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Root biomass along subtropical to alpine gradients: global implication from Tibetan transect studies

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Abstract

Much uncertainty in estimating root biomass density (RBD, root mass per unit area) of all roots regionally exists because of methodological difficulties and little knowledge about the effects of biotic and abiotic factors on the magnitude and distribution pattern of RBD. In this study, we collected field data of RBD from 22 sites along the Tibetan Alpine Vegetation Transects executed with the same sampling method that covered a relatively undisturbed vegetation gradient from subtropical forests to alpine vegetation. Our field data indicated that RBD significantly decreased with increasing altitudes ($r^2 = 0.60$, $P < 0.001$) but had low or non-robust correlations with aboveground biomass density ($r^2 = 0.10$–0.34), suggesting that RBD can be predicted without reference to shoot biomass. The transect data further revealed that temperature and/or precipitation were likely the major limiting factors for geographical distribution patterns of RBD. The relationships could be expressed as logistic function with a maximum RBD of 200 Mg/ha ($r^2 = 0.59$–0.65, $P < 0.001$). A simple empirical model was developed from the logistic regressions and then globally tested against data for 295 field plots of undisturbed to semi-disturbed vegetation ranging from the boreal zone to the tropics. In general, the model explained 80% of the RBD variation for 30 field plots along the North–South Transect of Eastern China ($r^2 = 0.80$, $P < 0.0001$) and less than half of the variation in the global dataset ($r^2 = 0.45$, $P < 0.0001$). The model predictions were strong for temperate evergreen forests, temperate/alpine shrubs and grasslands, boreal tundra, and Mediterranean deserts. Such a global scaling exercise revealed the global distribution pattern of RBD broadly over a range of major biomes, suggesting the possibility to develop a new method for large-scale estimation of root biomass.

Keywords: Tibetan Plateau; Vegetation; Transect; Root biomass; Climate; Model

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1. Introduction

Some improvements have been achieved in understanding global patterns of rooting depths (Canadell et al., 1996; Jackson et al., 1996; Schenk and Jackson, 2002a, 2002b), fine root production (Jackson et al., 1997) and root turnover (Gill and Jackson, 2000). However, much uncertainty in estimating root biomass density (RBD, root mass per unit area) of all roots regionally exists because of methodological difficulties and little knowledge about the effects of biotic and abiotic factors on the magnitude and distribution pattern of RBD (Santantonio et al., 1977; Vogt et al., 1996; Cairns et al., 1997). Based on the worldwide literature data, Vogt et al. (1996) and Cairns et al. (1997) found no significant or consistent patterns for root-to-shoot ratios for forests across different climatic forest types and soil order. In previous studies, average root/shoot (R/S) ratios for forests are commonly developed from the literature to quantify RBD at regional scales when only aboveground biomass density (ABD, shoot mass per unit area) is available (e.g. Birdsey, 1992; Brown et al., 1993; Schroeder and Winjum, 1995). However, the synthesis by Cairns et al. (1997) for the world's forests indicates that none of the tested independent variables such as ABD, latitude, temperature, precipitation, ratios of temperature to precipitation, tree type, soil texture, and tree/stand age had important explanatory value for R/S ratios. The Cairns et al. synthesis suggests that RBD for forests should be estimated directly rather than by using R/S ratios.

Variations in carbon allocation to roots may be related to a complex functional balance between root and shoot allocation (Raich and Nadelhoffer, 1989; Hendricks et al., 1993; Noordwijk et al., 1998), and costs and benefits of constructing fine roots (Eissenstat, 1992; Schenk and Jackson, 2002b). The variable conclusions arrived at from previous root allocation studies needs to be clarified. Part of the reason for this lack of consistency in conclusions about root allocation could be explained by the fact that most of the previous synthesis studies relied on data available in the literature rather than on data acquired using a systematic experimental design. One approach for collecting data for RBD estimates using a systematic approach can be accomplished through a transect study covering a broad range of biotic and abiotic conditions. Few transect studies have examined RBD along climatic and/or altitudinal gradients and quantified its relationship to climate (Schulze et al., 1996).

Weber's Law from Duvigneaud (1987) indicates that well-balanced natural plant communities, regardless of species composition, should have similar net primary productivity (NPP) and biomass accumulation under the same environmental conditions. Weber's Law is similar to the Law of Constant Yield derived from the Two-Thirds Thinning Law in population ecology, and further suggests the 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 using a logistic function at a global scale. However, it is unclear that biomass accumulation across biomes also follows such a logistic pattern. The Tibetan Plateau is an ideal place to study adaptations of natural ecosystems to climatic gradients because the vegetation, varying from forests to non-forest systems, is relatively undisturbed by humans, and the South Asian Monsoon produces wide ranges of temperature and moisture gradients (Li and Zhou, 1998). We have applied the law and logistic function to establish a climate-based statistical model of NPP of natural vegetation on the Tibetan Plateau, in which a combination of annual mean temperature and annual precipitation explains 70% of the NPP variation for the 180 vegetation sites derived from 1970 to 1980's inventory plots over the plateau (Luo et al., 2002a). More recently, our independent data sets from 22 sites along the Tibetan Alpine Vegetation Transects (TAVT) (1999–2000) also indicate that the general distribution patterns of NPP, ABD, and leaf area index (LAI) have threshold-like logistic relationships with climatic factors of temperature and precipitation (Luo et al., 2002b, 2004a). The lower correlations of ABD and LAI with climatic factors of temperature and precipitation ($r^2 = 0.28$–0.53, $P < 0.02$) suggested that the distribution patterns of ABD and LAI are limited by additional climatic factors such as solar radiation, wind, moisture and related water/energy balances. A synthesis of the global literature reveals that annual mean temperature and/or annual precipitation may be important predictors for belowground biomass in grasslands (Gill et al., 2002), global root turnover rates (Gill and Jackson, 2000) and global rooting depths (Schenk and Jackson, 2002a). It is possible that temperature and precipitation are the major limiting factors for patterns of RBD distribution of natural vegetation while additional climatic factors limit ABD. We hypothesize that RBD across biomes should show more significant threshold-like logistic pattern in response to the temperature and precipitation gradients along the TAVT. This would be helpful to understand the mechanisms underlying the NPP, LAI and biomass variations and to further develop a new method for large-scale estimation of root biomass for all natural ecosystems.

