

This article was downloaded by: [T&F Internal Users], [Rob Blackmore]

On: 11 April 2012, At: 06:24

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Scandinavian Journal of Forest Research

Publication details, including instructions for authors and subscription information:
<http://www.tandfonline.com/loi/sfor20>

Change of allometry between coarse root and shoot of Lodgepole pine (*Pinus contorta* DOUGL. ex. LOUD) along a stress gradient in the sub-boreal forest zone of British Columbia

Hans Pretzsch^a, Enno Uhl^a, Peter Biber^a, Gerhard Schütze^a & K. David Coates^b

^a Forest Growth and Yield, Technische Universität München, Freising, Germany

^b Ministry of Forests, Lands and Natural Resource Operations, Smithers, BC, Canada

Available online: 02 Apr 2012

To cite this article: Hans Pretzsch, Enno Uhl, Peter Biber, Gerhard Schütze & K. David Coates (2012): Change of allometry between coarse root and shoot of Lodgepole pine (*Pinus contorta* DOUGL. ex. LOUD) along a stress gradient in the sub-boreal forest zone of British Columbia, *Scandinavian Journal of Forest Research*, DOI:10.1080/02827581.2012.672583

To link to this article: <http://dx.doi.org/10.1080/02827581.2012.672583>



PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.tandfonline.com/page/terms-and-conditions>

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae, and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand, or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

ORIGINAL ARTICLE

Change of allometry between coarse root and shoot of Lodgepole pine (*Pinus contorta* DOUGL. ex. LOUD) along a stress gradient in the sub-boreal forest zone of British Columbia

HANS PRETZSCH¹, ENNO UHL¹, PETER BIBER¹, GERHARD SCHÜTZE¹ & K. DAVID COATES²

¹Forest Growth and Yield, Technische Universität München, Freising, Germany, and ²Ministry of Forests, Lands and Natural Resource Operations, Smithers, BC, Canada

Abstract

This transect study in 41–178 year-old stands of Lodgepole pine (*Pinus contorta* DOUGL. ex. LOUD.) in the southern boreal forest of British Columbia, Canada, analyses how site conditions modify the coarse root–shoot dynamics of trees. The allometric relationship between diameter growth of coarse roots and trunk is scrutinised for long-term site dependence, and short-term reactions to periodic climate conditions. Along a gradient from poor to rich sites, we analysed 54 trees. The sampling scheme provided two increment cores each from the three main roots and the shoot at breast height per tree. From the year-ring series, we calculated diameter time series for each shoot and each root. With these data, we show (1) that the trees' coarse root diameter and shoot diameter are linearly related in a double-logarithmic coordinate system, thus representing constant allometry on the long run. Statistical analysis of these long-term trajectories reveals that (2) the relative allocation to coarse roots versus shoot is much higher on poor sites compared to rich sites. A closer look at the short-term reaction to stress events in the period from 1995 to 2000, where several dry years occurred, underpins that (3) a lack of water supply triggers biomass allocation in favour of coarse roots at the expense of shoot growth most pronouncedly on poor sites. Implications of this morphological plasticity for allometric theory, method development, tree and stand dynamics and carbon storage assessment are discussed.

Keywords: Morphological plasticity, root–shoot allometry, root–shoot ratio, stress–gradient hypothesis, carbon storage, site–growth relationship.

Introduction

Trees have to cope with various kinds of stress which the environment holds as surprise in store for them in their long course of life. The most recent trend which challenges plants' capability for acclimation is climate change (Jentsch et al., 2007; Matyssek et al., 2010; Pretzsch & Dieler, 2010; Rötzer et al., 2009). According to Helms (1998), p. 1), we define acclimation as "... a change in the morphology or physiology of an organism in response to environmental change, that is a temporary increase in resistance to stress ...". Plasticity of crown and root structure is an indispensable requirement for acclimation, as it enables an adjusted resource supply even under scarce resource supply, for example by change of the root–shoot relationship.

Intra-individual root–shoot allometry

The focus of this study is on the analysis of the allometric root–shoot growth of selected dominant individuals over time. The approach is based on the methodology successfully tested in a pilot study by Nikolova et al. (2011). Growth of coarse roots is related to shoot growth to detect allometric relations and allocation patterns. With our study, we applied the methodology to an ecological gradient in order to explicitly detect effects of site conditions on the partitioning of resources using Lodgepole pine (*Pinus contorta* DOUGL. ex. LOUD.) – a tree species with easily measurable year rings.

The coarse roots as well as the stem diameter represent of course only one part of the below respectively above ground growth of trees. Growth

Correspondence: Prof. Dr. Hans Pretzsch, Forest Growth and Yield, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany. E-mail: Hans.Pretzsch@lrz.tum.de

(Received 31 August 2011; accepted 29 February 2012)

of fine roots and branches can differ considerably in the amount and dynamic of the coarse organs. So the analysed allometric relationships indicate just a part of the root–shoot dynamic, however, stem and coarse roots represent a substantial part of it, and are in a structural functional relationship with the smaller tree organs, as the latter ensure the supply and disposal of the former. In contrast to our intra-individual analysis of the root–shoot relationship most related studies (i.e. Weiner & Thomas, 1992) base on inter-individual sampling and evaluation. By the latter, roots of a number of individuals are excavated and weighted or measured, stems and branches are measured. Advantage is that larger parts of the root and shoot system can be integrated in the study, as the trees are harvested. Disadvantage is that these sampling procedures destroy the tree, disable the compilation of time series of root–shoot growth and substitute an artificial time series for a real time series. Such a substitution of intra-individual for inter-individual records invites to mix differences in root–shoot allometry due to relative size, competitive status, and micro-sites with real allometric effects that matter partitioning. Furthermore, selective studies rarely generate statistical relations between driving forces and growth reaction and are less appropriate for causal analyses. Biological interrelations concerning growth are unveiled best when analysed along a broad range of site conditions. Site dependent, species-specific growth reactions and structural evolution are exemplary described by Pretzsch et al. (2010) and Pretzsch and Dieler (2012).

Year-ring chronologies based on sampling of cross sectional discs along stems and root systems have been used as indicators of whole-tree resource allocation under differing climatic conditions (Drexhage et al., 1999; Krause & Eckstein, 1993) or after insect outbreaks (Krause & Morin, 1999). So far, such analyses concentrated on ring-width variations or structural changes on a macroscopic level. The selection of cross-sectional discs from roots and shoots of adult trees, however, is related with several methodological difficulties, such as restrictions to use individuals felled by wind-throw or after commercial cut, and subsequent mechanical uprooting and excavation of the root system (Bolte et al., 2004). Therefore, at present there is a lack of quantitative information about forest trees' root–shoot allometry response to changes in the resource availability.

Theoretical background

Since its beginning allometric research was driven by the search for an overarching, universal allometric

exponent. Often it was proposed that volume or mass related allometric functions scale with exponents based on 1/3 due to the volume dimensionality (Bertalanffy, 1951; Gorham, 1979; Yoda et al., 1963, 1965). More recently, West et al. (1997, 2009), Enquist et al. (1998, 2009) and Enquist and Niklas (2001) presented a general explanation of allometric scaling with exponents to be derived from 1/4 based on the fractal network of transportation systems in organisms.

In contrast to the assumption of general scaling rules for metabolism, the morphology of plants appears to be rather variable and plastic. Stable metabolic scaling and variable scaling of crown and root structure are not necessarily contradictory (Pretzsch & Dieler, 2010, 2012). Maybe morphological plasticity is even a requirement for holding trees on a rather stable leaf mass–plant mass or root mass–plant mass trajectory under variable or changing environmental conditions.

Allometric equations offer an appropriate approach to describe the size development of a plant and the relationship of one organ or dimension to another. Supposing x and y quantify the size of two different plant dimensions, the growth $x'(dx/dt)$ and $y'(dy/dt)$ is related to the size x and y as $y'/y = \alpha x'/x$. More common are integrated ($y = ax^\alpha$) or logarithmic representations ($\ln y = \ln a + \alpha \times \ln x$). These equations address the relative change of one plant dimension, dy/y (e.g. the relative height growth) in relation to the relative change of a second plant dimension dx/x (e.g. the relative diameter growth).

