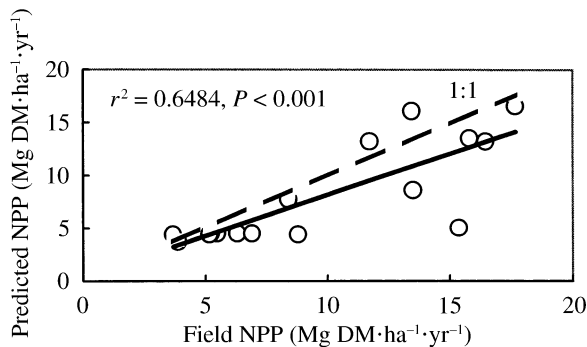


FIG. 7. Comparison of predicted NPP from the QZNPP model with field NPP from 16 natural vegetation plots (Table 3, Sites 1–16).

DM·ha⁻¹·yr⁻¹, from Table 7) was overestimated in comparison with its mean live biomass density (2.01 Mg DM/ha) estimated from inventory data (from Table 6). We had no field data for the deserts on the plateau for calibrating the model.

Figure 8 shows NPP and mean annual air temperature and precipitation. Mean annual temperature was from -5°C to 15°C and precipitation varied between 50 mm and 1500 mm. Net primary productivity increased with increasing temperature and precipitation. It approached a maximum value of ~20 Mg DM·ha⁻¹·yr⁻¹ where the temperature was >11°C and the precipitation was >1100 mm. This upper limit of NPP was consistent with the results of the maximum biomass plots presented in Table 4 except for the secondary poplar forest where the NPP was up to 23.87 Mg DM·ha⁻¹·yr⁻¹. Based on the available field NPP data over China collected in Li and Luo (1996) and Luo (1996), the NPP

upper limit of the subtropical and tropical forests in eastern China (except plantations and young secondary forests with stand ages of <70 yr) was ~26 Mg DM·ha⁻¹·yr⁻¹, which was higher than the simulated value (20 Mg DM·ha⁻¹·yr⁻¹) from the QZNPP model based on the plot data of natural vegetation of the plateau. In the vegetation classification system of China (Wu 1980), there were Eastern and Western Divisions in the subtropical evergreen broad-leaved forest and tropical forests (Table 8). The Western Division, including the southeastern Tibetan Plateau and the Yunnan-Guizhou Plateau, had lower temperatures and less precipitation than the Eastern Division. Therefore, the NPP upper limit used in the QZNPP model should reflect the differences between vegetation divisions in China. On the other hand, the QZNPP model simulated the positive effect of the monsoon climate in China, where the warmest season coincided with the wettest season, by using the product of temperature multiplied by precipitation. However, we should note that this NPP upper limit would be more suitable for well-adapted old forests than young secondary forests such as poplar stands.

Based on the field data in Table 3 (Sites 17 to 19), annual production of wheat croplands on the plateau was from 12.4 Mg DM/ha to 30.8 Mg DM/ha with two to seven times greater than local potential NPP (from 4.0 Mg DM/ha to 7.3 Mg DM/ha) of natural vegetation. This implied that intensive cultivation such as irrigation and fertilization could greatly increase carbon sequestration in this arid and vast region. This result further suggested the importance of agricultural management practices in sequestering carbon, especially in arid regions.

