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Structure and growth of trees modified by the environmental conditions in forests and urban areas

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„Ein aufrechter Baum: Er trägt seine Äste und diese Zweige und diese Blätter. Und jeder einzelne Teil wächst harmonisch, großartig, seit der Künstler Gott ihn geschaffen hat.“

Antoni Gaudi

Vorwort

Da ist das Ding! Bis zur Fertigstellung der vorliegenden Arbeit war es ein langer Weg. Im Folgenden möchte ich all denen danken, die einen maßgeblichen Anteil an der erfolgreichen Realisierung dieser Arbeit hatten.

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Weiterhin bedanke ich mich bei meinen Doktorandenkollegen für das tagtägliche Miteinander, die gegenseitige Unterstützung und die einmaligen Momente abseits des Lehrstuhls, allen voran bei Dominik Bayer, Michael Heym, Diana Perkins, Dr. Andreas Rais, Cynthia Schäfer und Klaas Wellhausen. Vielen Dank für die schöne Zeit mit Euch.

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Es ist schön, dass es Dich gibt.

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List of Abbreviations

ba	Basal area
cb	Height to crown base
cr	(Mean) Crown radius
cpa	Crown projection area
d_0	Diameter at root collar
dbh	Diameter at breast height
DMI	De Martonne Aridity Index
h	Tree height
hcb	Height to crown base
iba	Basal area increment
npa	Non-paved area
P	Annual precipitation sum
r	Crown radii
RSE	Residual standard error
rw	Ring width
SCON	Degree of confinement due to soil sealing (surface confinement)
SE	Standard error
SDI_l	Local Stand Density Index
T	Mean air temperature
UHI	Urban Heat Island
W	Total biomass weight

List of Species

Abies sachalinensis MAST.	Sakhalin fir	Sachalin-Tanne
Aesculus hippocastanum L.	Horse-chestnut	Gewöhnliche Roßkastanie
Araucaria cunninghamii Aiton ex D. Don	Hoop pine	Neuguinea-Araukarie
Khaya senegalensis (DESR.) A. JUSS.	African mahogany	Afrikanisches Mahagoni
Picea glauca (MOENCH.) VOSS	White spruce	Weiß-Fichte
Platanus x hispanica MÜNCHH.	London plane	Ahornblättrige Platane
Quercus nigra L.	Water oak	Wassereiche
Quercus robur L.	Pedunculate oak	Stieleiche
Robinia pseudoacacia L.	Black locust	Gewöhnliche Robinie
Tilia cordata MILL.	Small-leaves lime	Winterlinde

Abstract

Through their functions and services trees play an important role, not only but particularly in urban areas, with different environmental conditions compared to forest stands. Due to climate change however, forecasts predict climatic conditions in rural areas, which are comparable to the current urban tree growth conditions. The analysis of urban tree growth today therefore bears the opportunity to project the effect of climate change on forest stands. Against this background the following thesis focused on the growth behavior of solitary versus stand-grown trees, as well as on assessing and predicting the related tree functions and services, in specific their carbon storage capacity.

To do so, urban trees in different metropolises worldwide were sampled. Thereby in each city a common local urban tree species was chosen (Brisbane - *Araucaria cunninghamii,* Hanoi - *Khaya senegalensis,* Houston - *Quercus nigra,* Cape Town – *Quercus robur*, Santiago de Chile – *Robinia pseudoacacia*, Paris - *Platanus x hispanica,* Munich -*Aesculus hippocastanum,* Berlin - *Tilia cordata*, Prince George – *Picea glauca*, Sapporo – *Abies sachalinensis*). To be able to analyze tree growth under urban versus rural environmental conditions, core samples were taken along gradients from the city centre to the periphery. In addition, young *Quercus robur* trees on four different forest investigation plots throughout Europe (Nelder trials) were sampled. Based on the obtained data allometric relationships were derived and growth reaction patterns to growing conditions were investigated. In specific, the influence of resource limitation, in form of stand density for forest trees or restricted non-paved area for urban trees, on tree growth was investigated. Further, differences between urban and rural trees and between recent and past climate conditions were examined.