Records of pairs of size measurements (e.g. x = stem diameter, y = root diameter) taken from n different individuals or from n subsequent measurements of the same individual over time provide $x_i, i = 1..n$ and $y_i, i = 1..n$. After logarithmic transformation of the bivariate size data ($\ln(x_i), \ln(y_i)$) linear regression techniques yield a and α of $\ln y = \ln a + \alpha \times \ln x$. The allometric exponent α can be perceived as a distribution coefficient for the growth resources between organs y and x : when x increases by 1%, y increases by $\alpha\%$. The allometric factor a is a species-specific normalisation constant. It differs, for example significantly between herbaceous and woody plants.

The optimal partitioning theory (OPT) and the allometric biomass partitioning theory (APT) are two alternative theories that have recently been advanced to describe the allocation in plants (Müller et al., 2000; Niklas, 2004; Pretzsch, 2009). Their different concepts become obvious by their assumptions on the behaviour of the parameters a and α . According to APT, resource allocation patterns between different organs change solely with plant size (i.e. allometrically) being insensitive to the

variation in the local environmental conditions (Enquist & Niklas, 2002; Müller et al., 2000). This means that parameter a can be modified by environmental factors, resource supply or growth, while the allometric exponent α is assumed to be constant and to have overarching validity. OPT states that a plant always invests into improving the access to the currently limiting factor. If for example the limiting factor is light or water, the plant invests in shoot or root growth, respectively (Bloom et al., 1985). With regard to the parameters of the allometric equation, this implies that both, exponent α as well as the normalisation factor a can be modified by environmental conditions in space and time.

If we assume that environmental factors and resource supply modify allometric exponents at all, then this is most probable for the relationship between root and shoot. For maximising their fitness, plants are supposed to partition resources and allocate biomass to organs in a way that remedies limitations to biomass production. This concept should also become obvious in the dynamics of root–shoot growth, as root growth should be increased when below-ground resources (water, nutrients) are limiting and shoot growth when above ground resources are scarce (light, CO_2). This behaviour is assumed to be responsible for the wide variation of the root–shoot ratio under different site conditions (Comeau & Kimmins, 1989; Keyes & Grier, 1981).

Objectives

In this article, we apply the allometric analysis of coarse roots and stem tested by Nikolova et al. (2011) for a broad set of samples along an ecological gradient. We use the relationship between the diameter growth of coarse roots and trunk of Lodgepole pine (*P. contorta* DOUGL. ex. LOUD.) in a sub-boreal forest for analysing (1) how growth of coarse roots and stem are related, (2) if and how site conditions modify the allocation to coarse roots versus shoot and (3) if and how short-term events of drought modify the allometry and matter allocation between coarse roots versus shoot on sites with poor to rich resource supply. The results are discussed in view of the allometric biomass partitioning theory (APT), the OPT and the relevance for forest monitoring (carbon storage) and forest management.

Materials and methods

Study area – climate and soil conditions

In this study, we focus on Lodgepole pine (*P. contorta* var. *latifolia* Engelm.) in mature upland coniferous forests in the region around Smithers, Northwest British Columbia, Canada ($54^{\circ}35'N$, $126^{\circ}55'W$). Our study sites are located in a 20×50 km area centred on Smithers (Figure 1). Thus, they belong to the southern boreal forest of British Columbia which is designated as the Sub-Boreal Spruce Biogeocli-

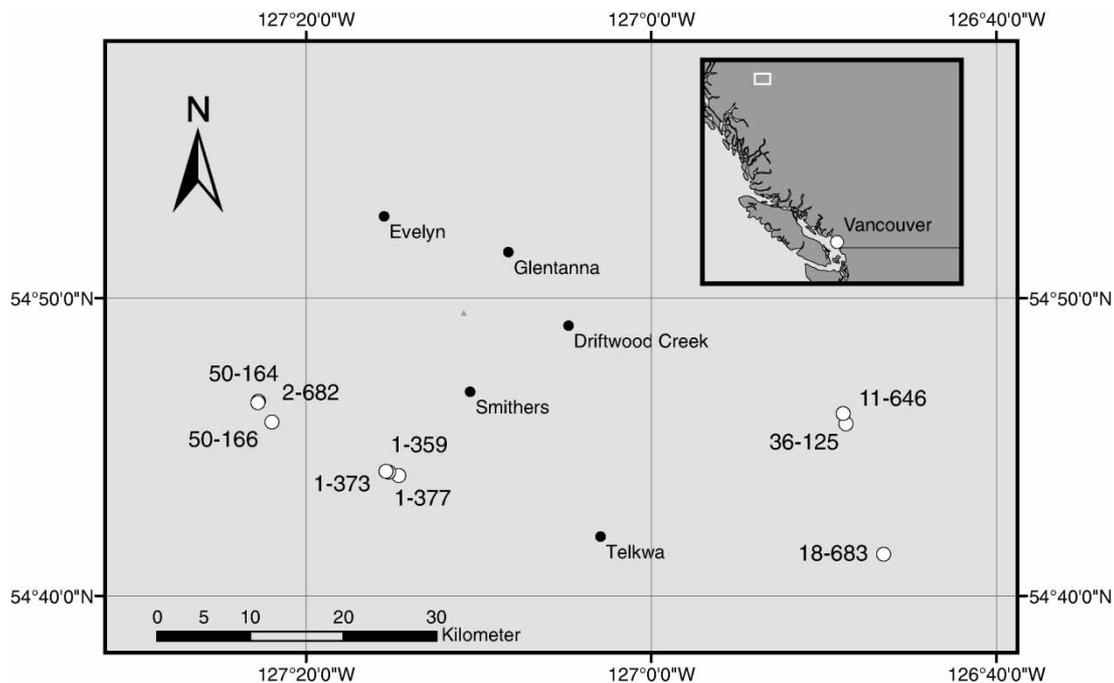


Figure 1. Location of the nine experimental plots near Smithers/British Columbia (No. 50-166, 50-164, 2-682, 1-373, 1-377, 1-359, 36-125, 11-646 and 18-683, from west to east). For large-scale orientation see map in inlet top right.

matic Zone (SBS) and is located in the montane landscape of the Central Interior, within the closed forest portion of the Cordilleran boreal region (Pojar, 1996). Climate in the SBS is continental with severe, snowy winters and relatively warm, moist and short summers (mean annual temperature range of -0.7 to 3.6°C ; mean annual precipitation of 400–750 mm, with 25–50% falling as snow), and a frost free period of 116 days (Banner et al., 1993). The moist and cold subzone of SBS the study sites belong to is called SBSmc2 (Pojar, 1996).

For scrutinising short-term drought effects on root–shoot allometry (question 3), we focussed on two subsequent six-year growth periods, 1989–1994 and 1995–2000, which show marked climatic differences. In the latter period, growth conditions were less favourable, that is drier and colder. Our choice is supported by Ouimet et al. (2008), who report trees suffering pronouncedly from an unusual climatic episode in 1995 and 1996.

In the study area, the first period, 1989–1994, is characterised by a 0.7°C higher mean periodic temperature compared to the long-term mean of 3.8°C (1942–2008) and a 0.6°C higher temperature than during the second period (all climate data obtained from the weather station Smithers A (Environment Canada, 2010)). Considering the mean temperature of the months April–September, the earlier period is about 1.0°C warmer than the later one. The growing season length (GSL) index (ETCCDI, 2011) shows a longer GSL of 11 days on average for the first period. In addition, the warm spell duration (WSDI) index (ETCCDI, 2011) demonstrates longer lasting warm episodes for the single years during the period from 1989 to 1994 (+6 days on average).

During 1989–1994, the annual precipitation was higher in every year than the long-term mean (513 mm) whereas during 1995–2000 the mean periodic precipitation only accounts for 490 mm with a higher variability ranging from 384 to 617 mm. The consecutive dry days (CDD) index (ETCCDI, 2011) is slightly higher within the second period.

