EFFICIENCY OF DIFFERENT FOREST TYPES IN CARBON STORAGE DEPENDS ON THEIR INTERNAL STRUCTURE

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ABSTRACT

Forest vegetation is a key factor in the maintenance of global carbon cycle balance under the present climate change conditions. Forest ecosystems are both buffers against extreme climatic events accompanying climate change and carbon sinks diminishing the environmental impact of anthropogenic greenhouse gas emissions. We investigated the influence of stand structure and site characteristics on the productivity and carbon storage capacity of temperate forest types. Predictors of species productivity were parameters such as stand density, age, height, average diameter and wood density. *Morus alba* (L.) was more productive than average both in terms of annual volume increment and annual biomass gain, while *Quercus sessiliflora* (Matt.) Lieb. and *Quercus frainetto* (Ten.) were significantly less productive than average. Differences in stand productivity were explained by stand density, age, height, altitude, type of regeneration and species composition. Statistically significant differences were measured between the productivity of stands dominated by different woody species, with low productive stands dominated by slow growing species with high wood density like *Quercus* or *Fagus*, and highly productive stands rich in fast growing species with low wood density like *Populus* or *Salix*. Stands with different plant communities in the underlying herbaceous layer also tended to have different levels of productivity.

KEY WORDS: carbon storage, productivity, temperate forests.

INTRODUCTION

Greenhouse gas emissions are considered the main driving force behind the ongoing alteration of global climate, with emissions from fossil fuels being the largest contributor to the anthropogenic greenhouse effect (Lehmann 2007). However, it is estimated that as much as 30% of the rise in carbon dioxide levels registered over the last centuries is due to land use changes, mainly deforestation (Fenning et al. 2008). Apart from reducing greenhouse gas emissions and searching for alternative sources of energy, current efforts to decrease the atmospheric concentration of carbon dioxide attempt its active withdrawal from the atmosphere and sequestration in aquatic or terrestrial ecosystems. Vegetation biomass and soil organic matter are efficient carbon sinks due to their large capacity of carbon fixation and storage for long periods of time (Alexandrov 2007; Nair et al. 2009). Temperate forests alone contain approximately 20% of the global vegetation biomass and store approximately 10% of the terrestrial carbon (Bonan 2008). Due to the slower carbon cycling rates, they are more effective in storing carbon over long periods of time than tropical and equatorial ecosystems. Tree trunks have the highest contribution to the carbon storage capacity of forest ecosystems, while leaves, sprouts and herbaceous layer form the litter and are subject to decomposition within 2 to 3 years (Gheorghe and Topa-Stan 2007; Nair et al. 2009).

Climate warming is expected to enhance plant growth in temperate ecosystems and therefore increase carbon sequestration. However, local conditions like drought duration and intensity and site characteristics like soil and vegetation structure strongly influence the response to climate variation. Moreover, the increased frequency of extreme drought events (Ciais et al. 2005) can severely impact terrestrial ecosystems reversing the effect of the increased mean temperatures and prolonged growing seasons and transforming forest ecosystems from carbon sinks into sources. Afforestation and reforestation efforts need therefore to be based on a thorough knowledge of the carbon storage capacity of different vegetation types and of its dependency on ecosystem structure and characteristics (Alexandrov 2007; Fenning et al. 2008; Nair et al. 2009). In spite of the recent advances in modelling and predicting the carbon storage capacity of forest ecosystems at regional as well as global level (e.g. Gough et al. 2008; Liu and Han 2009), the quality of such predictions is limited by the availability and quality of input data. Since obtaining such data is extremely time and cost intensive, it becomes important to select a minimal set of determinant parameters based on which reliable predictions of the carbon storage capacity of different forest ecosystems can be done. Among the structural parameters controlling the productivity, and therefore the amount of carbon stored in a forest ecosystem, trees species, density, age and height (depending in managed forests on the length of the harvest cycles) are generally recognized as the determinant ones. Our aim was to investigate the degree to which these structural parameters or other site-specific features can influence and predict stand productivity and implicitly carbon storage capacity of different temperate forest types.