Differences in the allomeric relationships were found for the different tree species in their respective environment, as well as for stand-grown versus open-grown trees. It is assumed that the differences in growth are a result of both, differences in the growth behavior between the species, but also differences in the environmental conditions. Thereby, for forest as well as for urban trees, warmer and drier climatic conditions led to higher tree growth and biomass productivity respectively. Further the results showed that for both, stand-grown and solitary grown trees, higher competition or inhibition respectively led to reduced growth and reduced biomass. The kind of inhibition differs (inter-tree competition versus sealed surface), but both lead to a reduced resource availability, which is likely to be the reason for the reduced growth. Regarding trees' carbon storage capacity, tree diameter and tree height were

identified as predictors for biomass, which is directly related to a tree’s carbon storage capacity. While these tree variables are also the ones which are used in existing equations in literature, the results from this research question the applicability of known equations. The findings rather indicate that additional predictors for biomass should be considered, which might also be site- or species-specific. One of them is stand density.

The results of this thesis, in specific the allometric relationships derived, can help for management decisions, e.g. planting decisions or tree maintenance and care. In addition, the findings regarding biomass productivity and the inclusion of stand density into biomass equations can help to improve the estimation of biomass and thus of the carbon storage capacity, in form of more adequate results.

Zusammenfassung

Dank ihrer Funktionen und Leistungen spielen Bäume eine wichtige Rolle, insbesondere auch in städtischen Gebieten, in denen andere Umweltbedingungen als in Wäldern vorzufinden sind. Im Zuge des Klimawandels werden jedoch für naturräumliche Gebiete ähnliche klimatische Bedingungen prognostiziert, wie sie momentan in Städten vorherrschen. Die Analyse des jetzigen Stadtbaumwachstums bietet daher die Möglichkeit die Auswirkungen des Klimawandels auf Bestandesbäume vorherzusagen. Vor diesem Hintergrund konzentriert sich die vorliegende Dissertation auf das Wachstumsverhalten von Stadtbäumen gegenüber Bestandesbäumen, sowie auf die Beurteilung und Vorhersage der zugehörigen Funktionen und Leistungen, insbesondere ihrer Kohlenstoffspeicherkapazität.

Hierfür wurden Stadtbäume in verschiedenen Metropolen weltweit beprobt. Dabei wurde in jeder Stadt eine häufig vorkommende Baumart gewählt (Brisbane - *Araucaria cunninghamii,* Hanoi - *Khaya senegalensis,* Houston - *Quercus nigra,* Kapstadt – *Quercus robur*, Santiago de Chile – *Robinia pseudoacacia*, Paris - *Platanus x hispanica,* München - *Aesculus hippocastanum,* Berlin - *Tilia cordata*, Prince George – *Picea glauca*, Sapporo – *Abies sachalinensis*). Um das Baumwachstum unter städtischen und außerstädtischen Umweltbedingungen analysieren zu können, wurden Bohrkernproben entlang eines Gradienten vom Stadtzentrum bis zu den Außenbezirken der Stadt entnommen. Zusätzlich wurden junge *Quercus robur* Bäume auf vier verschiedenen forstlichen Untersuchungsflächen (Nelder-Flächen) innerhalb Europas beprobt. Auf Basis dieser Messdaten wurden allometrische Beziehungen aufgestellt und Wachstumsreaktionen in Bezug auf die Wachstumsbedingungen analysiert. Konkret wurde, anhand der Bestandesdichte für die Waldbäume und anhand der Oberflächenversiegelung für die Stadtbäume, der Einfluss von Ressourcenlimitierung auf das Baumwachstum untersucht. Weiterhin wurden Unterschiede zwischen innerstädtischen und außerstädtischen Bäumen, sowie zwischen gegenwärtigen und vergangenen Klimabedingungen erforscht.