The climatic differences between the two periods probably resulted from both, short-term variability in the Pacific Northern Hemisphere inherent to the climate system, as well as from a transition of warm episode conditions (El Niño) in the tropical Pacific to cold episode conditions (La Niña) in winter 1995/1996 (NOAA, 1996; Ouimet et al., 2008).

Soils in the SBSmc2 subzone are mostly Dystric Brunisols, Brunisolic Luvisols or Orthic Gray Luvisols with sandy loam to clay loam textures, rooting depths of around 35 cm and coarse fragment content ranging from 0 to 65% (Banner et al., 1993).

Topographical and geomorphic variation over the landscape result in a range of site productivity conditions (Banner et al., 1993). The driest, poorest sites are typically found on moisture-shedding slopes with shallow, rocky, coarse-textured soil, an acidic surface soil horizon and a thin forest floor dominated by fungi. Lodgepole pine dominated stands are most abundant on the poorer and drier soils in the region.

The medium or mesic sites have medium-textured, well-drained soil, with little soil acidification and a thicker forest floor with influences from fungi and soil fauna. Mesic sites with mature forests in the SBSmc2 subzone have been characterised by Kranabetter et al. (2007). Forest floors are typically acidic (pH of 4), approximately 3.5 cm deep, moderately moist throughout the growing season (averaging 150% w/w) and characterised by low rates of N mineralisation. Mineral soils are similarly limited in N availability, with low amounts of organic matter (%C of approximately 2%) and moderate moisture deficits (averaging 25% w/w) during the growing season. Foliar analyses typically reveal N deficiencies (%N of approximately 1.2%) for conifers on mesic sites, often with secondary limits in S, but no other macro- or micro-nutrient deficiencies (Kranabetter & Simard, 2008).

The richest sites are located in moisture-receiving areas with year-round seepage from upper slopes. They tend to have finer-textured soils with organic matter incorporated into the mineral soil by active soil fauna and quickly decomposing herbaceous flora. In the following, we refer to the site conditions as poor, medium and rich.

Lodgepole pine in the study area

Mature forests in the SBSmc2 subzone generally established after an earlier landscape-level stand destroying fire, while, in contrast, managed stands in the area are generally of clear-cut origin and less than 40 years old. Mature upland coniferous forests are dominated by Lodgepole pine (*P. contorta* var. *latifolia* Engelm.), Interior spruce [a complex of White spruce (*Picea glauca* Moench), Voss and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), Subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) and Trembling aspen (*Populus tremuloides* Michx.)]. Paper birch (*Betula papyrifera* Marsh.), Black cottonwood (*Populus balsamifera* ssp. *trichocarpa* Torr. & Gray) and willow (*Salix* spp.) occur, but are less common. Mesic sites often support mixed forests of the three major conifer species. Trembling aspen can be common after disturbance on mesic sites, but was infrequent in our sample plots. Interior spruce and subalpine fir are the dominant tree species in mature

forests on the more productive site types of the SBSmc2 subzone.

The root system of lodgepole pine is generally shallow but can vary considerably in form, depending on soil type (Cochran, 1985; Krajina et al., 1982). In well-drained medium-textured soils, the taproots and vertical sinkers are common but they gradually become less significant as individual trees mature. Sinker roots can also form near the base of large lateral roots and are important for support. Shallow roots are common above hardpan or in shallow, rocky soils (Cochran, 1985; Krajina et al., 1982).

Plot selection and measurements

Our study took advantage of a set of stem-mapped long-term trial plots established by the Bulkley Valley Centre for Natural Resources Research and Management (<http://www.bvcentre.ca>). These plots were specifically established along a gradient of below-ground resource supply (from dry and poor to wet and rich) and competitive tree canopy neighbourhoods (density and species). Site productivity at each sample plot was assessed in nearby soil pits according to the British Columbia Biogeoclimatic Classification System (Banner et al., 1993) using soil horizons, texture, depth, coarse fragment content, slope position, humus form and indicator plants to determine below-ground resources.

The plot design allows analyses of allometric relations and allocation along both, a spatial gradient represented by different site conditions, as well as a temporal gradient that covers different climatic conditions.

For this study, we selected nine subplots with ages between 41 and 178 years from the above-mentioned set. In August 2010, we sampled between three and eight dominant Lodgepole pines per subplot, in total 54 trees. Direct neighbours were never chosen as sampling trees in order to avoid

strong interactions. From all trees height (measured with the ultrasonic hypsometer HAGLÖF VER-TEX), and diameter at breast height (girth tape with pi-scale) were measured. For each tree, we individually determined the site index after Thrower & Associates Ltd (1994), and found a good conformity between this site index and the qualitative site classification available for the plots (Banner, et al., 1993; Kranabetter et al., 2007). Our data represent site indexes from 11.3 to 22.7 m (reference age 50 years), i.e. they cover poor to rich sites. See Table I for a summary of subplot characteristics.

We applied standard techniques of increment boring (Nikolova et al., 2011) to stem and selected coarse roots of each sample tree. Two increment cores were taken at breast height (1.3 m) from each sample tree's stem in perpendicular directions, that is 45° and 315° relative to the widest stem diameter. From each sample tree, the three tallest lateral structural roots were partly excavated. We measured the root diameter and cored twice per individual root at positions about 30–50 cm from their offset at the trunk. This distance was determined according to Krause and Morin (1995), who found the number of missing or discontinuous rings in roots to increase with increasing distance between coring position and the outer edge of the stem base. Roots were typically elliptical with the largest radius perpendicular to the forest floor. In order to get representative and rather unbiased root diameter and diameter growth measurements we took two increment cores each in $\pm 45^\circ$ to the plumb-line (Figure 2). When taking increment cores from stem and roots, we made an effort to hit the pith in order to trace the increment back as far as possible.

Sample and data preparation

The increment cores were sanded with a belt sander using paper with 80–120 grits. After that, the year-ring widths were measured using a digital positiometer

Table I. Subplot characteristics calculated from measured trees.

Subplot	Age (a)	dq (cm)	hq (m)	ba (m ² ha ⁻¹)	Site index (m)	Site classification
1–359	64	29.3	21.1	35.7	18.6	Poor
1–373	80	23.9	21.8	33.3	17.3	Poor
18–683	52	21.3	15.7	23.7	15.3	Poor
1–377	111	25.0	23.6	47.7	17.0	Medium
2–682	73	19.6	20.2	33.7	16.6	Medium
11–646	41	24.3	18.4	33.3	20.7	Medium
36–125	61	21.4	22.6	42.3	20.4	Rich
50–164	167	28.6	27.8	47.0	18.1	Rich
50–166	178	39.4	33.0	39.5	22.5	Rich

Note: dq, hq: quadratic mean diameter and corresponding height, respectively. ba: basal area, site index after Thrower & Associates Ltd. (1994), site classification: qualitative site classification as available for the plots.

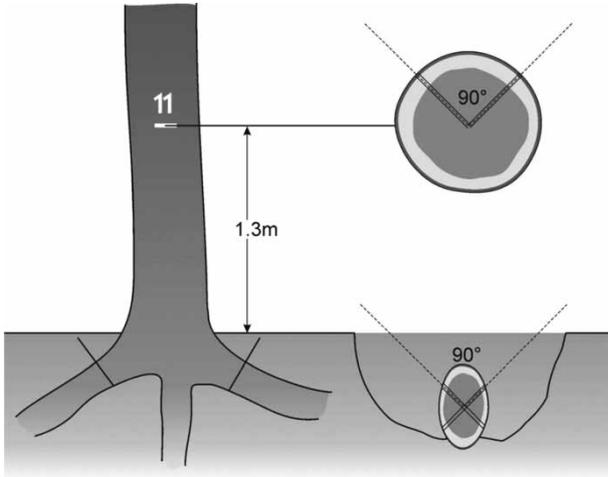


Figure 2. Principle of sampling increment cores from the trunk and three main roots of the tree. Positions selected for increment boring at stem and roots (upper cross section) and directions of crosswise boring (lower cross section).

after Johann (Biritz + Hatzl GmbH, Austria). Non-perpendicularly drilled year-rings as occur near the centre of a stem or a root were not included in the further analysis. Damaged cores and insufficient core orientation towards the root centre made us exclude 7 roots out of 162 from the study. We consider this loss of information negligible for the statistical analyses.