MATERIALS AND METHODS

A number of 116 forest ecosystems spread along an altitudinal gradient from the lower Danube floodplain (15 m asl) to Făgăraş Mountains, Romania (1800 m asl) were selected. The stands covered a wide range of vegetation and substrate type, age and regeneration type. To avoid stands likely to be impacted by management practices (timber exploitation) a lower density limit of 0.8 was imposed for stand selection. Structural parameters were provided for all stands by the Forest Research and Management Institute (ICAS) (planning studies between 2004-2007). Those parameters were: tree species, region of provenance and abundance, average age, diameter at 1.3 m and height, timber volume ($m^3\ ha^{-1}$) (or standing biomass, $kg\ ha^{-1}$), stand altitude, exposition and density, production, vitality and type of regeneration (seed vs. vegetative). Wood density was obtained from Filipovici (1964).

For each stand five areas of 500 m^2 surface were selected for the survey of tree and herbaceous layers. Tree species with abundances higher than 10% were considered dominant per stand and considered separately for all analysis. Species with abundances lower than 10% were grouped according to wood density and considered together as soft wooded (wood density between 0.25-0.40 g/cm^3) or hard wooded (wood density between 0.80-0.98 g/cm^3) in subsequent analysis.

The type of herbaceous layer was established based on the dominant species in the forest floor using Braun-Blanchet scores of 5 (frequencies of 75-100%). For this, a 1 m^2 quadrate divided in 1 dm^2 sections was placed in 20 randomly selected positions, and the number of sections where a species was encountered was counted to obtain species frequency per quadrate. Average frequencies for the 20 random quadrates gave species frequency for the given forest stand.

Stem productivity was estimated according to Whittaker and Woodwell (1968) as biomass accumulated per area and time unit. Briefly, five circular plots of 500 m^2 were randomly selected for each stand. For each plot and dominant species, five representative trees were selected. Two stem cores per tree were harvested at 1.3 m height on perpendicular directions with a Pressler increment borer and used for productivity, growth and age determination. Age of tree samples was calculated by counting the growth rings and used subsequently in a diameter vs. age regression to estimate the age of other trees from the same species. Basal increase area was calculated according to Mitsch (1991) as

$$A_i = \pi\,[r^2 - (r-i)^2] \tag{1}$$

where r is tree radius at 1.3 m height and i is the mean across five years of the annual radial increment. Annual stem productivity P_i was calculated as

$$P_i = 0.5\,\rho\,A_i\,h \tag{2}$$

where ρ is wood specific density and h is the tree height (Whittaker and Woodwell 1968). Site stem productivity PW was calculated as

$$PW = \Sigma\,[P_i]\,BA/BC \tag{3}$$

where BA is the average basal area/m^2 for the given site and BC is the total basal area of the sample trees.

For representative groups carbon stock was calculated using CO2FIX31EXE based on leaf and woody biomass carbon stocks, timber volume, wood density and leaf biomass. Carbon content was measured in a CE Instruments EA-1110 CHNS-O elemental analyser for leaves and woody biomass. For each dominant species, approximately 50 g dry leaf biomass and 10 stem cores (two per each of five randomly selected trees) were dried to constant mass and ground to fine powder in a ball mill before carbon measurements. Litter traps (10 traps with 0.5 cm loops placed at 1.5 m above ground) were used to estimate total leaf biomass production for each of the dominant species, based on which leaf carbon stock was calculated. Timber volume was estimated based on published dendrological tables (Giurgiu et al. 1972) from tree diameter at 1.3 m and height and then was used together with wood density (Filipovici 1964) to estimate woody biomass. Woody biomass thus estimated was used to calculate woody carbon stocks. Root stocks were estimated as 13% of woody carbon stocks (Giurgiu et al. 1972).

Statistical analyses were performed with R2.7.0 (R-Development-Core-Team 2006). R package *nlme* (Pinheiro et al. 2006) was used to fit linear mixed effects models. Predictors of productivity and differences between stand and species productivity were investigated using linear mixed-effects models (*lme*) and linear models (*lm*), respectively. Full models included second order polynomials of all continuous variables and interactions of significant predictors ($p<0.05$). The models were constructed according to Aiken and West (1991) whereby when higher-order (interaction and polynomials) terms were included in the model then all the related lower-order terms were also included. To avoid co-linearity orthogonal polynomials were included in the models. Best models were selected from the candidate models based on likelihood ratio tests.