In this study, we present field data of RBD from the systematically designed experimental sites along the Tibetan Alpine Vegetation Transects (TAVT) executed with the same sampling method during 1999–2000. The goals are to improve our knowledge about geographical distribution patterns of RBD, and to explore if RBD for any ecosystem type can be predicted without reference to shoot biomass. Our tasks are to: (1) analyze the relationship between RBD and ABD across biomes and the altitudinal trend in RBD along the TAVT, (2) model the relationships between RBD of natural vegetation and climatic factors (temperature and precipitation) based on the TAVT data, and (3) develop a climate-based empirical model for large-scale estimation of RBD and examine how generally applicable the simple model is to the major biomes in eastern China and in the world.

2. Data and methods

2.1. Field data in Tibetan Alpine Vegetation Transects (TAVT)

The TAVT includes the altitudinal transect in the eastern slope of Gongga Mountains of Eastern Tibetan Plateau and the longitudinal–latitudinal transect of Central Tibetan Plateau (Fig. 1). The altitudinal transect starts from the subtropical evergreen broad-leaved forest at 1900 m above sea level (ASL) to the timberline at 3700 m ASL. The longitudinal–latitudinal transect covers latitudes from 29°32′N to 35°13′N and longitudes from 91°08′E to 94°43′E, with about 1000 km in length and 40 km in width. The transect starts from the forest zone of Sergyemla Mountains (3000–4800 m ASL) in the southeastern 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). During July–September of 1999 and 2000, we located each of 22 sites along the whole TAVT using a global positioning system (GPS). We measured biomass density both belowground and aboveground for different relatively undisturbed vegetation types including forests, shrubs and grasslands (Table 1). In these field sites, root biomass was measured to the depth of the deepest visible root (0.6–1.5 m in forests, 0.3–0.5 m in alpine shrubs and grasslands), which generally exceeds the depth in most field studies reported in the literature (generally 0.1–0.8 m; see Schenk and Jackson, 2002a).

Aboveground live-biomass densities of grasslands (sites 1–5) and alpine shrubs (sites 6–8) were measured by harvesting quadrats (4 m^2 for shrubs and 0.25 m^2 for grasslands). In each forest plot (0.04–0.5 ha), tree height and diameter at breast height (DBH) were measured for all trees over 3 cm in DBH. Aboveground live-biomass density (ABD) of all trees in the 13 forest plots (sites 9–11, 13–22; no ABD measurements in site 12) was estimated by allometric regressions based on measured tree height and DBH, while the undergrowth biomass were measured by harvesting quadrats (4 m^2). More detailed information about the allometric regressions and variations in aboveground biomass density across the whole TAVT is found in Luo et al. (2002b).

Because estimates of forest RBD based on standard methods are much less common (Santantonio et al., 1977; Cairns et al., 1997), a sampling method was used to measure RBD in a manner that equated to stand-level variables. We selected a standard tree with average tree height and quadratic mean DBH calculated from the average per-tree basal area. Location of the standard tree avoided large gaps and characterized a normal density distribution of trees. RBD generally decreased with the increasing distance from the stem base to the crown edge despite the high spatial variation across the plot. Root biomass samples were taken in positions of the upper and lower slopes around the standard tree. Two samples were taken 50 cm apart from the tree stem, and another two samples from the edge of the tree crown. Fine

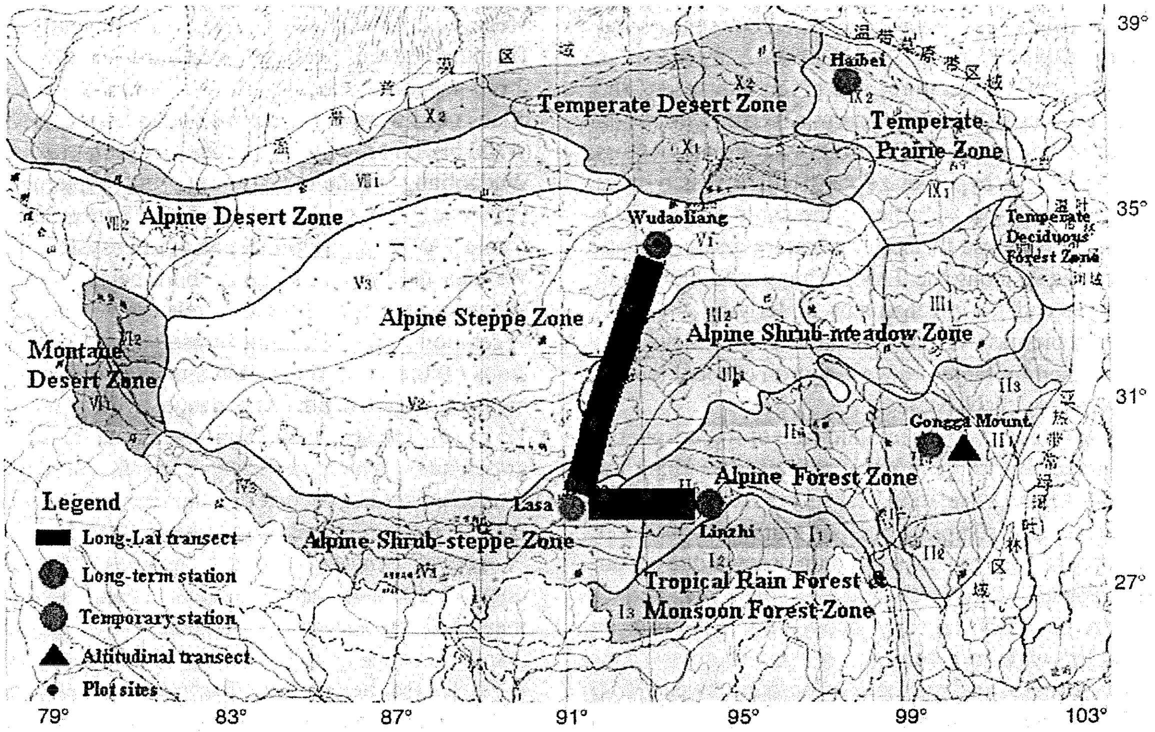


Fig. 1. Map of the Tibetan Alpine Vegetation Transects (TAVT). The vegetation zonations were adapted from Zheng (1996).

(<5 mm) to medium (5–10 mm) and coarse (>10 mm) roots were harvested by digging up all the roots in 0.25 m^2 quadrats to the depth of the deepest visible root (0.6–1.5 m). We separated live from dead and hand sorted live medium and coarse roots. Because fine roots in both forests and grasslands generally have a lifespan of days to weeks (Gill and Jackson, 2000), we collected both live and dead fine roots by washing through a sieve. Subsamples of all roots were dried to a constant weight at 70 °C to determine the ratios of dry to fresh mass. A mean RBD in dry mass for live medium and coarse roots and live and dead fine roots in the plot was averaged from the four measurements.