Each of the three individual root-year-ring series per tree was matched separately with the previously synchronised and averaged stem year-ring series of the corresponding sample tree. Neither in the stems nor in the roots hints for absent year-rings were detected. Thus, successful cross-dating was possible. From these increment series, we calculated backwards diameter time series for each stem and each root. For the sake of clarity, we refer to a tree's diameter at breast height always as dshoot and to the diameter of a root as droot in the further text.

Combining the individual droot and dshoot series per root and tree, we obtained series that cover in average 30 (minimum 9, maximum 100) annual droot-dshoot-pairs. The three droot series per tree were saved individually but also averaged by year to produce one representative time-series for the root growth of the respective tree. A summary of the measured tree, stem and root data is presented in Table II. The stem and root diameters measured in August 2010 range from 14.5 to 45.1 cm (stems), and from 6.8 to 36.3 cm (roots), respectively. The minimum annual growth rate of both root and shoot diameter is 0.04 mm whereas roots show a higher maximum. The mean annual growth rate of droot and dshoot account for nearly the same.

Resulting from the procedure described earlier, droot-dshoot time series from 54 trees and 155 roots, counting back for 30 years in average, were

Table II. Overview of measured tree variables.

	Unit	Min-Max	Mean	SD
Stem Age	a	41–178		
Diameter at breast height	cm	14.5–45.1	25.1	6.7
Height	m	11.6–35.1	22.2	5.1
Site index (Thrower & Ass. 1994)	m	11.3–22.7	17.5	2.7
Year-ring width	mm	0.04–6.93	1.19	0.95
Root Diameter	cm	6.8–36.3	17.5	6.4
Year-ring width	mm	0.04–9.29	1.18	0.92
Length of droot-dshoot time series used for allometric analysis	#	9–100	30	17

available for descriptive and statistic analyses (question 1 and 2). In search for short-term drought effects (question 3) we clipped out the root-dshoot diameters from 1988 to 2000 in order to cover the increment years 1989–1994, and 1995–2000 (see climate characteristics described earlier).

Statistical methods

Long-term root-dshoot allometry and its site dependency (question 2)

We applied and compared a multitude of statistical model formulations that were basically apt to describe the possible site-dependent long-term allometric relationship between dshoot and droot. They took into account the nested data structure (plot, subplot, tree, root), the time series character of our data, and variance inhomogeneity. Using the Akaike Information Criterion (AIC) as a benchmark in the sense of Burnham and Anderson (2004), we found the site index si after Thrower & Associates Ltd (1994) performing best as a descriptor for the influence of site quality on the droot-dshoot allometry. In order to ensure the fitting algorithm converging despite the complex error structure modelled, we combined the nesting levels plot and subplot to one level 'subplot-in-plot'. Most important is to have the single tree as a nesting level, because per tree there mostly are three droot values for one dshoot value.

The AIC-based model comparison identified the following parsimonious linear mixed effects model as our means to answer question (2):

$$\begin{aligned} \ln(\text{droot}_{ijkt}) &= \beta_0 + \beta_1 \cdot \ln(\text{dshoot}_{jt}) + \beta_2 \cdot \ln(\text{dshoot}_{jt}) \cdot \ln(\text{si}_{ij}) \\ &\quad + b_i + b_{ij} + b_{ijk} + \varepsilon_{ijkt} \end{aligned} \quad (1)$$

In Equation 1, si represents the tree-specific site index, and the indices i, j, k refer to subplot-in-plot,

tree, and root respectively. The year to which the respective diameters are attributed is represented by t . For example, $\text{dshoot}_{t=1983}$ indicates a stem diameter at the end of 1983's vegetation period. $\beta_0, \beta_1, \beta_2$ are parameters to estimate. Here, β_0 is an estimate for the natural logarithm of the allometric factor a as described in the introduction section, while $\beta_1 + \beta_2 \ln(\text{si})$ gives a site dependent estimate for the allometric exponent $\alpha_{r,s}$ which expresses the scaling between root and shoot diameter. If $\beta_2 > 0$, $\alpha_{r,s}$ increases with site quality, indicating a higher relative investment into root growth on better sites and vice versa. AIC comparisons showed that si needed to be included in interaction with dshoot only.

In contrast to the conditions for applying a classic regression model, the assumption of uncorrelated errors ε_{ijkl} is not justified here due to the nested structure and the time series character of our data. Accounting for the former b_i, b_{ij}, b_{ijk} in Equation 1 represent normally distributed random effects ($b_i(0, \tau_1^2), b_{ij}(0, \tau_2^2), b_{ijk}(0, \tau_3^2)$) on the respective nesting levels. For describing the latter, serial correlation, we used an MA(q) model (Pinheiro & Bates, 2000; Zuur et al., 2009)

$$\varepsilon_{ijkl} = \sum_{n=1}^q \theta_n \cdot \eta_{ijkl\ t-n} + \eta_{ijkl\ t} \quad (2)$$

where θ is a parameter vector of length q to be estimated, and η is i.i.d. noise. This means that serial autocorrelation is described on individual-root level. In addition, we found that variance inhomogeneity with tree age had to be considered. Following Pinheiro and Bates (2000) we used the following variance function

$$\text{Var}(\varepsilon_{ijkl}) = \sigma^2 \cdot \text{age}_{ijkl}^{2 \cdot \delta} \quad (3)$$

with age being the tree age, σ^2 the residual variance and δ a parameter to be estimated.

The model was fitted using the Maximum Likelihood method. The residuals were visually assessed for normality, homogeneity and the absence of serial correlation as proposed by Pinheiro and Bates (2000) and Zuur et al. (2009).

Short-term drought effects on $\alpha_{r,s}$ (question 3)

As mentioned earlier, the favourable (moist and warm) increment period 1989–1994 was compared with the adversarial period 1995–2000. Thus, we extracted all root and stem diameters recorded for the end of the years 1988–1994 and attributed them to the first period. In the same way, all diameters from 1994 to 2000 had to be accounted to the second period. Note that the diameters of 1994 turn

up in both periods as they represent the endpoint of the first period and the start point of the second period at the same time. We took the natural logarithms of all stem diameters dshoot and all root diameters droot and centred them on individual stem level and individual root level by subtracting their period-wise means:

$$\text{lc.dshoot}_{ijklp} = \ln(\text{dshoot}_{ijklp}) - \overline{\ln(\text{dshoot}_{ijkp})} \quad (4)$$

and

$$\text{lc.droot}_{ijklp} = \ln(\text{droot}_{ijklp}) - \overline{\ln(\text{droot}_{ijkp})} \quad (5)$$

Here, the indices i, j, k, l, t mean plot, subplot, tree, root and year, respectively. The index p denotes the moist (1989–1994) or the dry increment period (1995–2000).

The centred logarithmic root and stem diameters as obtained from Equations 4 and 5 were included in the following mixed linear model

$$\begin{aligned} \text{lc.droot}_{ijklp} &= \beta_1 \cdot \text{lc.dshoot}_{ijklp} + \beta_2 \cdot \text{lc.dshoot}_{ijklp} \cdot \text{per}_p + \beta_3 \\ &\cdot \text{lc.dshoot}_{ijklp} \cdot \ln(\text{si}_{ijk}) + \beta_4 \cdot \text{lc.dshoot}_{ijklp} \cdot \text{per}_p \\ &\cdot \ln(\text{si}_{ijk}) + (b_i + b_{ij} + b_{ijk} + b_{ijkl}) \cdot \text{lc.dshoot}_{ijklp} \\ &+ \varepsilon_{ijklp} \end{aligned} \quad (6)$$

where per is a dummy variable, indicating the moist increment period with $\text{per} = 0$, and the dry period with $\text{per} = 1$, respectively. $\beta_1 + \beta_2 \cdot \text{per} + \beta_3 \cdot \ln(\text{si}) + \beta_4 \cdot \text{per} \cdot \ln(\text{si})$ is a site and period specific estimation of $\alpha_{r,s}$. As, in contrast to the model shown in Equation 1, the time series of interest are very short, we didn't use serial correlation models as in Equation 2, but included the random effects $b_{i, \dots, ijkl}$ which represent the nesting levels plot, subplot, tree and root ($b_{i, \dots, ijkl} \sim N(0, \tau_{1, \dots, 4}^2)$). The ε are i.i.d. error terms. As for the long-term effects model (Equation 1), the residuals were assessed visually.

