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Biomass partitioning and growth efficiency in four naturally regenerated forest tree species.

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Abstract

Current forest growth models and yield tables are almost exclusively based on data from mature trees, reducing their applicability to young and developing stands. To address this gap, young European beech, sessile oak, Scots pine and Norway spruce trees approximately 0 to 10 years old were destructively sampled in a range of naturally regenerated forest stands in Central Europe. Diameter at base and height were first measured in situ for up to 175 individuals per species. Subsequently, the trees were excavated and dry biomass of foliage, branches, stems and roots was measured. Allometric relations were then used to calculate biomass allocation coefficients (BAC) and growth efficiency (GE) patterns in young trees. We found large differences in BAC and GE between broadleaves and conifers, but also between species within these categories. Both BAC and GE are strongly age-specific in young trees, their rapidly changing values reflecting different growth strategies in the earliest stages of growth. We show that linear relationships describing biomass allocation in older trees are not applicable in young trees. To accurately predict forest biomass and carbon stocks, forest growth models need to include species and age specific parameters of biomass allocation patterns.

Keywords:

Biomass allocation, forest trees, growth efficiency, allometric equations

Introduction

Accurate estimates of forest tree biomass are growing in importance. In view of climate change, scientists are starting to consider all tree biomass compartments, both for their energy and carbon content (Nabuurs, Garza-Caligaris, Kanninen, Karjalainen, Lapvetelainen et al., 2002). Traditionally, only merchantable biomass contained in the stem was of interest and a wide range of methods was developed for its estimation (Hakkila, 1989). Since biomass (carbon) allocation plays a critical role in forest ecosystem carbon cycling (Litton, Raich & Ryan, 2007), we urgently need to develop and improve the techniques for rapid and reliable assessment of non-stem forest biomass (Lehtonen, 2005; Pregitzer & Euskirchen, 2004). One of the most efficient ways to achieve this goal is to use allometric equations based on tree diameter and/or height. The equations and biomass allocation patterns estimated for larger and older trees are not generally applicable to young trees, hence the need for biomass models of forest trees in the initial stages of their growth (Wirth, Schumacher & Schulze, 2004).

As trees grow, age- and size-related changes in tree shape and form alter the contribution of tree biomass compartments to whole-tree biomass increment (Bartelink, 1998). The difference in biomass production and allocation between young and mature trees is often quite stark. As trees mature, the ratio of fine roots to foliage significantly increases (Ryan & Waring, 1992), the rate of stem growth decreases relative to that of foliage and fine roots (Waring & Schlesinger, 1985), while biomass accumulation in stem and coarse roots increases (Wieser, 2007). Over recent decades, the area of regenerating and young forests has been significantly expanding due to the damage inflicted on forests by climate change and its inherent negative phenomena (storms, drought episodes, forest fires). To account for these changes, we urgently need to close the gap in datasets and in models related to small tree biomass and its partitioning.

From initial establishment, through competitive growth and into maturity, the foliage requirement relative to other biomass compartments changes (Mäkelä & Valentine, 2001). Tree crown structure, characterised by its size (biomass or surface area) and distribution of individual crown elements (branches, shoots and foliage), is a key variable in forest ecology. The relationship between foliage and biomass growth is strongly related to productivity. Often termed “growth efficiency” (GE; e.g. Gersonde & O’Hara, 2005), it can be expressed as stem biomass increment per unit foliage area or foliage biomass. At present, we are lacking inter-specific comparisons of GE that could help us to elucidate ecological demands and growth strategies of tree species (Jack, Sheffield & McConville, 2002).

This study is principally aimed at using allometric equations to calculate biomass allocation patterns and growth efficiency in main biomass compartments of young European beech (*Fagus sylvatica* L.), sessile oak (*Quercus petrea* [Matt.] Liebl), Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* [L.] Karst) trees. The chosen species represent key components of temperate European forests and such models would have wide applicability in European forestry and carbon accounting. Alongside presenting the biomass allocation models, the main contribution of this work is thus a demonstration of the suitability of allometric equations for inter-specific comparisons of biomass allocation and growth efficiency.