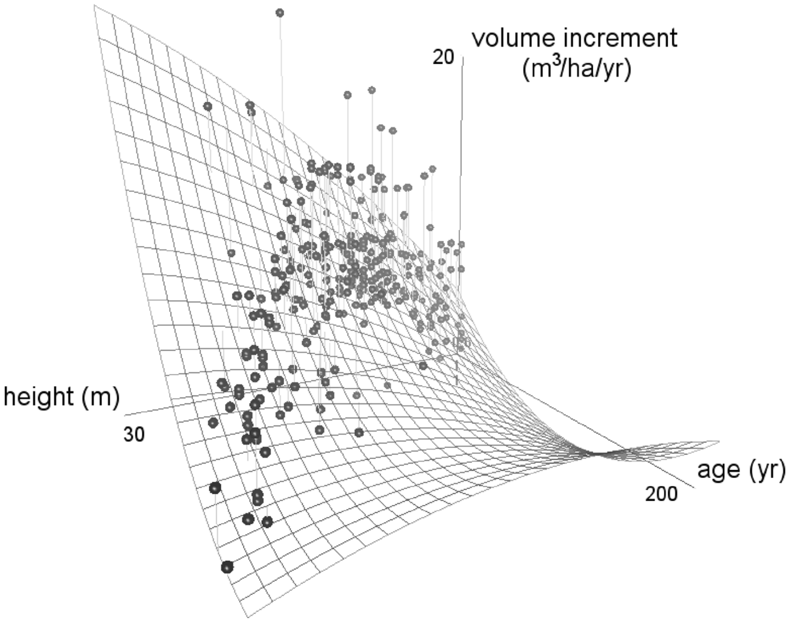

Fig. 1. Dependence of annual volume increment of species on age and height.

RESULTS AND DISCUSSION

Predictors of productivity

We investigated the predictors of productivity both in terms of annual volume increment and of biomass growth. For this we used linear mixed-effects models (*lme*) with the species productivity (log transformed for normality) as dependent variable and the species nested in stands as random factors. All parameters which could influence the level of productivity were included as predictors in the full model: average age, average diameter at 1.3 m, height, species type (coniferous vs. broad leafed), abundance and wood density, total timber volume (m^3 ha^{-1}) (or standing biomass, kg ha^{-1}), vitality, stand altitude, exposition and density, type of regeneration (seed vs vegetative) and region of provenance (autochthonous vs. allochthonous). To allow for non-linear effects, second order polynomials were included in the model for all continuous variables. Interactions among all significant predictors were considered and the best models were selected from the candidate models based on likelihood ratio tests.

Following the stepwise simplification of the model, the minimal model for the prediction of annual volume increment retained the average age, height, diameter and wood density as predictors of productivity while accounting for species density. The only significant interaction was between second order polynomials of age and height (Fig. 1). The second model explained differences in biomass gain

TABLE 1. Predictors of species annual volume increment and annual biomass gain.

Predictor	Annual volume increment			Annual biomass gain		
	Estimate ± SE	Test	P value	Estimate ± SE	Test	P value
intercept	1.06±0.19			6.92±0.2		
density density^2	13.5±0.34 -4.33±0.34	$F_{2,24}$ = 924.441	0.000	13.38±0.34 -4.12±0.34	$F_{2,24}$ = 929.1385	0.000
age age^2	-1.59±2.90 0.73±1.66	not tested #		-1.54±2.91 0.98±1.67	not tested #	
height height^2	4.15±1.41 0.29±1.13	not tested #		4.18±1.42 0.35±1.14	not tested #	
diameter	-0.01±0.01	$F_{1,24}$ = 4.850	0.038	-0.01±0.01	$F_{1,24}$ = 4.873	0.037
wood density wood density^2	-2.23±0.39 1.69±0.36	$F_{2,153}$ = 26.095	0.000	0.9±0.13	$F_{1,154}$ = 49.322	0.000
age*height age^2*height age*height^2 age^2*height^2	-75.71±46.76 16.83±20.80 23.12±20.13 -13.15±6.38	$F_{4,24}$ = 7.969	0.000	-79.9±46.96 15.3±20.97 25.34±20.21 -13.63±6.44	$F_{4,24}$ = 8.007	0.0003