Sowohl für Bestandes-, als auch für Einzelbäume, konnten Unterschiede in den allometrischen Beziehungen für die verschiedenen Baumarten in ihren jeweiligen Umgebungen festgestellt werden. Es wird angenommen, dass die Unterschiede im Wachstum auf Unterschiede im Wachstumsverhalten der Baumarten, aber auch auf Unterschiede in den Umweltbedingungen zurückzuführen sind. Dabei konnte sowohl für Bestandes- wie auch für Einzelbäume nachgewiesen werden, dass unter wärmeren und trockeneren Bedingungen eine höhere Wachstumsrate und eine höhere Biomasseproduktion

erzielt wurde. Des Weiteren zeigten die Ergebnisse, dass bei beiden, bei Bestandes- und Einzelbäumen, höhere Konkurrenz beziehungsweise Einschränkung zu reduziertem Wachstum und Biomasseproduktion führten. Die Art der Einschränkung unterscheidet sich (Konkurrenz auf Zwischenbaumebene versus Oberflächenversiegelung), aber in beiden Fällen führt sie zu einer reduzierten Ressourcenverfügbarkeit, welche vermeintlich der Grund für die Wachstumsreduktion ist. Bezüglich der Kohlenstoffspeicherkapazität eines Baumes konnten der Baumdurchmesser und die Baumhöhe als Prädiktoren für die Biomasse, welche direkt mit der Kohlenstoffspeicherkapazität verknüpft ist, herausgearbeitet werden. Obwohl diese Baumvariablen auch jene sind, die in bestehende Biomassegleichungen aus der Literatur eingesetzt werden, stellen die Ergebnisse die Anwendung dieser Gleichungen in Frage. Die Ergebnisse zeigen viel mehr, dass weitere, möglicherweise auch standort- oder artspezifische, Prädiktoren berücksichtigt werden sollten. Einer von ihnen ist die Bestandesdichte.

Die Ergebnisse dieser Dissertation, insbesondere die aufgezeigten allometrischen Beziehungen, können bei Managemententscheidungen, wie beispielsweise Pflanzentscheidungen oder Baumvorsorge- und Baumerhaltungsmaßnahmen, helfen. Weiterhin können die Ergebnisse für die Biomasseproduktion und die Berücksichtigung von der Bestandesdichte in Biomassefunktionen zu einer verbesserten Schätzung und somit zu realistischeren Ergebnissen der Biomasse und der Kohlenstoffspeicherkapazität beitragen.

I. Cumulative Thesis

Publication and submission record

The present thesis is submitted as a cumulative dissertation based on the following three first authorships, complemented by the further publications listed below:

Dahlhausen, J., Uhl, E., Heym, M., Biber, P., Ventura, M., Panzacchi, P., Tonon, G., Horváth, T., Pretzsch, H. (2017). Stand density sensitive biomass functions for young oak trees at four different European sites, *Trees*, 31(6): 1811-1826; http://dx.doi.org/10.1007/s00468-017-1586-7

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Pretzsch, H., Biber, P., Uhl, E., Dahlhausen, J. Schütze, G., Perkins, D., Rötzer, T., Caldentey, J., Koike, T., van Con, T., Chavanne, A., du Toit, B., Foster, K., Lefer, B. (2017): Climate change accelerates growth of urban trees in metropolises worldwide. *Scientific Reports*, 7:15403; http://dx.doi.org/10.1038/s41598-017-14831-w

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Dahlhausen, J., Uhl, E., Heym, M., Biber, P., Ventura, M., Panzacchi, P., Tonon, G., Horváth, T., Pretzsch, H. (2017). Stand density sensitive biomass functions for young oak trees at four different European sites, Trees, 31(6): 1811-1826

The quantification of tree biomass plays an important role in the light of climate change, due to the carbon storage ability of trees. While the biomass productivity of trees or single compartments has been studied in several research articles, only few took the belowground biomass into consideration. Additionally, few studies so far have dealt with young trees or considered further influencing factors like the growing conditions i.e. the prevailing stand density. In the study at hand, young *Quercus robur* trees were sampled on Nelder trials, which comprise different stand densities, on four European sites along a climatic gradient. The climatic gradient extends from hot and dry (Sant Agata Bolognese, Italy), over slightly colder but drier conditions (Györ, Hungary) to wet and colder conditions (Neckarsulm, Germany) and finally cold and dry conditions (Ingolstadt, Germany). Methodologically, logarithmic transformed power functions were estimated for total, as well as for above- and belowground biomass. The biomass proportions of the compartments leaves, branches, stem and roots were estimated using Dirichlet regressions. The results revealed that plant size, in form of diameter at root collar and height, predicts total biomass, as well as above- and belowground biomass. For total and belowground biomass the stand density was additionally an important predictor, not so for aboveground biomass. Omitting the Stand Density Index (SDI_I) resulted in an overestimation of biomass productivity. Further, the biomass allocation between the compartments was found to be modified by tree diameter and SDI_I, but not by tree height. Finally yet importantly, the study revealed that the consideration of belowground biomass is critical, as it accounted for 10 to 30% of total biomass when stand density was high and for even 30 to 50% of total biomass when stand density was low. The biomass quantification presented in this article contributes to the literature by accounting for a broader variety of competitive situations than has previously been considered.