Material and methods

Site and stand characteristics

We selected forest stands in Central Slovakia as the principal area for the field measurements. For each species, we purposefully excluded the localities found at the extremes of their natural distribution in order to ensure the widest possible applicability of our allometric relations. For each species, we identified seven separate stands originating from natural regeneration where all mature trees had been removed (Table 1). All stands belonged to the first age class (0-10 years) and the stocking rate of the target tree species (beech, oak, pine and spruce) was always 90-100% (see Appendix A: Tables 1-4). A circle of ca. 400 m^2 was randomly positioned within each stand and all measurements were carried out on trees found within this area.

Tree measurements

All sampling was carried out during the summer months of 2005-2007, when maximum foliage was present in all species to support the validity of inter-specific comparisons. To assess tree height and diameter distribution at each site, 100-150 randomly selected trees were measured. These were evenly divided into 10 height classes and 2-3 random individuals from each height class were destructively sampled. This resulted in 20-25 sampled individual trees per site, or 160-175 per species across all seven sites. Before excavation, Diameter At Base (DAB) was measured *in situ* twice for each sample tree in two perpendicular directions, together with tree height.

The trees selected for destructive sampling were excavated with care to include all roots over 1 mm in diameter and transported to the laboratory. Trees were then divided into roots (including the below-ground part of the stump), stems, branches and foliage. All samples were first left to dry in a well-ventilated laboratory at room temperature for about one month and then dried at 105 °C until constant weight. Size and weight measurements were used to calculate allometric relations based on DAB and tree height.

Biomass functions

The majority of allometric equations and biomass models use Diameter at Breast Height (DBH) as the standard predictor variable. Due to the small size of our sample trees, we utilised DAB as a substitute for this universal forest mensuration parameter. Despite the fact that height is not usually used in tree biomass functions and models, we used it as a predictor since it might offer several benefits in relation to small trees. It is substantially easier to measure than DAB in very young forest stands and by using height it is possible to link up models describing initial growth stages with models of fully grown stands, rather than having separate models based on DAB and DBH.

In this work we tested the predictive power of the following functions (e.g. Tobin, Čermák, Chiatante, Danjon, Di Iorio et al. 2007):

$$B = e^{\left(b_0 + b_1 \ln DAB\right)} \lambda \tag{1}$$

$$B = e^{\left(b_0 + b_1 \ln h\right)} \lambda \tag{2}$$

$$B = e^{\left(b_0 + b_1 \ln DAB + b_2 \ln h\right)} \lambda \tag{3}$$

where

B is dry biomass, DAB is diameter at base, h is tree height, b_0, b_1 and b_2 are model coefficients and λ is the logarithmic transformation bias (e.g. Pajtík, Konôpka & Lukac, 2008).

Following on from this step, we used equations (1-3) to calculate biomass allocation coefficients (BAC) and growth efficiency (GE) in relation to DAB and tree height. First, allometric models based on equations (1-3) were used to calculate biomass compartment increments for all four tree species. Biomass increment of the whole tree can be expressed as a sum of increments of all compartments:

$$\Delta B_t = \Delta B_s + \Delta B_f + \Delta B_b + \Delta B_r \tag{4}$$

where

ΔB_t is the increment of total tree biomass, ΔB_s the growth of stem biomass, ΔB_f the growth of foliage biomass, ΔB_b the growth of branch biomass and ΔB_r the growth of root biomass.

However, since stem biomass increment is the most used and measured type of increment in forestry, ΔB_f, ΔB_b and ΔB_r can be readily expressed as:

$$\Delta B_f = BAC_f . \Delta B_s \tag{5}$$

$$\Delta B_b = BAC_b . \Delta B_s \tag{6}$$

$$\Delta B_r = BAC_r . \Delta B_s \tag{7}$$

where

BAC_i is the biomass allocation coefficient; BAC_f for foliage, BAC_b for branches and BAC_r for roots.