Main effects involved in statistically significant ($p<0.05$) interactions were not tested.

among different species using the same predictors as for the annual volume increment. The minimal models are given below while estimates and their standard errors are found in Table 1.

$$\log(\text{annual volume increment}) = \text{density} + \text{density}^2 + \text{age} + \text{age}^2 + \text{height} + \text{height}^2 + \text{diameter} + \text{wood density} + \text{wood density}^2 + \text{age}{*}\text{height} + \text{age}^2{*}\text{height} + \text{age}{*}\text{height}^2 + \text{age}^2{*}\text{height}^2$$

$$\log(\text{biomass gain}) = \text{density} + \text{density}^2 + \text{age} + \text{age}^2 + \text{height} + \text{height}^2 + \text{diameter} + \text{wood density} + \text{age}{*}\text{height} + \text{age}^2{*}\text{height} + \text{age}{*}\text{height}^2 + \text{age}^2{*}\text{height}^2$$

The minimal models confirm that species productivity is influenced by tree age (Bradford and Kastendick 2010) and implicitly tree height and diameter, as well as by wood density – a species-specific parameter further confirmed to have a strong influence upon the productivity of stands dominated by different tree species. Furthermore, stand density had a highly significant influence on stand productivity, a fact bearing high relevance for forest management practices aiming to maximize the carbon storage capacity of forest ecosystems as previously recognised (Nair et al. 2009). The results were very similar when productivity was expressed either as annual volume increment or as annual biomass gain. The parameters found to predict species productivity are in full accord with previously established methods in the field like the increment index method (Giurgiu 1998).

Forest biomass was previously shown to depend on stand age following a power-law monomial (Alexandrov 2007). Based on these results, forest age was proposed as a useful criterion to be considered in the general guidelines for forest management practices aiming at the protection and enhancement of forest carbon sinks. Our model extends this observation and highlights trees age and height as predictors of annual volume increment.

Species characterized by an annual volume increment higher than average (one sample t tests against overall mean, significant differences following Bonferroni correction) were: *Picea abies* (L.) Karst, *Morus alba* (L.) and *Populus alba* (L.) (Fig. 2), all of them fast growing species with low wood density. *Salix alba* (L.) was marginally more productive than average. Among the species with significantly lower than average annual volume increment were: *Quercus sessiliflora* (Matt.) Liebl. and *Quercus frainetto* (Ten.), both slow growing species with high wood density. In terms of biomass gain, *Morus alba* (L.) was significantly more productive than average while *Picea abies* (L.) Karst, *Abies alba* (Mill.), *Quercus sessiliflora* (Matt.) Liebl. and *Quercus frainetto* (Ten.) were significantly less productive than average (Fig. 2). Mixed stands of hard wood species also gained significantly more biomass than average which is in agreement with previously observed patterns of forest diversity influence on productivity (e.g. Oberle et al. 2009; reviewed in Thompson et al. 2009). However, these results should be interpreted in the context of model predictions showing that under elevated CO_2 levels, coniferous species could benefit in average from a higher long-term biomass gain as compared to deciduous species (130% as compared to 49%) (Saxe et al. 1998).

Differences in stands productivity

Further we investigated the influence of stands' position and characteristics on their productivity (annual stand vo-