Author contributions

Jens Dahlhausen conducted the field and laboratory work, and data analysis and wrote the manuscript. Hans Pretzsch initiated the study and contributed to the manuscript. Enno Uhl conceptualized the study design and revised the manuscript. Maurizio Ventura, Pietro Panzacchi and Tamás Horváth contributed to the development of the study design, supported the data acquisition and revised the manuscript. Michael Heym supported the data analysis. Peter Biber supported the statistical analysis and revised the manuscript. Giustino Tonon revised the manuscript.

Dahlhausen, J., Biber, P., Rötzer, T., Uhl, E., Pretzsch, H. (2016). Tree species and their space requirements in six urban environments worldwide, Forests 7(6): 111

Trees in urban environments grow under different conditions compared to forest stands. While trees play an increasingly important role in urban environments, not least due to its functions and services like carbon storage, research on the temporal dynamic of tree growth in urban surroundings is scarce. Addressing this research gap, the present article deals with allometric relationships of stem diameter, tree height, and crown radius for six tree species in six metropolises worldwide (Brisbane - *Araucaria cunninghamii,* Hanoi - *Khaya senegalensis,* Houston - *Quercus nigra,* Paris - *Platanus x hispanica,* Munich -*Aesculus hippocastanum,* Berlin - *Tilia cordata*). As such, species-specific allometries were derived for a set of common urban trees, under the conditions they are typically found and best adapted to. Based on increment cores, the relationship between basal area and basal area increment was identified and the temporal dynamics for each species in relation to the allometric parameters and growth extensions were extrapolated. Further, space and resource limitation in form of sealed surface was assessed, to evaluate its influence on tree growth. Finally, biomass equations were applied for estimating aboveground woody biomass and the resulting carbon storage capacity of the different tree species. The results revealed species-specific allometries of urban trees. The highest growth rates for stem diameter and crown radius were found for *Q. nigra* and *K. senegalensis*, whereas *T. cordata* and *A. hippocastanum* remained on a lower level. Regarding the sealed surface, the tree species *A. hippocastanum* and *K. senegalensis* were found to be significantly restricted in tree growth where non-paved area is limited. Aboveground biomass, which is directly linked to the tree's ability to store carbon, was found to be highest for *Q. nigra* and lowest for *T. cordata*. The reported quantitative information about how typical urban tree species develop worldwide, in specific regarding space requirements, is useful for urban managers. In specific, the presented results can be applied to improve urban tree treatment, thereby enhancing the benefits of urban trees and reducing the cost of maintenance and care.

Author contributions

Jens Dahlhausen performed the data analysis, large parts of the data collection, and primarily wrote the paper. Hans Pretzsch, Thomas Rötzer, and Enno Uhl conceived and designed the experiment. Peter Biber contributed statistical analysis tools and statistical paragraphs to the manuscript. Thomas Rötzer and Enno Uhl revised the manuscript.

Dahlhausen, J., Rötzer, T., Biber, P., Uhl, E., Pretzsch, H. (2017): Urban climate modifies tree growth in Berlin. International Journal of Biometeorology