In shrub and grassland plots, root biomass was measured by digging up all the roots in a 0.25 m^2 quadrat to the depth of the deepest visible root (0.3–0.5 m). We also collected live and dead fine roots in shrub and grassland plots and live medium and coarse roots in shrub plots.

Because few meteorological stations (about 50 stations) exist in the Central Tibetan Plateau, the climatic data of the sites along the longitudinal–latitudinal transect were obtained from a Chinese temperature and precipitation database at resolution of $2.5' \times 2.5'$ (ca. 4–5 km) simulated by parameter-elevation regressions on independent slopes model (PRISM; Daly et al., 2002) according to GPS locations (latitude, longitude and altitude). The PRISM's database was based on the averages of 30-year (1961–1990) observation data of monthly minimum and maximum mean temperatures and monthly precipitation from about 2450 temperature stations and 2600 precipitation stations in China and neighboring countries (Daly et al., 2000). The independent meteorological observation records from 18 ecological research stations over China were used to validate the PRISM grid data sets (Zhu et al., 2003). The climatic data of the sites along the altitudinal transect were estimated from the 10 years meteorological observations measured at 1600 and 3000 m, by Alpine Ecosystem Observation and Experiment Station, Chinese Academy of Sciences (Zhong et al., 1997). The site temperatures were calculated using a lapse

Table 1
Site description of the Tibetan Alpine Vegetation Transects (TAVT)

Site no.	Place name	Vegetation type	Longitude	Latitude	Altitude (m)	RBD (Mg//ha)	ABD (Mg/ha)
1	Wudaoliang	Alpine *Stipa* steppe	93°04′05″E	35°12′56″N	4626	6.36	0.59
2	Tuotuo river valley	Alpine *Stipa* steppe	92°32′52″E	34°18′51″N	4582	9.23	0.76
3	Anduo	Alpine *Stipa* steppe	91°48′19″E	32°27′33″N	4871	7.51	1.11
4	Damxung	Alpine *Kobresia* meadow	91°08′44E	30°29′50″N	4288	31.90	0.48
5	Gandansi	Alpine *Kobresia* meadow	91°29′12″E	29°45′11″N	4100	15.72	0.98
6	West Mila Mt.	Alpine shrub–meadow of *Rhododendron–Kobresia*	92°18′53″E	29°45′14″N	4652	8.62	9.29
7	Peak of Sergyemla Mts.	Alpine shrub of *Rhododendron*	94°39′07″E	29°36′38″N	4560	11.29	7.50
8	Maizhokunggar	Alpine dry shrub of *Lonicera–Artemisia*	91°38′03″E	29°47′50″N	3780	14.88	9.53
9	East Mila Mt.	*Betula* deciduous forest	93°30′00″E	30°00′00″N	3620	17.99	33.90
10	Nyiyang River Valley	*Quercus* evergreen forest	94°01′19″E	29°45′35″N	3080	52.26	75.88
11	Nyiyang River Valley	Mixed forest of *Pinus densata* and *Quercus* evergreen trees	94°14′32″E	29°45′13″N	3100	28.54	83.04
12	West Sergyemla Mts.	Mixed forest of *Pinus densata* and *Quercus* evergreen trees	94°30′27″E	29°34′02″N	3200	23.39	–
13	West Sergyemla Mts.	Alpine fir forest of *Abies georgei* var. *smithii*	94°33′27″E	29°33′32″N	3780	21.40	995.98
14	West Sergyemla Mts.	Timberline forest of *Abies georgei* var. *smithii*	94°35′31″E	29°34′52″N	4073	20.63	141.78
15	West Sergyemla Mts.	Timberline woodland of *Sabina saltuaria* and *Rhododendron*	94°37′22″E	29°36′55″N	4450	26.61	127.08
16	East Sergyemla Mts.	Alpine fir forest of *Abies georgei* var. *smithii*	94°42′51″E	29°39′04″N	3800	48.98	841.42
17	East Gongga Mts.	Evergreen broad-leaved forest	102°03′26″E	29°36′16″N	1900	67.45	165.20
18	East Gongga Mts.	Evergreen-deciduous broad-leaved forest	102°01′28″E	29°35′13″N	2200	95.10	348.63
19	East Gongga Mts.	Mixed forest of spruce-fir and deciduous trees	102°01′20″E	29°35′10″N	2850	35.63	481.61
20	East Gongga Mts.	Alpine fir forest of *Abies fabri*	101°59′55″E	29°34′34″N	3050	35.48	162.91
21	East Gongga Mts.	Alpine fir forest of *Abies fabri*	101°59′55″E	29°34′34″N	3000	23.81	369.40
22	East Gongga Mts.	Timberline forest of *Abies fabri*	101°58′05″E	29°32′44″N	3700	6.98	242.23

RBD and ABD are for root biomass density and aboveground biomass density (in dry matter), respectively.

rate of 0.6 °C per 100 m of altitude. Annual precipitation at elevations below 2500 m ASL was estimated from the meteorological observatory at 1600 m ASL in increments of 120 mm per 100 m (from 1600 to 2500 m ASL). Annual precipitation at elevations above 2500 m was estimated from the meteorological observatory at 3000 m in decrements (between 2500 and 3000 m) or increments (above 3000 m) of 74 mm per 100 m. The climatic conditions across the sites along the transects showed a broad range of temperature and precipitation, with annual mean temperature from −4.2 to 10.4 °C, and annual precipitation from 270 to 2400 mm.

2.2. Literature data used for model validation

Two groups of site data sets from the literature were used to assess how generally applicable the relationships between RBD and climatic factors derived from the TAVT data are to major biomes in eastern China and in the world. They included the gradient site data along the North–South Transect of Eastern China, one of the IGBP transects in China and the worldwide literature data (see Appendices A–C in supplementary files of the on-line version of this article). The gradient site data were from 30 field plots of 17 natural reserve areas across eastern China ranging from the boreal zone to the