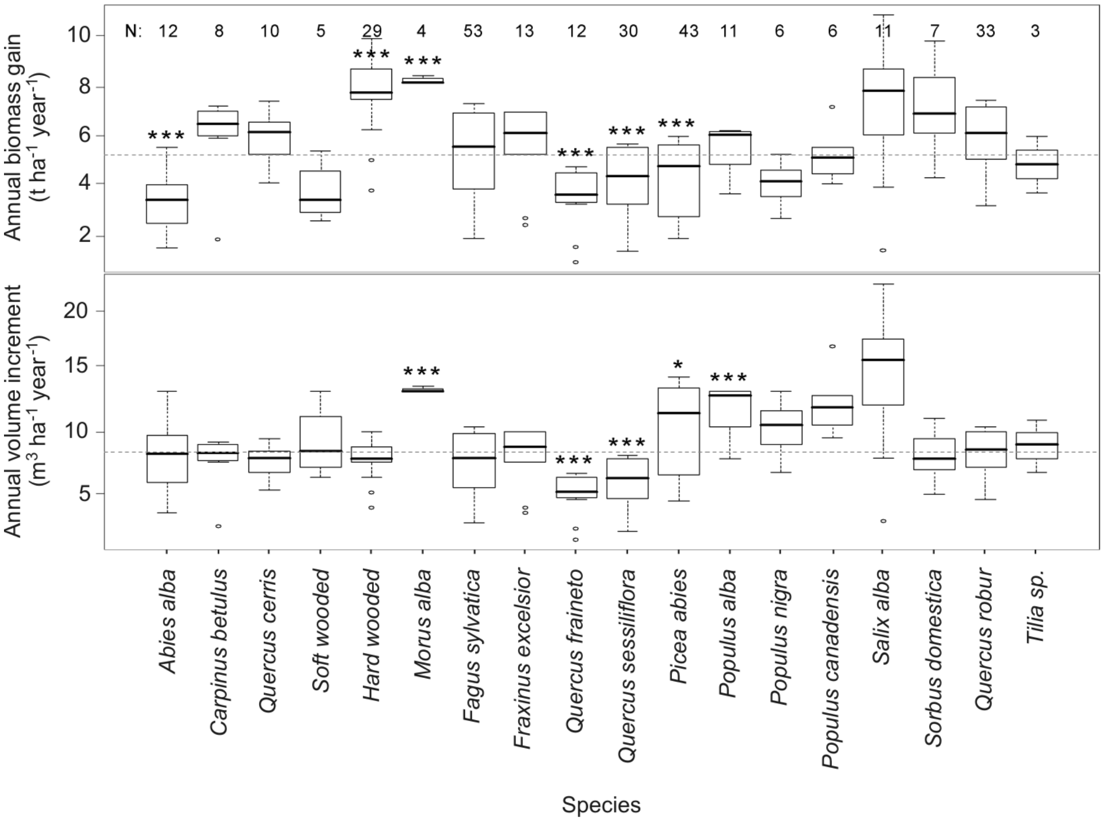

Fig. 2. Differences in species annual volume increment and gain in biomass. Dotted line denotes the overall mean. Stars indicate adjusted p-values (Bonferroni correction) of one sample t-tests against overall mean (* $p<0.05$, ** $p<0.01$, *** $p<0.001$).

TABLE 2. Predictors of annual stand volume increment and annual stand biomass gain.

Predictor	Annual volume increment			Annual biomass gain		
	Estimate ± SE	Test	P value	Estimate ± SE	Test	P value
intercept	10.22±2.9			1480±1566		
density	9.53±3.45	$F_{1,107} = 7.612$	0.007	3923±1732	$F_{1,104} = 5.129$	0.026
age	-15.8±5.4	$F_{2,107} = 5.142$	0.007	-21470±12870	not tested [#]	
age^2	-0.31±2.45			-9670±6066		
height	16.48±4.3	$F_{2,107} = 22.741$	0.000	11850±7086	not tested [#]	
height^2	-9.94±2.36			-4926±4143		
wood density	-14.36±1.94	$F_{1,107} = 54.967$	0.000			
regeneration	-0.002±0.001	$F_{1,107} = 14.116$	0.000	-624.6±239.3	$F_{1,104} = 6.812$	0.010
altitude	-1.69±0.45	$F_{1,107} = 6.232$	0.014	-0.91±0.24	$F_{1,104} = 14.192$	0.000
number of species	-0.27±0.14	$F_{1,107} = 3.670$	0.058	-142.2±72.96	$F_{1,104} = 3.798$	0.054
age*height				107300±143300	$F_{4,104} = 3.984$	0.005
age^2*height				67540±58490		
age*height^2				-9609±59440		
age^2*height^2				-20300±16190		