For all statistical evaluations, we used the free software R, version 2.13.1 (R Development Core Team, 2011), especially the package nlme by Pinheiro et al. (2011).

Results

Growth relation between stem and coarse roots

The $\ln(\text{droot}) - \ln(\text{dshoot})$ -trajectories of all analysed roots provide the basis for the statistical evaluation. In Figure 3a, we exemplify how we combined the results of the increment measurements of all three individual roots with the stem growth. That yielded three, in few cases only two

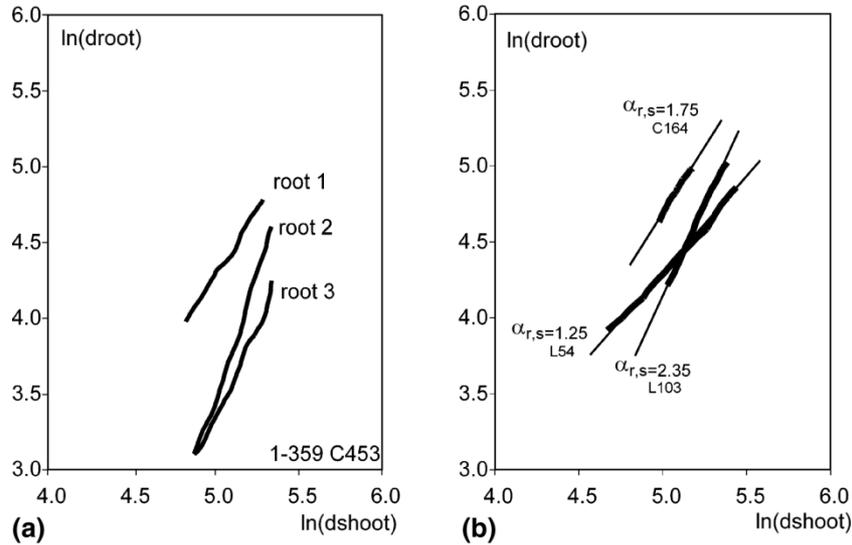


Figure 3. Example of coarse root diameter–stem diameter relationships plotted in the double-logarithmic grid. (a) Observed $\ln(\text{droot})$ – $\ln(\text{dshoot})$ -trajectory for the three main coarse roots of tree No. C 453 (tree height 16.1 m, trunk diameter 20.8 cm, root diameters 13, 10 and 7 cm, tree age 64 years). (b) Observed trajectory and linear fit for the $\ln(\text{droot})$ – $\ln(\text{shoot})$ -relationship of three selected trees on poor to rich sites (No. L 54: $h = 21.9$ m, $d = 23.0$ cm, mean diameter root = 12.9 cm, tree age 61 years; No. C 164: $h = 19.0$ m, $d = 17.7$ cm, mean diameter root = 14.6 cm, tree age 73 years; No. L 103: $h = 16.4$ m, $d = 21.8$ cm, mean diameter root = 15.2 cm, tree age 52 years). The $\alpha_{r,s}$ values of 1.25, 1.75 and 2.35 indicate the range in which most of the slopes are lying.

$\ln(\text{droot})$ – $\ln(\text{dshoot})$ -trajectories per tree. The mean trajectory of the measured root growth per tree is shown exemplarily in Figure 3b for three different trees. From Figures 3 and 5, which shows the trajectories for all 155 roots, can be seen that the relation between root and shoot growth is generally linear in a log–log scale. The specific slope of such a trajectory depends on site quality and estimates the allometric relation between droot and dshoot.

Long-term root–shoot allometry

Before fitting Equation 1 simultaneously to the whole data, we explored the distribution and the range of the long-term allometric slopes $\alpha_{r,s}$ by simply fitting the model $\ln(\text{droot}) = \ln(a) + \alpha_{r,s} \cdot \ln(\text{dshoot}) + \varepsilon$ to each individual droot–dshoot series separately by ordinary least squares regression. Figure 4 shows the empirical probability density function of the estimated $\alpha_{r,s}$ values. The range of $\alpha_{r,s}$ roughly covers the span between 0 and 8 and thus reveals a remarkable plasticity of the long-term root–shoot relationship. However, there is a pronounced peak at $\alpha_{r,s} = 1.75$ which indicates a kind of species-specific or regional-specific set point value.

The best maximum likelihood fits of Equation 1 were obtained including an MA(2) serial correlation model, in other words with q from Equation 2 set to $q = 2$. The parameter estimates are shown in Table III. Evidently, parameter $\beta_2 = -0.2741$ reflects a highly significant modification of the root–shoot relationship by the site conditions. Due to the

negative β_2 , the $\alpha_{r,s}$ -value, that is the slope of the $\ln(\text{droot})$ – $\ln(\text{dshoot})$ -relationship is steeper on poor sites and shallower on richer sites. This significant reduction of biomass investment into coarse roots with increasing site index is shown in Figure 5. The combination of the $\ln(\text{droot})$ – $\ln(\text{dshoot})$ -relationships modelled as straight lines with slopes $\alpha_{r,s} = 1.59$ – 2.03 (black) and the measurement results (grey) display how Equation 1 with the obtained

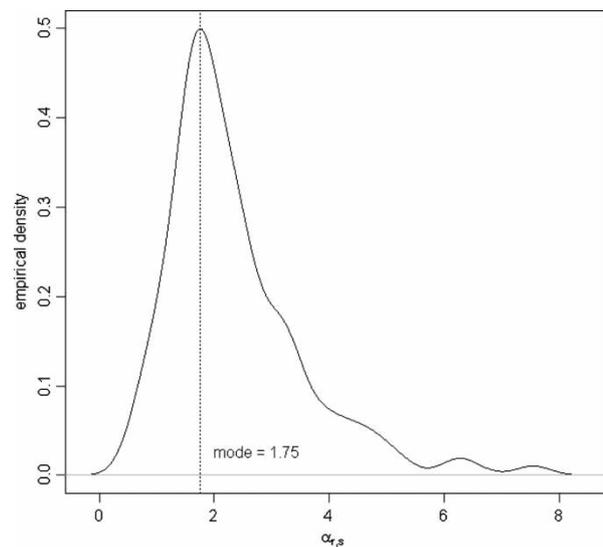


Figure 4. Empirical probability density of the long-term allometric exponent $\alpha_{r,s}$ resulting from separate OLS fits for each $\ln(\text{droot})$ – $\ln(\text{dshoot})$ time series. The mode of the density function is $\alpha_{r,s} = 1.75$.

Table III. Parameters of the fitted model from Equation 1 combined with an MA(2) serial correlation model (Equation 2), and a variance function (Equation 3).

Parameter	Value	Standard error
β_0	-2.9458***	0.0922
β_1	2.5743***	0.1868
β_2	-0.2741***	0.0651
θ_1	1.8323	
θ_2	0.9999	
δ	-0.7399	
τ_1	0.2248	
τ_2	0.1499	
τ_3	0.3355	

τ_1, \dots, τ_3 : Standard deviations of the random effects.

*, ** and *** indicate significance levels of $p < 0.05, 0.01$ and 0.001 , respectively.

β -values covers the slope and the range of the observed trajectories. For $si = 16.4$ which represents mean site conditions, the model predicts $\alpha_{r,s} = 1.81$, which is near to the mode of the $\alpha_{r,s}$ -distribution (1.75) obtained by separate individual fits (Figure 4). The estimates for the serial correlation model's parameters θ_1 and θ_2 (Equation 2; Table III) follow the invertibility conditions as shown by Anderson (1976). According to Anderson, marginal non-invertibility that is possibly indicated by θ_2 being very near to 1, is not problematic in practice. The variance function parameter $\delta < 0$ (Equation 3; Table III) indicates a decreasing residual variance with age.