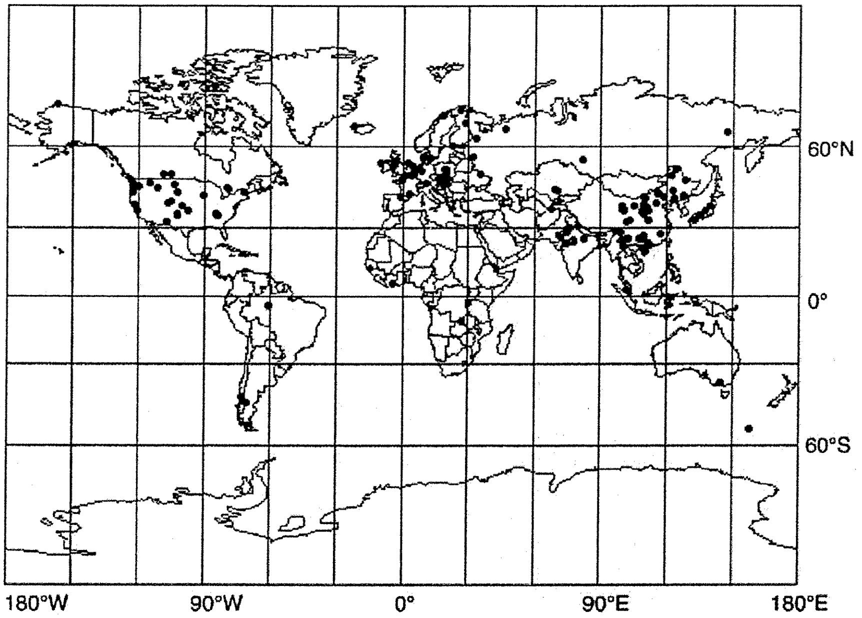


Fig. 2. Global map of the 295 field plots of root biomass measurements from the worldwide literature (see Appendices A–C in supplementary files of the on-line version of this article), used for the model validation.

tropics. In the worldwide literature data, there were 59 plots of boreal/alpine coniferous forests, 51 plots of temperate coniferous or sclerophyllous evergreen forests, 51 plots of temperate deciduous broadleaved forests, 36 plots of tropical/subtropical broadleaved forests, 9 plots of tropical savanna, 12 plots of alpine/subalpine shrubs, 24 plots of temperate/alpine meadows, 17 plots of temperate prairies/steppes, 31 plots of boreal tundra, and 5 plots of Mediterranean desert. In general, methods of sampling root mass included spatially distributed soil cores or pits for fine to medium roots and partial to complete excavation and/or allometry for coarser roots. The information about root sampling depth, size classes and distinction between live and dead is limited and incomplete. To be compatible with the mature forests in the TAVT, we excluded data from juvenile plantations or secondary forests generally with a stand age of less than 50 years. Fig. 2 is the global map for 295 field plots of RBD that met the selection criteria.

Most of related climatic data were obtained from the corresponding sites. For a few tropical rainforests sites, the climatic data were estimated from the nearest weather stations. Mean annual temperature and annual precipitation were used for most of the ecosystems including all forests, shrubs, grasslands and deserts. Additional data of July and January mean temperatures were collected for boreal tundra. The site climatic conditions showed a broad range of temperature and precipitation, with annual mean temperature from −18.8 to 23.8 °C, and annual precipitation from 54 to 2787 mm.

2.3. Relationships between root biomass density and climatic factors along the TAVT

We used two logistic equations to express the relationships between RBD and temperature and/or precipitation as follows:

$$\mathrm{RBD} = \frac{k}{(1+\exp(a+bx))} \quad \text{or}$$

$$\mathrm{RBD} = \frac{k}{(1+\exp(a+bx+cx^2))}$$

where x is the climatic independent variable of temperature and/or precipitation, singly or in combination, exp the base of natural logarithm, RBD root biomass density (Mg dry matter per hectare, Mg DM/ha), k maximum RBD, and other parameters of a, b, and c are the equation constants.

Among the interactive regressions, the fittest independent variables (x) included January, July and annual mean temperatures (°C), annual precipitation (mm), and the product of annual mean temperature (°C) and precipitation (mm), respectively. Mean temperatures for the year, January and July were highly correlated ($r^2 = 0.95$–0.99) but had low or non-robust correlations with annual precipitation ($r^2 = 0.37$–0.44). Based on the global literature data, a global maximum RBD of 217 ± 83 Mg/ha exists in mature tropical rainforests of Brazil and Ghana where the aboveground biomass is about 851 ± 409 Mg/ha (Santantonio et al., 1977; Cairns et al., 1997). In China, the maximum RBD was generally less than 200 Mg/ha (Luo, 1996; Li and Luo, 1996). In this study we set the parameter k to equal 200 Mg/ha. The TAVT data were used to determine the equation constants of a, b, and c by method of least squares of regression analysis (Fig. 3).