[#] Main effects involved in statistically significant ($p<0.05$) interactions were not tested.

lume increment and stand biomass gain respectively). The linear model (*lm*) contained stand productivity as dependent variable and several predictors: stand age (maximum age of all present species), stand height (maximum height of all present species), stand type (all conifers, all broad leafed or mixed stand), stand altitude, stand exposition and density, average diameter at 1.3 m and wood density, number of tree species with relative abundance higher than 10% and the dominant type of regeneration per stand (seed vs vegetative). Standing biomass (kg ha^{-1}) was additionally included as predictor of the annual biomass gain, and total timber volume (m^3 ha^{-1}) and wood density as predictors of annual volume increment. As in the previous models, second order polynomials were included in the full model for all continuous variables and interactions of significant predictors were considered.

Following the stepwise simplification, the minimal model retained as predictors of the annual stand volume increment the stand density, age, height, and altitude, the type of regeneration, average wood density and number of species. The minimal model for the prediction of annual stand biomass gain retained the same predictors, except for wood density. Additionally a highly significant interaction between stand age and height was retained in the simplified model. The minimal models are given below while estimates and their standard errors are found in Table 2.

annual stand volume increment = stand density + stand age + stand age^2 *+ stand height + stand height*^{2} *+ average wood density + type of regeneration + altitude + number of species*

annual stand biomass gain = stand density + stand age + stand age^2 *+ stand height + stand height*^{2} *+ type of regeneration + altitude + number of species+ age*height + age*^{2}**height + age*height*^{2} *+ age*^{2}**height*^{2}

The minimal models explained differences between stand productivity expressed as annual volume increment and annual biomass gain based on the same predictors except for wood density, used to estimate standing biomass and therefore not included in the second model. As expected, the models confirm the significant influence of stand age, altitude and species diversity and composition upon the productivity.

The importance of species composition, particularly of the dominant species in predicting stand productivity was further investigated. Stands dominated by *Quercus sessiliflora* (Matt.) Liebl. or *Quercus robur* (L.) had significantly lower than average annual volume increments (one sample t tests against overall mean, Bonferroni correction) while stands dominated by *Picea abies* (L.) Karst or *Populus alba* (L.) had annual volume increments above average (Fig. 3). However, *Quercus robur* (L.) dominated stands were more productive than average in terms of annual biomass gain while *Quercus sessiliflora* (Matt.) Liebl. dominated stands had marginally significant lower productivity (Fig. 3). As expected, low productive stands were dominated by slow growing species with high wood density (e.g. *Quercus*, *Fagus*), while highly productive stands were rich in fast growing species with low wood density (e.g. *Populus*, *Salix*). For management purposes, these results should also be considered in the context of different global warming scenarios. For example, in a simulation using BIOMASS, *Pinus sylvestris* and *Picea abies* stands were predicted to respond to a 2-4°C elevation of mean annual air temperature with an increase in annual biomass gain of 5-27% due mainly to the earlier start of the growing season and the