When selecting the model formulation as shown in Equation 1, it was an important decision whether to include the influence of site conditions $\ln(si)$ as an interaction with $\ln(dshoot)$ only (Equation 1), or to include it as a main effect in addition. The latter would mean a site influence not only on $\alpha_{r,s}$, but also on the allometric factor a . A fit with this additional effect and all other settings the same otherwise, yielded a clearly non-significant main effect for $\ln(si)$ ($p = 0.25$) and a small AIC difference of 0.67 in favour of the simpler model (Equation 1).

Short-term drought effects on $\alpha_{r,s}$

The parameter estimates for the model shown in Equation 6 (Table IV) reveal two counteracting trends. First, parameter β_2 is significantly greater than zero, indicating an increase of $\alpha_{r,s}$ under unfavourable conditions which matches well with the insights drawn from the long-term data. However, β_4 is significantly smaller than zero which means that the better the site, the more the former trend is weakened or even reversed. Figure 6 illustrates this outcome: On a poor site ($si = 11.0$) the model predicts $\alpha_{r,s} = 2.27$ for the favourable growth period, and $\alpha_{r,s} = 2.76$ for the dry period, indicating a stronger relative investment in root growth under adverse conditions. For a rich site ($si = 24.5$) the model expects $\alpha_{r,s} = 3.08$ in the moist and $\alpha_{r,s} = 2.02$ in the dry period. Obviously, root-shoot allometry reacts site-specifically to a short-term change of site conditions, and this happens in a way that may even counteract the long-term trend.

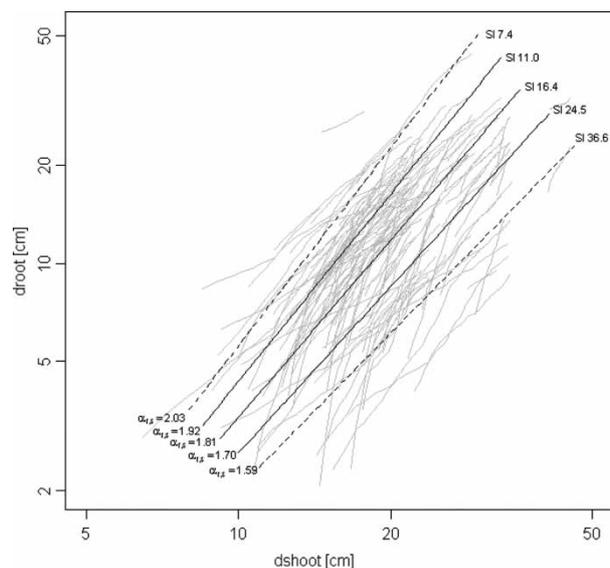


Figure 5. Long-term site dependent root-shoot diameter allometry as predicted by the fitted model according to Equation 1 and Table III. Solid lines: Site conditions as approximately covered by our data. SI: Site index after Thrower & Associates Ltd. (1994). Dashed lines: model extrapolations for very rich and very poor site conditions. Grey lines: measured trajectories.

Table IV. Model fit according to Equation 6: Parameters β_1, \dots, β_4 , and estimated standard deviations τ_1, \dots, τ_4 of the random effects.

Parameter	Value	Standard error
β_1	-0.1790	2.5972
β_2	5.1695***	0.4978
β_3	1.0184	0.9062
β_4	-1.9474***	0.1721
τ_1	0.3703	
τ_2	0.0002	
τ_3	0.6126	
τ_4	1.0626	

*, ** and *** indicate significance levels of $p < 0.05$, 0.01 and 0.001, respectively.

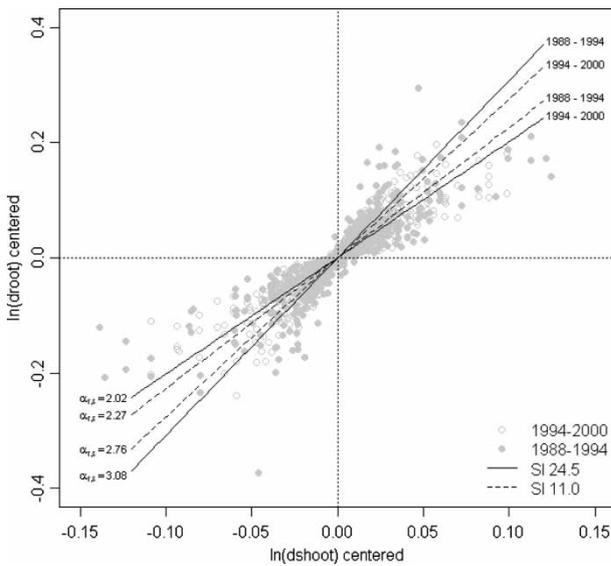


Figure 6. Centred logarithmic root–shoot diameter pairs (Equations 4 and 5) and site-dependent reaction of $\alpha_{r,s}$ on climatically favourable (1988–1994) and less favourable (1995–2000) conditions as predicted by the fitted model according to Equation 6 and Table IV. SI 24.5 and SI 11.0 represent a rich and a poor site, respectively.

Discussion

The allometric relationship between coarse root and shoot growth contributes to better understanding the consistency between the APT and the OPT (see introduction). Obviously, as we could show, the allometric exponent of the coarse root–shoot relationship is depending on site conditions. In other words, the allometric exponent is not constant as assumed by APT. However, it seems to be rather stable under long-term acting site conditions. Our data reveal a clear tendency, that the steepness of the slope is high on poor sites and rather shallow on rich sites. By this, the trees seem to optimise their root–shoot allometry depending on short-term changing site conditions whereas on a given site they rather

follow constantly the site-specific slope (schematically shown in Figure 7). The extent of detected short-term reactions even depends on the long-term site conditions. This underlines the high degree of morphological plasticity of trees (Weiner, 2004). Note that the slopes we report may be different for other tree species.

Our finding that on poor sites the slope steepens more pronouncedly when confronted with short-term unfavourable conditions than on richer sites seems plausible. On richer sites, which do not limit the trees so much even in adverse times, this reaction is weaker. However, there seems to be no intuitive explanation for the reverse reaction on rich sites. Further studies are needed to affirm or dismiss this effect.

Root–shoot allometry versus root–shoot ratios

Our results show that when plants grow larger coarse root biomass increases quicker than stem biomass. On average, root biomass grows by 1.75% when shoot biomass increases by 1% ($\alpha_{r,s} = 1.75$). Only for sites with ample water and nutrient supply applies $\alpha_{r,s} < 1.0$. Values of $\alpha_{r,s}$ above 1.0 as well as its increase when below-ground resources become scarce is in line with other allometric studies (see e.g. Bloom et al., 1985; Nikolova et al., 2011; Shipley & Meziane, 2002). Such findings have considerable consequences for the interpretation of studies which base their findings on root–shoot ratios (e.g. Meier & Leuschner, 2008a,b). Any positive allometric exponents indicate, that the root–shoot ratio increases continuously with plant size. When the root–shoot ratios of two groups of plants are compared (e.g. stressed versus unstressed plants) and the unstressed plants' size is ahead of the stressed ones the root–shoot ratios of the unstressed plants should be higher simply because of their advanced size. In other words, one should not jump to conclusions that a lower root–shoot ratio of stressed plants means changed allometry and inconsistency with allometric theory. Rather before a comparison of the root–shoot ratios of two groups the size effect should be eliminated as follows:

Suppose root biomass scales with an exponent of $\alpha_{r,s} = 1.75$ to shoot biomass $w_r \propto w_s^{1.75}$, then the root:shoot ratio $r_{r,s}$ would increase with size like $r_{r,s} \propto w_r/w_s \propto w_s^{0.75}$. So, if shoot biomass – used as indicator of plant size – increases by 1% the root–shoot ratio does not remain constant but increases by 0.75%.