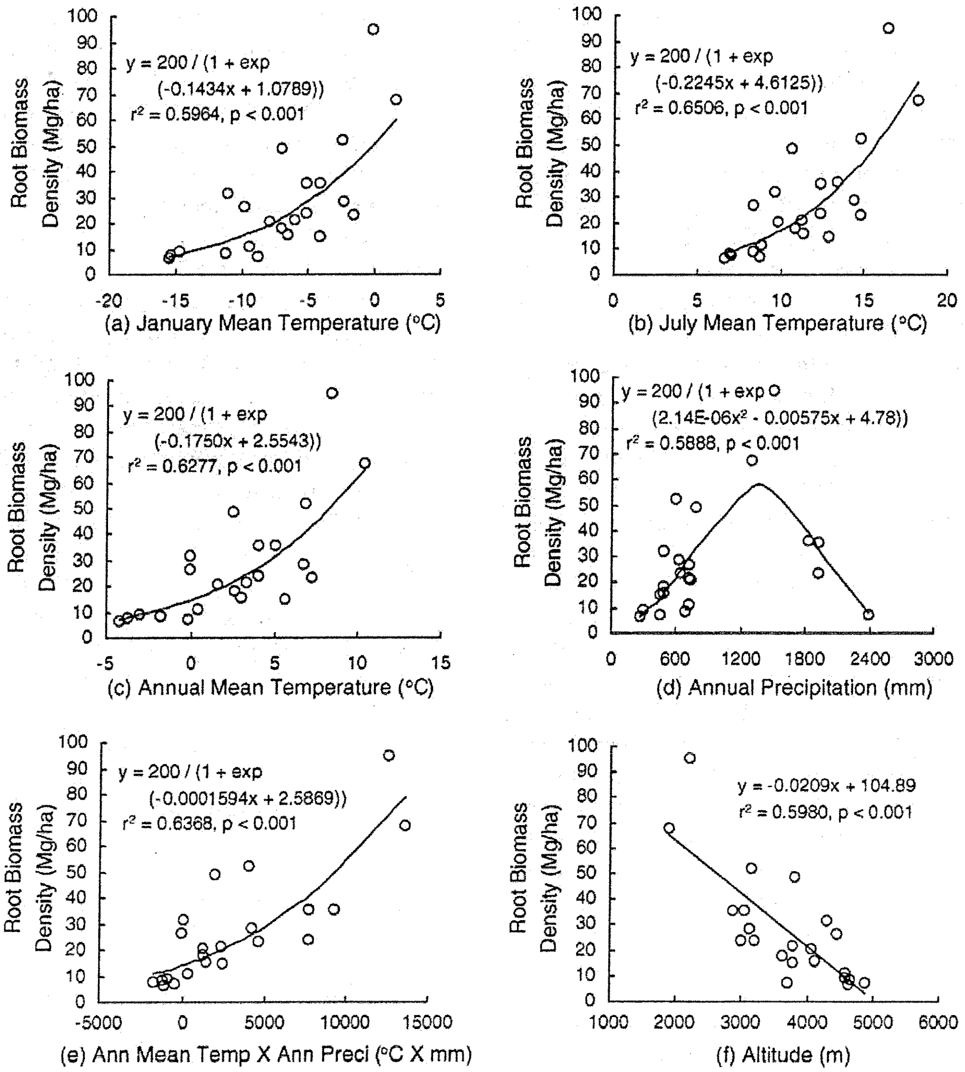


Fig. 3. Relationships of root biomass density (Mg DM/ha) with mean temperatures for: (a) January, (b) July and (c) the year, and (d) annual precipitation, (e) temperature and precipitation combination, and (f) altitude based on the TAVT data.

2.4. A climate-based empirical model for large-scale estimation of RBD

One goal in this study was to explore if RBD can be predicted without reference to shoot biomass. Based on the logistic equations developed on the TAVT data (Fig. 3a–e), a simple climate-based empirical model was constructed here, called model for regionally estimating root biomass density (MRERBD). Such a modeling exercise would be helpful to reduce the uncertainty arising from different sampling depths and measuring methods.

At large scales, limiting climatic factors of RBD might vary with different vegetation types. In the model, we further assumed RBD was limited by: (1) a combination of temperature and precipitation for all forest and shrub systems (Brown and Lugo, 1982; Vogt et al., 1996), and for typical grasslands where annual mean temperature was less than 9 °C (the upper limit of steppe distribution in China; Wu, 1980); (2) precipitation for deserts, as well as for arid grasslands where annual mean temperature was more than 9 °C (Evenari et al., 1976; Schulze et al., 1996); (3) temperatures in warmest or coldest months for boreal tundra (Epstein et al., 2000) where the July isotherm is commonly used for the zonal division of tundra (Wielgolaski, 1975). The model is composed of two modules, i.e. MRERBD-1 and MRERBD-2. The MRERBD-1 module contained the logistic equations with single independent variables of January, July and annual mean temperatures and annual precipitation (Fig. 3a–d), while the MRERBD-2 module comprised the logistic equation with independent variables of annual mean temperature and precipitation in combination (Fig. 3e). Calculations by the MRERBD-2, which were based on combination of annual mean temperature and precipitation, were used for forests and shrubs, and typical grasslands where annual mean temperature was less than 9 °C. Annual precipitation-based calculations by the MRERBD-1 were used for deserts and arid grasslands where annual mean temperature was more than 9 °C. Otherwise, the MRERBD-1 was used to predict RBD of forest tundra as the minimum from temperature-based calculations both in January and July, and RBD of other tundra as the temperature-based calculation in July. The literature data were used to assess how generally applicable the simple model is to the major biomes in eastern China and in the world.

3. Results

3.1. Relationships of root biomass density and temperature and precipitation along the TAVT

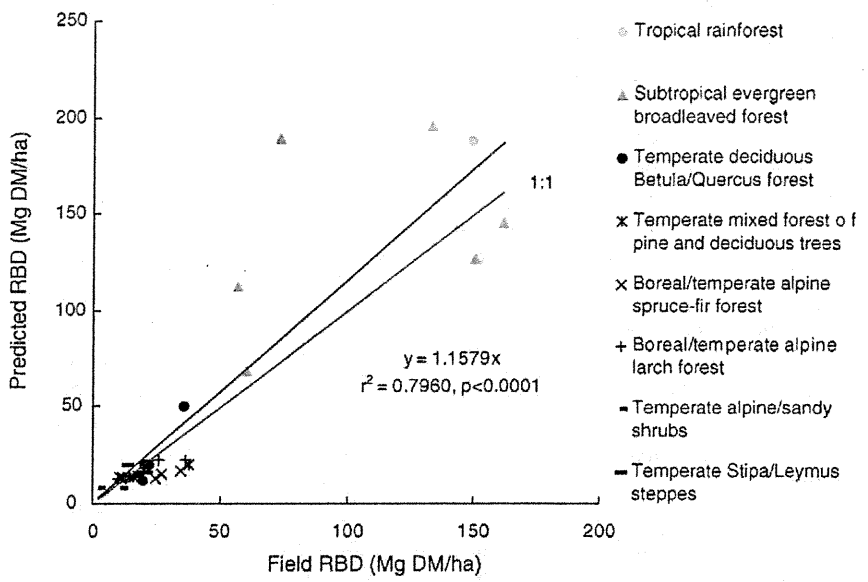
Root biomass density along the Tibetan transects varied with different vegetation types: 6–10 Mg/ha for alpine steppes, 9–32 Mg/ha for alpine shrubs and meadows, 18–52 Mg/ha for dry valley forests, 67–95 Mg/ha for subtropical forests, 23–36 Mg/ha for alpine mixed forests, 21–49 Mg/ha for alpine spruce-fir forests, and 7–27 Mg/ha at the timberline (Table 1). The analysis of variance indicated that RBD in subtropical forests was higher than all the other vegetation types (statistically significant at $P < 0.05$), but the RBD among the other vegetation types were not statistically significant. Moreover, RBD had low or non-robust correlations with ABD ($r^2 = 0.10$–0.34, simple linear regressions of different data transformations such as linear, power, log and exponential functions) (from Table 1).

Along the TAVT, RBD significantly decreased with increasing altitudes described by a linear relationship ($r^2 = 0.60$, $P < 0.001$) (Fig. 3f). Logistic regressions for the TAVT data revealed that the fittest independent variables of mean temperatures and annual precipitation, singly or in combination, accounted for 59–65% of the variation in RBD with a statistical significant level at $P < 0.001$ (Fig. 3). July mean temperature ($r^2 = 0.65$, $P < 0.001$), annual mean temperature ($r^2 = 0.63$, $P < 0.001$) and combination of annual mean temperature and annual precipitation ($r^2 = 0.64$, $P < 0.001$) had the highest predictive value for RBD, followed by January mean temperature ($r^2 = 0.60$, $P < 0.001$) and annual precipitation ($r^2 = 0.59$, $P < 0.001$). Combinations of July and January mean temperatures with annual precipitation both showed low correlations with RBD ($r^2 = 0.23$–0.30, $P < 0.05$, data not shown).