In other words, coefficient BAC_i describes the ratio between a particular biomass compartment increment (ΔB_f, ΔB_b, ΔB_r) and stem biomass increment (ΔB_s). Biomass increment is usually computed for a certain time period, however, using allometric equations (1-3) we can calculate the value of BAC_i for a specific DAB. The biomass increment of a component *i* is calculated as the difference in biomass at DAB and at DAB plus annual diameter increment. As an example, we used three levels of annual DAB increment of 2.5, 5.0 and 7.5 mm and annual height increment of 0.1, 0.3 and 0.5 m. These annual increments represent ranges typically found in all four species of interest, as predicted by the yield tables (Halaj & Petráš, 1998). The average annual DAB increment at our sites was 3.0 mm in beech, 4.5 mm in oak, 5.7 mm in pine and 4.6 mm in spruce. We used allometric equations (1-3) to expand the BAC$_i$ ratio (8) to the following forms (9-11):

$$BAC_i = \frac{\Delta B_i}{\Delta B_s} \qquad (8)$$

$$BAC_i = \frac{B_{i(DAB+\Delta DAB)} - B_{i(DAB)}}{B_{s(DAB+\Delta DAB)} - B_{s(DAB)}} = \frac{(e^{(b_{i0}+b_{i1}\ln(DAB+\Delta DAB))}\lambda) - (e^{(b_{i0}+b_{i1}\ln DAB)}\lambda)}{(e^{(b_{s0}+b_{s1}\ln(DAB+\Delta DAB))}\lambda) - (e^{(b_{s0}+b_{s1}\ln DAB)}\lambda)} \qquad (9)$$

$$BAC_i = \frac{B_{i(h+\Delta h)} - B_{i(h)}}{B_{s(h+\Delta h)} - B_{s(h)}} = \frac{(e^{(b_{i0}+b_{i1}\ln(h+\Delta h))}\lambda) - (e^{(b_{i0}+b_{i1}\ln h)}\lambda)}{(e^{(b_{s0}+b_{s1}\ln(h+\Delta h))}\lambda) - (e^{(b_{s0}+b_{s1}\ln h)}\lambda)} \qquad (10)$$

$$BAC_i = \frac{B_{i(DAB+\Delta DAB,h+\Delta h)} - B_{i(DAB,h)}}{B_{s(DAB+\Delta DAB,h+\Delta h)} - B_{s(DAB,h)}} = \frac{(e^{(b_{i0}+b_{i1}\ln(DAB+\Delta DAB)+b_{i2}\ln(h+\Delta h))}\lambda) - (e^{(b_{i0}+b_{i1}\ln DAB)+b_{i2}\ln h)}\lambda)}{(e^{(b_{s0}+b_{s1}\ln(DAB+\Delta DAB)+b_{s2}\ln(h+\Delta h))}\lambda) - (e^{(b_{s0}+b_{s1}\ln DAB+b_{i2}\ln h)}\lambda)} \qquad (11)$$

In the next step, we calculated growth GE of all four species as a ratio of relevant biomass compartment increments (stem, branches, roots and the total of the three) to standing foliage biomass. In effect, GE describes biomass production per unit foliage:

$$GE_i = \frac{\Delta B_i}{B_f} \qquad (12)$$

where

ΔB_i is the increment of a component *i* and B_f is foliage biomass.