If measurement would yield $r_{r,s,1} = 1.1$ for trees under drought stress (group 1) and $r_{r,s,2} = 1.30$ for the reference (group 2) a different allocation key between the groups seems obvious. In this case that might be interpreted as a contradiction to the OPT,

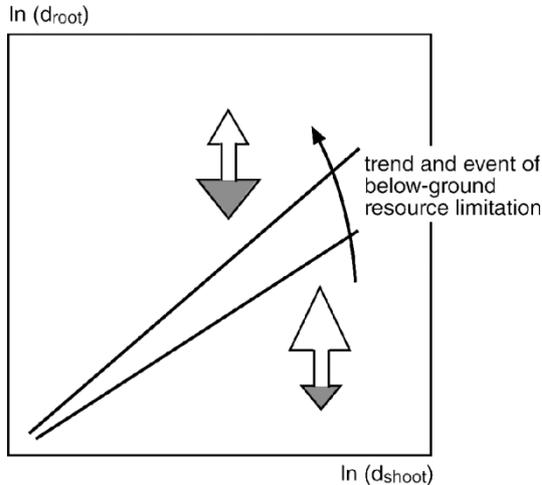


Figure 7. Allometric relationship between diameter growth of coarse roots and shoot in schematic representation. Trends and events of below-ground resource limitation shift the allocation pattern towards root growth, that is the allometric relationship becomes steeper. The more limited the below-ground resources the higher the portion of biomass allocation to coarse roots and vice versa.

as trees seem to invest less into root growth when scarcely supplied with water. However, if we consider that tree size in group 1 is just $w_{s,1} = 4$ kg compared with $w_{s,2} = 5$ kg in group 2 we can calculate the ratio which would be expected for stressed trees after elimination of the mere size effect and assuming $\alpha_{r,s} = 1.75$ ($\hat{r}_{r,s,1} = r_{r,s,1} (w_{s,2}/w_{s,1})^{\alpha_{r,s}} = 1.1(5/4)^{0.75} = 1.30$). So, the ratio expected for the group 1 trees after elimination of the size effect is $\hat{r}_{r,s,1} = 1.30 = r_{r,s,2}$. In other words, the ratio of group 1 is different from that of group 2, but behind the difference is merely the slowing down of size growth in group 1 and not an altered biomass allocation key.

In this way, the size effect can be eliminated, and allocation effects can be distinguished from simple size effects. There is only evidence of group differences when the group means still differ after elimination of the size effect. Our study provides evidence that root–shoot development is non-isometric (i.e. $\alpha_{r,s} \neq 1$), which may be confused with simple size effects when root–shoot ratios are not adjusted as for example by Meier and Leuschner (2008a,b).

Methodological perspectives

Knowledge on root growth of mature trees is mainly limited by the highly complicated sampling procedures. A new method of combined root–shoot analysis by increment boring has been successfully applied along an ecological gradient in a boreal forest ecosystem. Without exhausting root excavations,

which are often hardly possible or realistic, this new method delivers useful information and indication on the root–shoot allometry of trees growing under different site conditions. By increment boring the effort is much lower, although only parts of the root system and thereby only parts of the root growth are sampled. We see a special potential in combining traditional total root excavations and root sampling by increment boring. This bears the potential to upscale from coarse root attributes to total root information. Additionally, it is a basis for an efficient scaling from easy accessible tree variables like diameter and height to otherwise hardly available and accessible root quantities. With future studies we want to extend our measurements to a broader number of species and a more expanded site spectrum.

Total biomass and carbon storage

The revealed root–shoot dynamics mean that differences in above-ground biomass productivity, normally addressed by foresters by means of site index, is less distinct, when we consider the sum of above- and below-ground biomass productivity. In less favourable years and on poor sites tree growth may be just more geared towards the exploitation of below-ground resources, while the productivity in total is not much different from the one under better conditions. The revealed principles and functions could be useful for estimation of species and site-specific biomass and carbon sequestration depending on easily accessible variables like tree diameter or tree height. This may be an important contribution for estimation of carbon storage of forest stands and carbon balance of forest ecosystems.

We conclude that:

- (1) The reactions on stress, no matter whether chronic or acute, can appear much less pronounced when being measured on total tree level in comparison with above ground level. These findings stimulate rethinking about the suitable approach of measuring and modelling tree and stand productivity, fitness and their dependency from site conditions. Stress, seen with “the plant’s eye” can be rather different from stress indicated by above ground productivity measures.
- (2) Combined trunk and coarse root increment coring, even when restricted to the three tallest roots, opens new insights into internal allocation patterns and their modification by external driving variables. For upscaling from coarse roots to the total root, our sampling method might be extended to more roots per tree or be

combined with root excavations and ingrowth core approaches.

- (3) The long-term root–shoot growth trajectories substantiate the APT as under given site conditions the root–shoot partitioning changes solely with plant size. The systematic change of the steepness of the root–shoot trajectory in dependence on chronic or acute resource limitation provides evidence for the OPT. A consistent interpretation of the shown root–shoot reaction patterns suggests a link between both APT and OPT.
- (4) Assuming that the three coarse roots represent the root–shoot relationship on different sites, trees allocate more into anchoring and stability on poor compared with rich sites. That suggests a trade-off between above ground productivity and storm stability; that is between growth and defence.
- (5) Assuming again that the three coarse roots represent the root–shoot relationship the revealed allocation pattern means that trees of a given size (dbh, height) on poor sites have much more below-ground mass than trees of the same size on rich sites. Studies like ours can contribute to developing site-dependent biomass functions or expansion factors which enable a more accurate estimation of below-ground biomass and C-storage in forest ecosystems.

Acknowledgements

The authors wish to thank the Deutsche Forschungsgemeinschaft for providing funds for forest growth and yield research as part of the Sonderforschungsbereich SFB 607 “Growth and Parasite Defense” and the British Columbia Ministry of Forests, Mines and Lands and Natural Resource Operations for funding the Canadian-German cooperative project, Crown competition, crown efficiency, tree growth and site type: quantification with terrestrial LIDAR“ (No. Y091162). We are grateful to Vanessa Foord from BC Forest Service, Prince George for providing condensed climate data. Thanks are also due to Moritz Pretzsch for uncovering and sampling the roots, Ulrich Kern for the graphical artwork, and three anonymous reviewers for their constructive criticism.

References

- Anderson, O. (1976). *Time series analysis and forecasting. The Box-Jenkins approach*. London and Boston: Butterworths, 182 p.
- Banner, A., MacKenzie, W., Haeussler, S., Thomson, S., Pojar, J., & Trowbridge, R. (1993). A field guide to site identification and interpretation for the Prince Rupert Forest Region. BC
- Ministry of Forest and Range, Victoria, BC. *Land management handbook* 26, 503 p.
- Bertalanffy, L. von (1951). Theoretische Biologie II. Band. Stoffwechsel, Wachstum. [*Theoretical biology II. Volume II. Metabolism, growth*]. Bern: A. Francke AG.
- Bloom, A. J., Chapin, F. S. & Mooney, H. A. (1985). Resource limitation in plants and economic analogy. *Annual Review of Ecology and Systematics*, 16, 363–392.
- Bolte, A., Rahmann, T., Kuhr, M., Pogoda, P., Murach, D. & Gadow, K. V. (2004). Relationships between tree dimension and coarse root biomass in mixed stands of European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* [L.] Karst.). *Plant and Soil*, 264(1–2), 1–11.
- Burnham, K. P. & Anderson, D. R. (2004). Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods & Research*, 33(2), 261–304.
- Cochran, P. H. (1985). Soils and productivity of lodgepole pine. In: D. M. Baumgartner, R. C. Krebill, J. T. Arnott, & G. F. Weetman (Eds.), *Lodgepole pine: The species and its management*, pp. 89–93. Pullman, Wash: Cooperative Extension, Washington State University.
- Comeau, P. G. & Kimmins, J. P. (1989). Above- and below-ground biomass and production of Lodgepole pine on sites with differing soil moisture regimes. *Canadian Journal of Forest Research*, 19, 447–454.
- Drexhage, M., Huber, F. & Colin, F. (1999). Comparison of radial increment and volume growth in stems and roots of *Quercus petraea*. *Plant and Soil*, 217, 101–110.
- Enquist, B. J., Brown, J. H. & West, G. B. (1998). Allometric scaling of plant energetics and population density. *Nature*, 395, 163–165.
- Enquist, B. J. & Niklas, K. J. (2001). Invariant scaling relations across tree-dominated communities. *Nature*, 410, 655–660.
- Enquist, B. J. & Niklas, K. J. (2002). Global allocation rules for patterns of biomass partitioning in seed plants. *Science*, 295, 1517–1520.
- Enquist, B. J., West, G. B. & Brown, J. H. (2009). Extensions and evaluations of a general quantitative theory of forest structure and dynamics. *Proceedings of the National Academy of Sciences*, 106(17), 7046–7051.
- Environment Canada. (2010). National climate data archive. Retrieved August 13, 2010, from http://climate.weatheroffice.gc.ca/climateData/canada_e.html
- ETCCDI. (2011). Climate extreme indices. SmithersA Station. International CLIVAR Project Office, Southampton. Retrieved December 12, 2011, from <http://cccma.seos.uvic.ca/ETCCDMI/data.shtml>
- Gorham, E. (1979). Shoot height, weight and standing crop in relation to density of monospecific plant stands. *Nature*, 279, 148–150.
- Helms, J. A. (1998). *The dictionary of forestry*. Bethesda, MD: The Society of American Foresters.
- Jentsch, A., Kreyling, J. & Beierkuhnlein, C. (2007). A new generation of climate change experiments: Events, not trends. *Frontiers in Ecology and Environment*, 5(7), 365–374.
- Keyes, M. R. & Grier, C. C. (1981). Above-and below-ground net production in 40-years-old Douglas-fir stands on low and high productivity sites. *Canadian Journal of Forest Research*, 11, 599–605.
- Krajina, V. J., Klinka, K. & Worrall, J. (1982). *Distribution and ecological characteristics of trees and shrubs of British Columbia*. Vancouver, BC: Faculty of Forestry, University of British Columbia.
- Kranabetter, J. M., Dawson, C. R. & Dunn, D. E. (2007). Indices of dissolved organic nitrogen, ammonium and nitrate across productivity gradients of boreal forests. *Soil Biology & Biochemistry*, 39, 3147–3158.