3.2. Variation in root/shoot ratio among different vegetation types along the TAVT

Root/shoot biomass ratio from the TAVT data varied with different vegetation types: 16.0–66.2 for alpine meadows, 6.8–12.1 for alpine steppes, 0.9–1.6 for alpine shrubs, 0.3–0.7 for dry valley forests, 0.3–0.4 for subtropical forests, and 0.02–0.2 for alpine forests

(a) North-South Transect of Eastern China



(b) Vegetation in the World

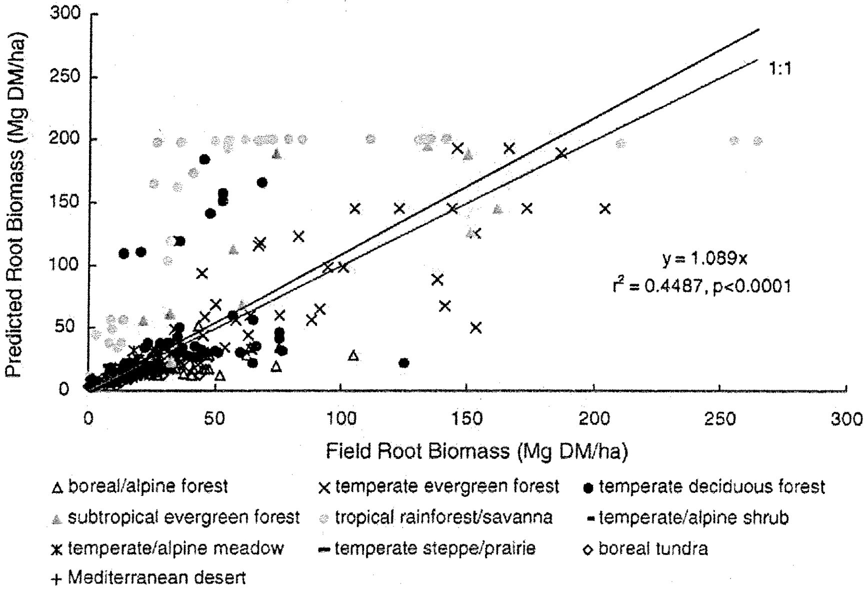


Fig. 4. Relationships between the predicted RBD by the MRERBD model and the literature RBD data from: (a) 30 plots along the North–South Transect of Eastern China, and (b) 295 global plots. Both literature data sets are available in Appendices A–C in supplementary files of the on-line version of this article.

(Table 1). The analysis of variance indicated that the root/shoot ratio in alpine meadows was higher than all the shrubs and forests (statistically significant at $P < 0.05$), but not significantly higher than the alpine steppes. Moreover, root/shoot ratios among the steppes, shrubs and forests were not statistically significant.

The root/shoot ratio tended to exponentially decrease with increasing precipitation and temperature (data not shown). Simple linear regressions of log-transformed data revealed that the correlation coefficient for annual precipitation ($r^2 = 0.54$, $P < 0.001$) was much higher than those for mean temperatures of the year ($r^2 = 0.17$, $P < 0.10$), January ($r^2 = 0.25$, $P < 0.05$) and July ($r^2 = 0.12$, not statistically significant at $P < 0.10$).

3.3. Validation of the MRERBD model developed from the logistic regressions

First we used the gradient site data for 30 field plots of 17 natural reserve areas in eastern China to validate the model predictions. The results indicated that the simple empirical model could explain 80% of the RBD variation for major undisturbed to semi-disturbed vegetation types across eastern China ($r^2 = 0.80$, $P < 0.0001$) (Fig. 4a).

Secondly, we examined further whéther the MRERBD model could be generally applicable to the worldwide literature. The model explained 45% of the variation in the global dataset (pooled data from 295 plots distributed globally from the boreal zone to the tropics; Fig. 4b). The trend line of predicted RBD versus literature RBD was very close to the one-to-one line with a statistical significance at $P < 0.0001$ ($r^2 = 0.45$), indicating that the simple empirical model simulated the global distribution pattern of RBD broadly over a range of major biomes. The model predicted well RBD for temperate evergreen forest ($r^2 = 0.70$, $P < 0.0001$), temperate deciduous broad-leaved forest in China ($r^2 = 0.68$, $P < 0.001$), and Mediterranean desert ($r^2 = 0.98$, $P < 0.01$) (Fig. 5),

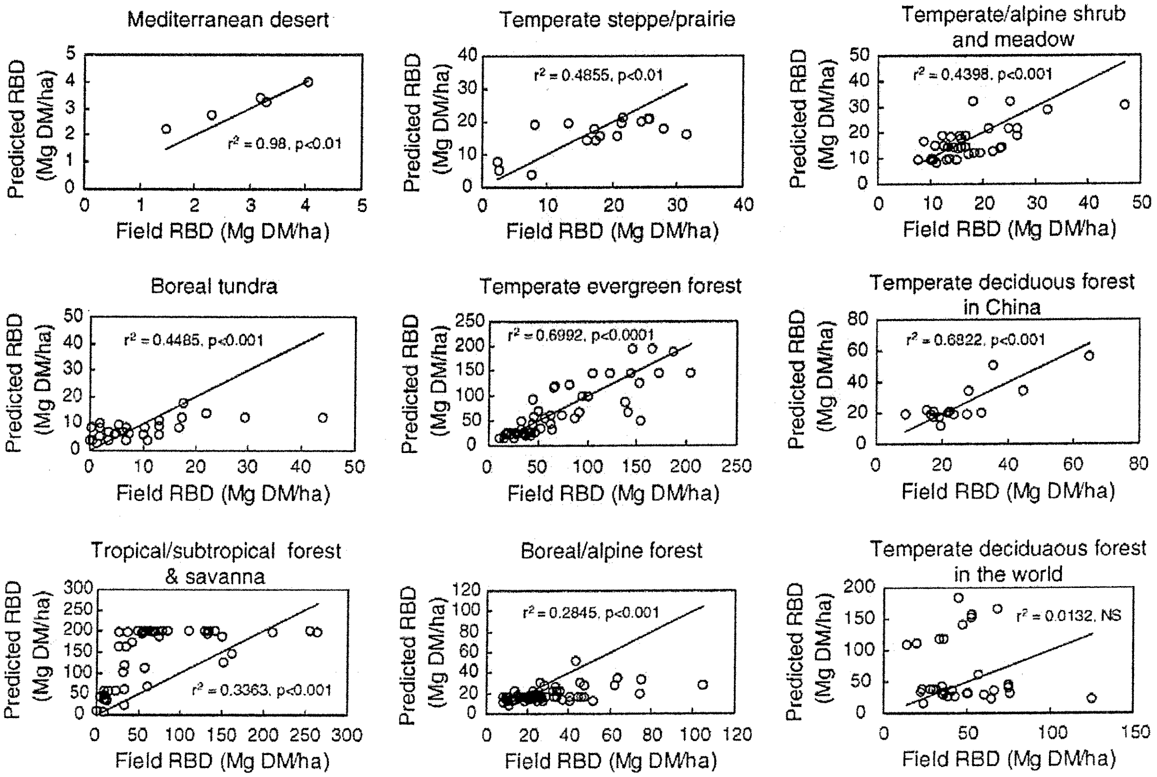


Fig. 5. Relationship between predicted RBD by the MRERBD model and the literature RBD for different vegetation types worldwide. The trend line is for one-to-one relationship.