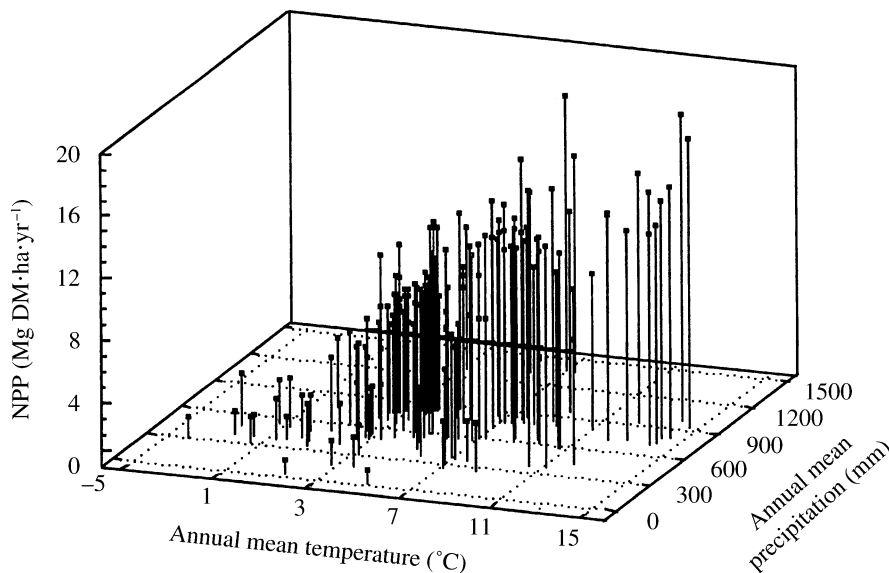


FIG. 8. Net primary productivity (NPP) plotted against mean annual temperature and precipitation for natural vegetation on the Tibetan Plateau.

TABLE 8. Climate factors of vegetation divisions in the tropical and subtropical zones in China (Wu 1980).

Vegetation division	Annual mean temperature (°C)	Highest monthly temperature (°C)	Lowest monthly temperature (°C)	Annual mean precipitation (mm)
Eastern Division of subtropical evergreen broad-leaved forest	18–21	27–29	2–12	1000–2000
Western Division of subtropical evergreen broad-leaved forest	15–20	20–24	8–12	900–1250
Eastern Division of tropical rain forest and monsoon forest	22–26	>28	13–21	>1500
Western Division of tropical rain forest and monsoon forest	16–23	24–28	12–16	>1200

Mean annual NPP of the natural vegetation on the Tibetan Plateau ($7.85 \text{ Mg DM}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) was consistent with the mean NPP of global vegetation ($7.82 \text{ Mg DM}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) from Lieth and Whittaker (1975), although the mean live biomass density of the plateau (19.05 Mg DM/ha) was much lower than the global mean biomass density (122 Mg DM/ha). Total annual NPP of the natural vegetation in the Xizang (Tibet) Autonomous Region and Qinghai Province was estimated as 0.57 Gg DM , of which 69.5% was produced by grasslands. Compared with mean annual NPP estimates for global grasslands (Lieth and Whittaker 1975), the alpine tundra and meadows ($3\text{--}6 \text{ Mg DM}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) and savanna ($17 \text{ Mg DM}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) of the Tibetan Plateau had much higher annual production than the global tundra and alpine grasslands ($1.4 \text{ Mg DM}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) and tropical savanna ($9 \text{ Mg DM}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$), but the alpine steppes ($4 \text{ Mg DM}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) had lower annual NPP than the global temperate grasslands ($6 \text{ Mg DM}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$).

Uncertainties in biomass estimates at large scales

Much uncertainty in biomass estimates of shrublands for the whole plateau occurred due to using mean biomass densities ($35.166 \pm 16.865 \text{ Mg DM/ha}$) that were based on limited field plot data for alpine shrubs. Considering that shrublands accounted for a small portion ($\sim 4\%$) of total vegetation area on the plateau, this uncertainty would not cause a great error in the total biomass estimates.

One limitation in this study was that litter and biomass losses to herbivores were not considered due to the lack of information. Based on Duvigneaud (1987), the proportion of litter biomass to total biomass in major biomes of the world is 2–7% for forests, 10–20% for tundra, 42–55% for grasslands, 28–38% for deserts. In this study, we attempted to reduce the underestimates of NPP caused by the lack of litterfall data, using the recent growth rate and leaf life span in forests and seasonal maximum live biomass in grasslands. Based on a compilation of data from grasslands and forests worldwide, Aber and Melillo (2001) estimated that herbivores were a pathway for the consumption of leaf growth in all grasslands that was nearly 10-fold higher than in forests with similar levels of foliage produced. Herbivores in forests and shrublands generally consumed $<10\%$ of annual net primary production aboveground, but close to 100% of annual aboveground pri-

mary production in parts of African grasslands. In other systems, such as the tundra, there might be large cyclical changes in herbivores.

In this study, we used a vegetation map from Hou (1979) to overlap the potential NPP map simulated by the QZNP model and then estimated mean annual NPP for different vegetation types (Table 7). These estimates contained some uncertainty because of land use and land cover changes in the past 20 yr. In our future work, using the updated remote sensing data of land cover classifications would help to reduce the uncertainty and improve the estimates.