- Kranabetter, J. M. & Simard, S. W. (2008). Inverse relationship between understory light and foliar nitrogen along productivity gradients of boreal forests. *Canadian Journal of Forest Research*, 38, 2487–2496.
- Krause, C. & Eckstein, D. (1993). Dendrochronology of roots. *Dendrochronologia*, 11, 9–23.
- Krause, C. & Morin, H. (1995). Changes in radial increment in stems and roots of balsam fir [*Abies balsamea* (L.) Mill.] after defoliation spruce budworm. *The Forestry Chronicle*, 71(6), 747–754.
- Krause, C. & Morin, H. (1999). Tree-ring pattern in stems and root systems of black spruce (*Picea mariana*) caused by spruce budworms. *Canadian Journal of Forest Research*, 29, 1583–1591.
- Matyssek, R., Wieser, G., Ceulemans, R., Rennenberg, H., Pretzsch, H., Haberer, K. et al. (2010). Enhanced ozone strongly reduces carbon sink strength of adult beech (*Fagus sylvatica*) – resume from the free-air fumigation study at Kranzberg Forest. *Environmental Pollution*, 158(8), 2527–2532.
- Meier, I. C. & Leuschner, C. H. (2008a). Genotypic variation and phenotypic plasticity in the drought response of fine roots of European beech. *Tree Physiology*, 28, 297–309.
- Meier, I. C. & Leuschner, C. H. (2008b). Belowground drought response of European beech: Fine root biomass and carbon partitioning in 14 mature stands across a precipitation gradient. *Global Change Biology*, 14, 2081–2095.
- Müller, I., Schmid, B. & Weiner, J. (2000). The effect of nutrient availability on biomass allocation patterns in 27 species of herbaceous plants. *Perspectives in Plant Ecology, Evolution and Systematics*, 3(2), 115–127.
- Niklas, K. J. (2004). Plant allometry: Is there a grand unifying theory? *Biological Reviews of the Cambridge Philosophical Society*, 79, 871–889.
- Nikolova, P. S., Zang, C. H., & Pretzsch, H. (2011). Combining tree-ring analysis on stems and coarse roots to study the growth of forest trees: A case study on Norway spruce (*Picea abies* [L.] H. Karst). *Trees Structure and Function*, 25(5), 859–872.
- NOAA. (1996). Climate conditions during the 1995.96 Northern Hemisphere Winter. In: Special climate summary-96/1. Retrieved December 12, 2011, from http://www.cpc.ncep.noaa.gov/products/special_summaries/96_1/
- Ouimet, R., Moore, J. D. & Duchesne, L. (2008). Effects of experimental acidification and alkalization on soil and growth and health of *Acer saccharum* Marsh. *Journal of Plant Nutrition and Soil Science*, 171, 858–871.
- Pinheiro, J. C. & Bates, D. M. (2000). *Mixed-effects Models in S and S-PLUS*. 528 p. Springer.
- Pinheiro, J. C., Bates, D. M., DebRoy, S., Sarkar, D. and the R Development Core Team. (2011). nlme: Linear and non-linear mixed effects models. R package version 3.1-101. Retrieved July 29, 2011, from <http://cran.r-project.org/web/packages/nlme/index.html>
- Pojar, J. (1996). Environment and biogeography of the western boreal forest. *The Forestry Chronicle*, 72, 51–58.
- Pretzsch, H. (2009). *Forest dynamics, growth and yield. From measurement to model*. Berlin, Heidelberg: Springer, 664 p.
- Pretzsch, H., Block, J., Dieler, J., Dong, P. H., Kohnle, U., Nagel, J. et al. (2010). Comparison between the productivity of pure and mixed stands of Norway spruce and European beech along an ecological gradient. *Annals of Forest Science*, 67, doi:10.1051/forest/2010037.
- Pretzsch, H. & Dieler, J. (2010). The dependency of the size-growth relationship of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* [L.]) in forest stands on long-term site conditions, drought events, and ozone stress. *Trees*, 25(3), 255–369.
- Pretzsch, H. & Dieler, J. (2012). Evidence of variant intra- and interspecific scaling of tree crown structure and relevance for allometric theory, *Oecologia*. doi: 10.1007/s00442-011-2240-5.
- R Development Core Team. (2011). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. ISBN 3-900051-07-0.
- Rötzer, T., Seifert, T. & Pretzsch, H. (2009). Modeling above and below ground carbon dynamics in a mixed beech and spruce stand influenced by climate. *European Journal of Forest Research*, 128, 171–182.
- Shipley, B. & Meziane, D. (2002). The balanced-growth hypothesis and the allometry of leaf and root biomass allocation. *Functional Ecology*, 16, 326–331.
- Thrower, J. S. & Associates Ltd. (1994). Revised height-age curves for lodgepole pine and interior spruce in British Columbia. Report to the B.C Ministry of Forests and Range, Research Branch, Victoria, B.C. 27 p. Retrieved July 29, 2011, from <http://www.for.gov.bc.ca/hre/sitetool/>
- Weiner, J. (2004). Allocation, plasticity and allometry in plants. Perspectives in Plant Ecology. *Evolution and Systematics*, 6(4), 207–215.
- Weiner, J. & Thomas, S. C. (1992). Competition and allometry in three species of annual plants. *Ecology*, 73(2), 648–656.
- West, G. B., Brown, J. H. & Enquist, B. J. (1997). A general model for the origin of allometric scaling laws in biology. *Science*, 276, 122–126.
- West, G. B., Enquist, B. J. & Brown, J. H. (2009). A general quantitative theory of forest structure and dynamics. *Proceedings of the National Academy of Science of the United States of America*, 106(17), 7040–7045.
- Yoda, K. T., Kira, T., Ogawa, H. & Hozumi, K. (1963). Self-thinning in overcrowded pure stands under cultivated and natural conditions. *Journal of the Institute of Polytechnics. Osaka City University. Series D. Biology*, 14, 107–129.
- Yoda, K. T., Shinozaki, K., Ogawa, J., Hozumi, K. & Kira, T. (1965). Estimation of the total amount of respiration in woody organs of trees and forest communities. *Journal of the Institute of Polytechnics. Osaka City University. Series D. Biology*, 16, 15–26.
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A. & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. Springer, 574 p.