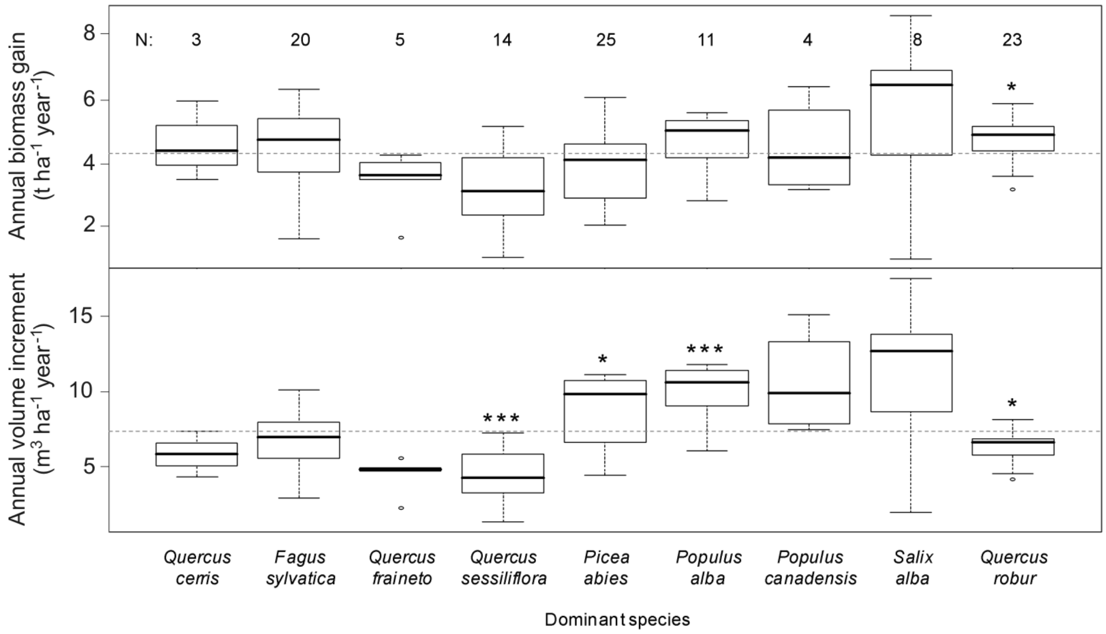

Fig. 3. Differences in the annual volume increment and biomass gain of stands with different dominant species. Dotted line denotes the overall mean. Stars indicate adjusted p-values (Bonferroni correction) of one sample t-tests against overall mean (* $p<0.05$, ** $p<0.01$, *** $p<0.001$).

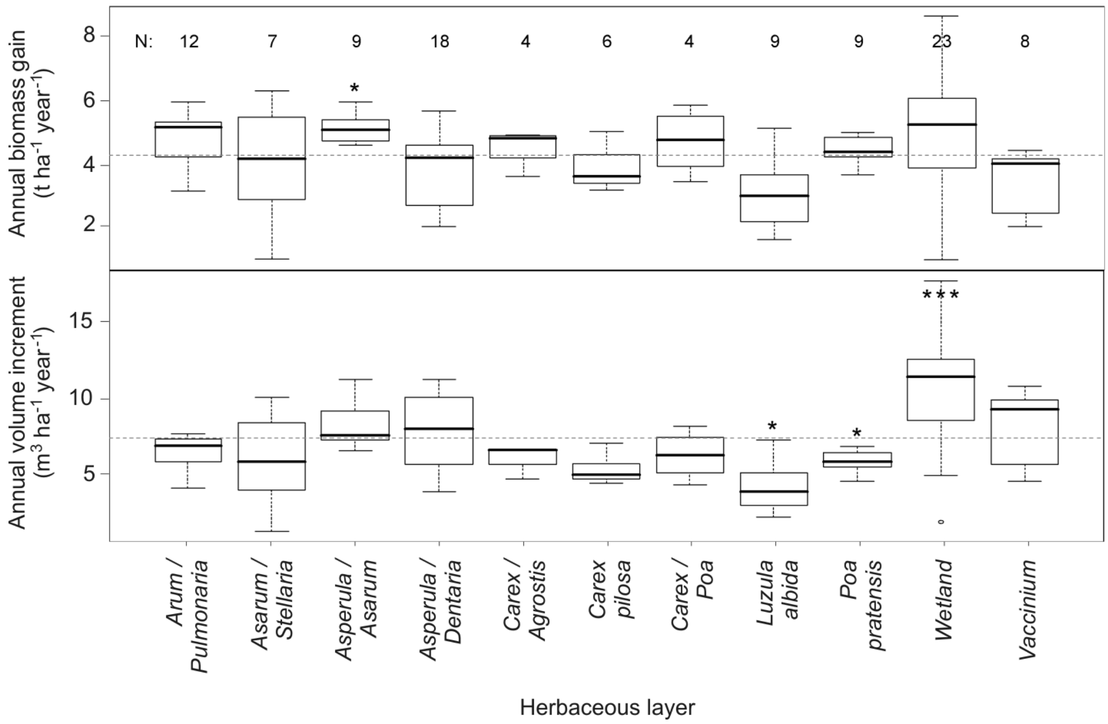

Fig. 4. Differences in the annual volume increment and biomass gain of stands with different herbaceous layers. Dotted line denotes the overall mean. Stars indicate adjusted p-values (Bonferroni correction) of one sample t-tests against overall mean (* $p<0.05$, ** $p<0.01$, *** $p<0.001$).