Similarly to the calculation of BAC, to obtain the estimates of GE we used three levels of annual DAB increment. Allometric equations (1-3) were used to expand the GE calculation (12), resulting in the following formulas:

$$GE_i = \frac{(e^{(b_{i0}+b_{i1}\ln(DAB_{B_f}+\Delta DAB))}\lambda)-(e^{(b_{i0}+b_{i1}\ln DAB_{B_f})}\lambda)}{B_f} \qquad (13)$$

$$GE_i = \frac{(e^{(b_{i0}+b_{i1}\ln(h_{B_f}+\Delta h))}\lambda)-(e^{(b_{i0}+b_{i1}\ln h_{B_f})}\lambda)}{B_f} \qquad (14)$$

$$GE_i = \frac{(e^{(b_{i0}+b_{i1}\ln(DAB_{B_f}+\Delta DAB)+b_{i2}\ln(h_{B_f}+\Delta h_{B_f})}\lambda)-(e^{(b_{i0}+b_{i1}\ln DAB_{B_f}+b_{i2}\ln h_{B_f})}\lambda)}{B_f} \qquad (15)$$

where

DAB_{B_f} is diameter DAB predicting foliage biomass B_f.

First, data for all trees were used to construct the allometric relations (equations 1-3). All subsequent comparisons of root/shoot ratios, BACs and GEs were carried out using the average tree from each stand (n=7) in conjunction with calculated species specific regression coefficients. Extra sum of squares F test was used to compare different model fits, any observed difference was considered significant at p<0.05. Unless otherwise stated, all significance values for BAC and GE comparisons are based on 5 mm diameter or 0.3 m height increment. Model fitting was carried out using the least squares method in Statistica 7.0 (StatSoft, Oklahoma, USA).

Results

Table 1 shows the mean values and the distribution of all measured dendrometric parameters and dry biomass weights for beech, oak, pine and spruce. We constructed allometric equations predicting dry biomass in young forest trees using DAB, tree height or both as predictors (see Appendix A: Tables 5-8). Stem diameter, traditionally a very accurate predictor variable, explained 87–94 % of measured dry compartment biomass variation in beech, 94-96 % in oak, 92-98 % in pine and 96-99 % in spruce (Equation 1). Using height as a single independent variable leads to lower values of the coefficient of determination (Equation 2; 85% vs. 94% on average across all compartments and species), while using both DAB and height slightly improves the coefficient of determination (Equation 3; 96% vs. 94%). In agreement with the high R^2 values, Akaike Information Criterion scores on average across all compartments and species are 134, 288 and 75 for Equations 1, 2 and 3 respectively, confirming the advantage of using DAB on its own or both DAB and height to predict dry biomass.

The results show large differences in biomass partitioning to below- and above-ground compartments among tree species. The initial decrease in root/shoot ratio with increasing tree size is more pronounced in broadleaves than in coniferous trees ($p<0.001$, Fig. 1). The largest change of this ratio with increasing tree size is apparent in oak, an increase of DAB from 5 to 70mm results in a three-fold decrease of the root/shoot ratio. The smallest changes were observed in pine, where the root/shoot ratio manifested a very mild decrease in our range of diameters. Initially, the broadleaves had larger values of root/shoot ratio than conifers, although the difference was not significant ($p=0.088$). With increasing stem diameter, however, the root/shoot ratio of each tree species did stabilise at around 0.2.

Marked differences were found between species in biomass allocation coefficients (Fig. 2). The relationship between BAC and DAB appears to be species-specific, but in general the trends of BAC with increasing DAB are conserved across species. BAC of foliage and roots decreases with increasing DAB, while that of branches remains stable - with the exception of beech ($p<0.001$). The ratio of foliage biomass increment to stem biomass increment in spruce is also appreciably higher (0.87) than in the other three species (0.04-0.37) at 60-70 mm DAB ($p<0.001$). Contrasting trends of root BAC can be shown for broadleaves and conifers, the broadleaves exhibit a very sharp decrease of BAC between 0 and 30mm DAB, while conifers are characterised by a more gentle decrease of BAC in this diameter class ($p=0.034$). To summarise, with increasing tree size the foliage and root increment decreases while the branch increment remains stable relative to stem diameter increment.

A similar situation was observed for foliage and root BAC when tree height was used as the predictor (see Appendix A: Fig. 1). Foliage BAC of spruce at 4 m height is significantly higher than in the other three species ($p<0.001$), however there is no difference in root BAC in broadleaves and in conifers ($p=0.812$). In contrast with diameter, increasing tree height results in a decrease of branch BAC in all tree species apart from beech ($p<0.001$).