Table 2
Mean field RBD compared with mean predicted RBD by the MRERBD model for 95 plots broadly distributed in the world

Vegetation type	Mean field RBD (Mg DW/ha)	Mean modeled RBD (Mg DW/ha)	Average error (%)	CV in field vs. modeled (%)	Field plots
Boreal/alpine needle-leaved forest	29.61 ± 18.76	18.91 ± 7.28	−36	63 vs. 39	59
Temperate evergreen needle- or broad-leaved forest	72.06 ± 50.95	66.67 ± 52.34	−8	71 vs. 79	51
Temperate deciduous broad-leaved forest	39.65 ± 21.32	53.18 ± 46.36	34	54 vs. 87	51
Subtropical and tropical evergreen broad-leaved forest (savanna)	72.50 ± 65.09	142.30 ± 69.95	96	90 vs. 49	45
Temperate/alpine steppe (prairie)	17.80 ± 8.57	15.92 ± 5.38	−11	48 vs. 34	17
Alpine shrub and temperate meadow	17.69 ± 7.60	16.14 ± 6.58	−9	43 vs. 41	36
Boreal tundra	9.82 ± 9.76	7.91 ± 3.81	−20	99 vs. 48	31
Mediterranean desert	2.86 ± 0.99	3.14 ± 0.65	10	35 vs. 21	5

The average error of estimation was calculated using the equation: ((mean modeled RBD − mean field RBD)/mean field RBD × 100). Positive values indicate the model overestimation, while negative values are for the model underestimation. Coefficient of variance (CV, %) = standard error/mean RBD × 100.

and explained less than half of the RBD variation in temperate steppe/prairie ($r^2 = 0.49$, $P < 0.01$), temperate/alpine shrub and meadow ($r^2 = 0.44$, $P < 0.001$), and boreal tundra ($r^2 = 0.45$, $P < 0.001$). Furthermore, there were general overestimates in tropical/subtropical forests/savanna ($r^2 = 0.34$, $P < 0.001$) and temperate deciduous forests in the world ($r^2 = 0.01$, not statistically significant at $P < 0.10$), and underestimates in boreal/alpine forests with high RBD of more than 30 Mg/ha ($r^2 = 0.28$, $P < 0.001$).

The relative standard error of estimation on average ranged between −20 and 10% in most of vegetation types including temperate evergreen forests (−8%), temperate/alpine shrubs and meadows (−9%), temperate steppes/prairies (−11%), boreal tundra (−20%), and Mediterranean deserts (10%) (Table 2). Overestimates existed in tropical and subtropical forests/savannas (96% higher) and warm-temperate deciduous forests (34% higher), and underestimates existed in boreal forests (−36% lower).

4. Discussion

4.1. Can root biomass be predicted without reference to shoot biomass?

Measurements of coarse and fine root biomass are generally made at specific sites, but the characteristics of the distribution over large areas are not well established (Vogt et al., 1996; Cairns et al., 1997; Cihlar et al., 2000). The empirical data from the systematically designed experimental sites along the TAVT indicated that RBD significantly decreased with increasing altitudes ($r^2 = 0.60$, $P < 0.001$) but had low or non-robust correlations with ABD ($r^2 = 0.10$–0.34), suggesting that RBD can be predicted without reference to shoot biomass. Our pattern analysis of the TAVT data further revealed that: (1) temperature and/or precipitation were the major limiting factors for geographical distribution patterns of RBD of natural vegetation and (2) relationships between RBD and limited climatic factors could be expressed as logistic equations with a maximum RBD of 200 Mg/ha (Fig. 3).

The simple climate-based empirical model developed from the logistic regressions explained 80% of the RBD variation for 30 field plots along the North–South Transect of Eastern China but less than half of the variation in the global 295 plots. The model predictions were strong for temperate evergreen forests, temperate/alpine shrubs and grasslands, boreal tundra, and Mediterranean deserts. Such a global scaling exercise suggested the possibility to develop a new method for large-scale estimation of root biomass, and may fix a gap in modeling global terrestrial carbon storage owing to the lack of standard methodology on calculating RBD.

4.2. *Effect of plant rooting depth on root biomass density*

We found that sampled maximum rooting depths explained 27% of the RBD variation ($P < 0.02$) for the 22 sites along the Tibetan transects (Fig. 6), indicating a tendency for root biomass to be correlated with plant rooting depth. Based on data from 250 studies, Canadell et al. (1996) found that the average maximum rooting depth for grasses and herbs was 2–2.5 m, but maximum rooting depth of trees and shrubs was considerably deeper, 5 and 7 m on average. More recently, based on a database of vertical root profiles from the literature with 520 profiles from 286 geographical locations, Schenk and Jackson (2002a) found that rooting depths, encompassing 95% of all roots, increased with decreasing latitude from 80° to 30° but showed no clear trend in the tropics. That study further indicated that annual potential evapotranspiration, annual precipitation, and length of the warm season were all positively correlated with rooting depths. Such a global pattern of plant rooting depth, in part, explains the global distribution of root biomass density of plants suggested in this study. It is possible that the inconsistent sampling depths and measuring methods might cause divergence of the measured data from the modeled patterns.

4.3. *Why could the logistic regressions found from the Tibetan transects be widely applied to other regions?*

We believe that the sound relationship between RBD and climatic factors was the result of the equilibrium status achieved after long-term interactions between the ecosystems and their environments in this extremely high plateau. 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 and Zhou, 1998). Uplifting of the plateau created and then strengthened the South Asian Monsoon, and has had tremendous impacts on the evolution and the development of species and ecosystems of the plateau itself and neighboring regions (Sun and Zheng, 1998).

