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Forest Ecology and Management 206 (2005) 349-363

Forest Ecology and Management

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

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Received 13 March 2004; received in revised form 12 November 2004; accepted 12 November 2004

## 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. © 2004 Elsevier B.V. All rights reserved.

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

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0378-1127/\$ – see front matter  $\odot$  2004 Elsevier B.V. All rights reserved. doi:10.1016/j.foreco.2004.11.016

## 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

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