We tested the influence of a range of stem increments on BAC. Varying the annual rate of stem diameter increment between 2.5 and 7.5 mm y^{-1} (Fig. 2) or height increment between 0.1 and 0.5 m y^{-1} (see Appendix A: Fig. 1) did not significantly affect the values of BAC for any of the species ($p=0.092$ to 0.407). Altering the rate of stem increment, for instance to reflect different site conditions, does influence the BAC only in very small trees. Once the DAB is greater than approximately 30 mm, this effect diminishes in all species.

Finally, having defined it as a ratio of biomass compartment increment to standing foliage biomass, we established the growth efficiency of all species. Fig. 3 shows the trends of stem (GE I) and woody biomass (stem + branches + roots, GE II) growth efficiency in relation to DAB. In general, GE indices exhibit decreasing trend with increasing tree size in all species apart from oak. The woody biomass GE, i.e. that of the stem, branches and roots together, is about twice as large as that of the stem alone. Similarly to the root/shoot ratio, evident differences in the values of GE at the high end of the DAB distribution exist between broadleaves and conifers (DAB 30 to 70 mm, p=0.007). Here, the GE of pine and spruce represents about a sixth of that of oak and beech. The decreasing trends of GE in species other than oak relate to the decreasing foliage BACs. In contrast, oak GE between DAB of 30 to 70 mm shows an increasing trend (P=0.019). In contrast to BACs, there is a strong influence of annual diameter increment on GE (p<0.001). GE increases about three-fold between two hypothetical values of stem diameter increment of 2.5 and 7.5 mm y^{-1} (Fig. 4) or height increment of 0.1 and 0.5 m y^{-1}(see Appendix A: Fig. 3).

Discussion

Biomass allocation

The large intra-specific variability in root/shoot ratio in trees of different ages is well established and very often simplified with linear models linking the root/shoot ratio to tree size or age (Giardina, Coleman, Hancock, King, Lilleskov et al., 2005). However, King, Giardina, Pregitzer & Friend (2007) pointed out a significant weakness of using the linear model using the example of *Pinus resinosa.* Similarly, Li, Kurz, Apps & Beukema (2003) have shown in their meta-analysis that a linear model could be applicable for softwood species and a non-linear model for hardwoods. Our results confirm that the root/shoot ratios of trees under 10 years old do not adhere to linear relationship with tree size. Interestingly, large differences exist between broadleaves and conifers in our forest stands. Very high initial values of root/shoot ratio in oak and beech rapidly decrease, while those of spruce follow a gentler decreasing trajectory or, in the case of pine, do not appear to relate to size. However, at about 70 mm DAB, the root/shoot ratio tends to stabilise around the value of about 0.20 in all species (Fig. 1). These results corroborate Harris (1992), who found that in most adult trees under normal conditions the root/shoot ratio is between 0.16 and 0.20. In their review of conifer seedling growth, Bernier, Lamhamedi & Simpon (1995) showed that the root/shoot ratio in Norway spruce starts from about 0.33, implying a larger contribution of roots to total tree biomass in young trees. Bearing in mind the difference between broadleaves and conifers, forest growth models should also take into account the non-linear nature of root/shoot ratio development if they are to be more realistic.