more rapid recovery from the winter season (Bergh et al. 2003). However, carbon gain was predicted to decrease because of the higher respiration. The same study predicted an opposite effect of increased temperatures for *Fagus sylvatica*, based on a lack of benefit from earlier bud break combined with increased water deficit and lower photosynthesis during summer. An increase of CO_2 concentrations was predicted to produce an additional increase in biomass gain up to 25-40% (Bergh et al. 2003).

Lastly, the correlation of the underlying herbaceous layer with different types of forest ecosystems prompted an investigation of the capacity of the herbaceous layer to predict stand productivity. Although the predictive value of the herbaceous layer was limited, some interesting observations have been made. Stands with herbaceous layers dominated by *Luzula albida* or *Poa pratensis* had lower annual volume increments than average, being mostly stands dominated by *Quercus* species, while the annual volume increment of stands with wetland vegetation (dominated by *Populus* and *Salix* species) were above average (one sample t tests against overall mean, differences after Bonferroni correction: very significant ($p<0.01$) and highly significant ($p<0.001$) statistical differences respectively) (Fig. 4). Stands with *Asperula-Asarum* associations in the herbaceo-

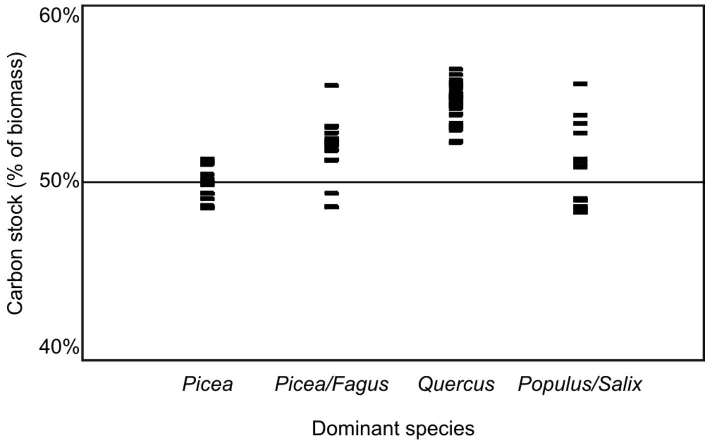

Fig. 5. Carbon stocks in forest stands with different dominant species.

us layer gained significantly more biomass than average, although these stands were mostly dominated by *Fagus sylvatica* (L.) (Fig. 4) – a species with average productivity.

Implications

The analysis highlighted the structural parameters which influence and predict stand productivity as well as the stand characteristics which explain the differences measured in stand productivity and implicitly in their carbon storage capacity. The most significant contribution to stand carbon storage capacity (both in terms of quantity and of the storage time) is that of the stems (Nair et al. 2009). Since the carbon stock represents approximately half of the biomass accumulated by a forest stand (Nair et al. 2009) (Fig. 5), such predictions and comparisons using stand productivity are valuable for predicting stand carbon storage capacity and should form the basis of forest management plans including those of aforestation and reforestation.

The models point to a trade-off between wood quality and growth rates: high wood density species are usually slow growing while fast growing species are frequently characterised by low wood density. While the first type of species can accumulate more carbon on the long term, fast growing species allow for rapid carbon fixation and faster rotation periods. Mixed stands of the two types of species have been recommended as most suitable for plantations (reviewed by Nair et al. 2009).

CONCLUSIONS

A detailed investigation of 116 temperate forest stands allowed us to identify the major predictors of stand productivity and carbon sequestration capacity. Such knowledge on the structural parameters which significantly influence stand capacity to generate ecological services (such as carbon sequestration) and goods (timber) and the trade-offs between them can greatly support forest management decisions and agroforestry strategies aiming for the sustainable use of resources and the maintenance of carbon cycle balance.

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