In natural vegetation on the Tibetan Plateau, relations of NPP (Luo et al., 2002a, 2004a), ABD (Luo et al., 2002b), leaf area index (Luo et al., 2004a), and whole-canopy mean leaf lifespan (Luo et al., 2004b) to temperature and precipitation also follow the Weber's Law and logistic patterns, indicating that the logistic pattern in RBD was well based. Convergence towards logistic patterns in dry matter production of natural vegetation along the TAVT confirms that in plant growth, natural selection favors a high carbon gain, close to the maximum that can be maintained in any given environment (Mooney, 1972; Grime, 1977; Chapin et al., 1987). 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).

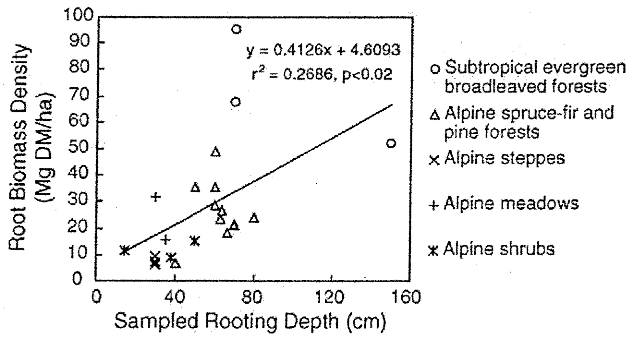


Fig. 6. Relationship between sampled maximum rooting depth and root biomass density. The data were from 22 field plots along the Tibetan Alpine Vegetation Transects in this study.

Along the TAVT, RBD significantly decreased with increasing altitudes ($r^2 = 0.60$, $P < 0.001$). Our previous study in the Gongga Mountains indicates that stand canopy at higher altitudes has longer leaf longevity and higher foliage mass, and root biomass is negatively correlated with whole-canopy mean leaf lifespan and foliage N-pool (Luo et al., 2004b). The closed canopy of trees with high leaf mass and long leaf longevity generally creates low soil temperature, which impairs root activity (Körner, 1998). Then carbon costs for nitrogen absorption by roots in alpine plants become more expensive and extending leaf lifespan is more economic (Luo et al., 2004b).

Mountain regions typically offer a wide variety of ecosystems within a small geographical area, thus providing a substitute for latitudinal changes (Becker and Bugmann, 2001). 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 rainforest to alpine vegetation (Li, 1985; Hou and Zhang, 1992; Zheng, 1996). Temperature was considered the limiting factor for the vegetation distribution in the Gongga Mountains because actual evapotranspiration is generally low and accounts for only 27% of the annual precipitation at 3000 m ASL (Zhong et al., 1997). Along the longitudinal–latitudinal transect in Central Tibetan Plateau, an extreme-climate environment controlled the vegetation distribution where we could find the obvious borders and ecotones from forests to shrubs and meadows limited by precipitation, and from alpine meadows to alpine steppes limited by temperature and precipitation.

4.4. Uncertainties in RBD estimates by the MRERBD model

Much uncertainty remains in RBD estimates of subtropical/tropical vegetation and temperate deciduous forests where the model tended to overestimate RBD (Fig. 5). We believe that the higher modeled values are a more realistic representation of RBD in these biomes because of the inadequate field sampling depth typically used. The global literature analysis by Schenk and Jackson (2002a) indicates that only 9% of the 475 root profiles are sampled to a depth at which no further roots are found, with few studies sampling root profiles to depths of 3 m or more. That study further indicates that rooting depths in tropical vegetation are only weakly correlated with climatic variables but are strongly correlated with sampling depths, suggesting that even after extrapolation, sampling depths are often insufficient to characterize root profiles and thus RBD. Measurements of RBD to date are likely underestimated for tropical/subtropical vegetation and warm-temperate deciduous forests because roots grow deeper than the depths typically sampled. For example, in the Edwards Plateau of central Texas, deciduous trees of *Quercus* species grew roots deeper than 5 m, with a maximum of about 25 m (Jackson et al., 1999). In eastern Amazonia, water uptake from 2 to 8 m soil depths contributes to more than three-fourths of the transpiration of evergreen forest in the dry season suggesting that roots penetrate to these depths (Nepstad et al., 1994).

The analysis by Cairns et al. (1997) reveals that forest RBD is positively correlated with stand age especially before 100 years old. Because most of the primary forests in tropical and subtropical regions have already disappeared due to human-induced disturbances, it is possible that the RBD measurements in the late secondary forests reported in the literature underestimate RBD in the primary vegetation.

One of the causes for the underestimates of RBD in forests, especially in boreal/alpine forests, by the MRERBD model is likely due to the difficulties in obtaining estimates of the complete biomass of root crown and coarse taproots rather than the fine roots in the TAVT sites. According to the global literature analysis by Vogt et al. (1996), there are much lower ratios of fine root biomass to total RBD in boreal/alpine forests (5–9%) than in temperate forests (10–34%) and tropical and subtropical forests (20–54%). Therefore, the measurements of RBD in the boreal/alpine forests of the TAVT sites using soil pits may cause more underestimated biases than in other forest types. Most investigations of roots are still exploratory in nature (Santantonio et al., 1977; Vogt et al., 1996; Cairns et al., 1997; Cihlar et al., 2000). It is almost impossible to assess the precision and accuracy of the existing root sampling schemes both in this study and the global literature. A possible improvement of the root sampling scheme in this study is the need to sample multiple standard trees within a plot; a task that takes a great deal of effort and causes a great deal of disturbance. Despite the uncertainty we believe that the RBD variation among the TAVT forest sites is mainly affected by climatic gradients because the same root sampling method is the same for all the sites and is comparable to the methods in the literature.

Estimates of root biomass density are fundamental to understanding carbon storage and the biogeochemical dynamics of terrestrial ecosystems. At large scales, regional inventory data such as forest growing stock and grass and crop yields are useful for reliably estimating aboveground biomass density, as it has been done for many regions of the world (Birdsey, 1992; Brown et al., 1993; Brown and Gaston, 1995). However, these inventory data do not provide a direct way of estimating RBD. Estimates of aboveground biomass based on well-established methods are relatively abundant, but estimates of root biomass based on standard methods do not exist.

The paucity of root biomass estimates is partly caused by the lack of accepted standards for sampling and estimation. There are a variety of ways of sampling roots, but none of them are standardized, particularly with respect to depth. The MRERBD model developed in this study may be appropriate for temperate evergreen forests, temperate/alpine shrubs and grasslands, boreal tundra, and Mediterranean deserts. We still need additional field work to further calibrate the model simulations in tropical/subtropical forests and boreal/alpine forests. The climate-based predictions in undisturbed to semi-disturbed vegetation may provide the baseline estimates of RBD across a large-scale landscape that is an important component in estimating global carbon stocks and the resulting fluxes when they are changed.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at 10.1016/j.foreco.2004.11.016.

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