Information concerning forest tree biomass allocation in all tree compartments rather than just root and shoot is very scarce even at present. Since most forest mensuration data relate to stem biomass, ideally the data describing other tree biomass compartments should be expressed relative to the stem. As trees age, an increasing proportion of stem growth to total tree growth is generally observed in most woody plants (Kozlowski & Pallardy, 1997). Kantola & Makela (2006) found that Norway spruce trees initially increase their biomass investment to branches, while allocation to foliage decreases. After canopy closure, needle biomass continues to decline while branch biomass remains stable relative to the stem. We did not observe the decrease in branch allocation in our young trees, however the decreasing foliage increment relative to stem increment is evident from the start. This trend is common in all four tree species we measured, the observed differences were only in the values of BAC_f. Contrary to Zhou, Peng & Dan (2006), who constructed a general model of biomass allocation in Canadian boreal ecosystems encompassing all species, we show that general BACs are not applicable even if separate models are used for broadleaves and conifers. We found large inter-specific differences in increment of foliages, branches and roots expressed relative to stem growth. Interestingly, while root BACs tend to stabilise around 0.3 in all species, the values of foliage and branch BACs differ between species, thus reflecting differences in their establishment and early growth strategies

Growth efficiency

Growth efficiency of individual trees is commonly defined as the stem volume increment per unit leaf area, assuming that both variables are the result of resource availability and biomass allocation (Waring et al., 1985). In order to use the output of allometric relations to predict GE, we opted for foliage biomass as the measure of productive tissue. We also calculated the GE of all woody tissues, rather than just the stem. At least some of the biomass allocation and structural relationships are thought not to be related to specific growing conditions (Berninger, Coll, Vanninen, Makela, Palmroth et al., 2005; Oren, Werk & Schulze, 1986), leaving age and size as the main drivers of changes in GE. Published data suggest that GE in forest trees is usually highest in dominant or co-dominant trees (Reid, Lieffers & Silins, 2004). Increasing relative tree size should result in higher GE due to improved resource acquisition capacity (Brunner & Nigh, 2000; Claveau, Messier, Comeau & Coates, 2002), but not in old trees where the dominance of non-photosynthesising tissues (Mäkelä, 1986) and restrictions on water supply to the canopy (Magnani, Mencuccini & Grace, 2000) lead to a decrease in GE. Old trees have more fine roots per unit foliage than younger individuals, a condition which probably contributes to a decline in GE and subsequent downward trend in net primary productivity (Mäkelä et al., 2001). As Kaufman & Ryan (1986) point out, suppressed and overtopped trees can reach GE values almost as high as the dominant individuals, mainly because they tend to maintain smaller mass of foliage relative to the stem.

Our results show higher GE in beech and oak than in pine and spruce. We used foliage biomass, rather than specific leaf area (SLA), as the basis for GE calculations. Since broadleaves maintain foliage with higher values of specific leaf area (SLA) than conifers (Bartelink, 1998), the difference in GE we observed between broadleaves and conifers could be related to different leaf area per unit mass of foliage. We did not observe any difference in GE when comparing pine to spruce, but there was a significant difference between beech and oak. While GE in beech decreases as the trees grow larger, that of oak increases. Since in this study we utilised only naturally regenerated stands, we hypothesize that this difference is related to species-specific growth strategy and very high density of selected stands. As beech is thought to be shade tolerant and keeps different sun and shade leaves, a substantial amount of foliage is thus maintained as the beech trees grow in size, leading to decreasing GE. Oak, on the other hand, is less shade tolerant and may be shedding the leaves shaded by the canopy. This process would lead to smaller foliage biomass as the oaks grow larger and compete for canopy space, ultimately increasing the GE in oak. However, further physiological measurements would be necessary to confirm this contention.

Conclusions

Our allometric model comparison shows that the most accurate biomass and GE predictions are achieved when using both DAB and tree height. We show that this approach is suitable for estimating biomass growth in different body parts of forest trees. Such biomass partitioning and GE data can then serve as inputs in models of forest gross and net primary productivity. We observed marked differences between young broadleave and coniferous trees in their biomass allocation patterns and in calculated values of GE, suggesting that tree species do differ in their early growth strategies. Further, our results clearly show different biomass partitioning patterns in young compared to older trees. We suggest that future investigations of GE should also include observations of fine root production, since photosynthate transfer to this biomass pool represents an important carbon sink and could affect estimates of GE.

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Appendix A: Supplementary Material

The online version of this article contains additional supplementary data. Please visit XXXXX.

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