Future directions

The largest uncertainties in the global carbon balance are associated with the net flux of carbon to or from terrestrial ecosystems (Sundquist 1993, Houghton 1995). One major source of uncertainty in estimating terrestrial carbon flux is the biomass density of forests (Dale et al. 1994) and the initial stocks of carbon in the undisturbed vegetation and soil (Houghton 1995). This uncertainty contributes 30–50% of the uncertainty in estimating the net flux of carbon in tropical forests (Houghton 1991). More recently, a report from the Global Terrestrial Observing System (GTOS) Terrestrial Carbon Observation (TCO) Synthesis Workshop (Cihlar et al. 2000) described large gaps in forest carbon stocks and productivity data at global to subnational levels: (1) limited access to the original plot-level measurements, (2) difficulty with releasing exact coordinates of plot data due to confidentiality concerns, (3) no well established way to convert merchantable volumes into total flux estimates due to limited information on measurements of other components such as root, leaf, branch, and litter, (4) uncertainties from a variety of inventory methods, (5) difficulty with obtaining accurate data on stock changes due to various disturbances, and (6) requirements for high resolution forest inventories at a local level depending on the Kyoto Protocol. A two-pronged approach was suggested in the report: (1) increase access to quality forest biomass data, and (2) develop methods for using the existing forest data and inventories to improve estimates of carbon fluxes. Brown et al. (1989) presented biomass estimation methods for tropical forests with applications to forest inventory data in which a series of regression equations were developed to estimate the

aboveground biomass of individual trees as a function of diameter at breast height (dbh), total height, wood density, and Holdridge life zone. More recently, biomass density was estimated using geographic information systems (GIS) modeling (Iverson et al. 1994), and a bookkeeping model based on the combination of historical land-use records and country-specific volume data (Flint and Richards 1994). Country-specific biomass estimates were much more accurate than continent-wide values used previously (Houghton et al. 1983, 1985, 1987, Houghton 1996) but still left a great deal to be desired for accuracy because of both natural geographic and human-induced spatial variability (Dale et al. 1994).

There had been a dramatic increase in the use of regional process-based ecosystem models to predict the primary productivity of the terrestrial biosphere, and to assess ecosystem response to changes in global climate and elevated atmospheric carbon dioxide concentration (Melillo et al. 1993, Smith and Shugart 1993, Ruimy et al. 1994, VEMAP Members 1995, Cao and Woodward 1998, Tian et al. 1998b, 1999, Schimel et al. 2000). The critical gaps in developing a dynamic biosphere model were: (1) the poorly developed links between empiricism and concepts used to construct models, especially the lack of data to parameterize and validate mechanistic models, (2) an incomplete fundamental knowledge about how complex terrestrial ecosystems work, and (3) a poor understanding of how to scale up from ecosystem processes to large regions (Tian et al. 1998a). Therefore, improvements of terrestrial carbon flux and stock estimates required spatially explicit data and local information on finer scales.

There are too few papers in international journals discussing the carbon cycle of Chinese vegetation (Gao and Zhang 1997, Fang et al. 1998, Gao et al. 1998, Gao and Lu 1998) in relation to the global carbon cycle (Bacastow and Keeling 1973, Woodwell et al. 1978, 1983, Broecker et al. 1979, Houghton et al. 1983, 1985, 1987, 1998, Detwiler and Hall 1988, Keeling et al. 1989, Tans et al. 1990, Hall and Uhlig 1991, Sarmiento et al. 1992, Melillo et al. 1993, Smith and Shugart 1993, Dixon et al. 1994, Ciais et al. 1995, Houghton 1996, Cao and Woodward 1998, Fan et al. 1998). Fang et al. (1998) presented an estimate of forest biomass of China based on country-level data collected between 1984 and 1988. However this report was based on limited direct information from the Tibetan Plateau where the highest wood volume per unit area of forests in China could be found (Li 1985, 1993). In future works, we need to estimate carbon stocks in litter and soil as well as change in stocks induced by anthropogenic disturbances.

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APPENDIX A

A description of the selected field plots of biomass and NPP on the Tibetan Plateau is available in ESA's Electronic Data Archive: *Ecological Archives* A012-008-A1.

APPENDIX B

Allometric regressions of live biomass for dominant tree species on the Tibetan Plateau are available in ESA's Electronic Data Archive: *Ecological Archives* A012-008-A2.

APPENDIX C

Equations for the average annual growth rate of stem volume as a function of age for 15 dominant tree species on the Tibetan Plateau based on the measurements of 704 trees in this region and the neighboring provinces are available in ESA's Electronic Data Archive: *Ecological Archives* A012-008-A3.