Urban climate is characterized among other things by higher (especially nocturnal) air temperatures compared to peripheral areas. This phenomenon is called Urban Heat Island (UHI) and results in distinct growth conditions for urban trees. For analyzing differences in tree growth in relation to climatic conditions, 252 small-leaved lime trees (*Tilia cordata* Mill.) were sampled along a gradient from the city center of Berlin to the periphery. Increment cores were taken for tracing back the tree growth of the last 50 to 100 years. For investigating the general growth trend, the Bertalanffy growth function was applied to the increment data of the earlier years. The expected growth for the recent decades was derived by extrapolating the growth equation. To determine whether expected and actual growth differ, the estimated values were compared to the measured growth data of the recent years. In addition, data on air temperature and precipitation from an urban versus a peripheral climate station in Berlin, as well as information on housing density, were taken into account. Considering the general growth trend, the results revealed a higher growth rate than estimated for young trees (< 40 years) in high-dense areas. In relation to the UHI effect, higher growth rates for trees younger 60 years were found in high dense areas between 1981 and 2000, but in low dense areas before and after this period. The opposite growth behavior was found for trees older 60 years, showing higher growth rates in high dense areas before 1979 and after 2000. In line with this, results of a linear model indicated that through local climate, housing density influenced urban tree growth within the last 20 years. Additionally, the data showed a significantly higher variance of the ring width index in areas with medium housing density compared to low housing density, but no temporal trend. Based on the results, the article discusses potential reasons and consequences for urban tree growth under changing climate conditions. This is of high relevance, as the urban environmental setting bears the opportunity to investigate possible effects of climate change on tree growth already today. While the growth patterns of forest stands cannot be transferred to urban trees, the analysis of urban trees is viewed as a possibility to predict future growth behavior of forest stands.

Author Contributions

Jens Dahlhausen undertook parts of the field work and was primarily responsible for the data analysis and for writing the manuscript. Hans Pretzsch, Thomas Rötzer, and Enno Uhl conceived and designed the project. Enno Uhl also conducted parts of the field work and revised the manuscript. Peter Biber contributed statistical analysis tools and revised the manuscript. Thomas Rötzer and Hans Pretzsch contributed to writing the manuscript.

Pretzsch, H., Biber, P., Uhl, E., Dahlhausen, J., Rötzer, T., Caldentey, J., Takayoshi, K., van Con, T., Chavanne, A., Seifert, T., du Toit, B., Farnden, C., Pauleit, S. (2015): Crown size and growing space requirement of common tree species in urban centres, parks and forests. Urban Forestry & Urban Greening 14(3):466-479

While trees fulfill many services and functions, they are also source of possible disservices like fallen branches. The trees' crown size is an important information for the assessment and prognosis of both. The crown size however is species-specific and among others dependent on tree age and resource supply. In addition, tree growth dynamics and consequently also the trees' crown size differ in urban versus forested areas. Addressing this topic, the present article analyzed the species-specific allometric relationship of crown radius and stem diameter for 22 common tree species in urban environments worldwide. The results revealed five crown extension types. For each of these five types further allometric relationships were derived. In addition, quantile regressions for the crown radius – stem diameter relationship revealed accelerated growth under open grown compared to forested areas. Again, species-specific differences in the growth dynamics could be observed. While the difference between open grown and stand grown *Tilia cordata* trees decreased with increasing tree size, the difference remained constant for e.g. *Aesculus hippocastanum*. These results highlight the importance of species-specific estimation of space requirements, which can support the initial choice of a species for a given environment to avoid later conflicts provoked by too large crown expansion. As such the results are of particular importance for urban planners.

Author Contributions

Jens Dahlhausen collected and prepared parts of the data and contributed to the analysis. Hans Pretzsch initialized the study, contributed to data collection, conceptualized the manuscript and contributed to writing. Peter Biber developed the methodological approach of the analysis and contributed to data preparation and writing. Enno Uhl and Thomas Rötzer conceptualized the study, contributed to data collection and to writing. Juan Caldentey, Takayoshi Koike, Tran van Con, Aurélia Chavanne, Thomas Seifert, Ben du Toit, Craig Farnden, supported the manuscript writing process with their local expert knowledge. Stephan Pauleit revised the manuscript.

Pretzsch, H., Biber, P., Uhl, E., Dahlhausen, J., Schütze, G., Perkins, D., Rötzer, T., Caldentey, J., Takayoshi, K., van Con, T., Chavanne, A., du Toit, B., Foster, B., Lefer, B. (2017): Climate change accelerates growth of urban trees in metropolises worldwide. Scientific Reports 7:15403

While the growth of forest trees under recent climatic conditions is well studied, little is known on whether these findings can be transferred to urban environments. Due to differences in the climatic conditions, differences in the growth behavior can be assumed. In addition, due to climate change, the urban climate today represents climatic conditions which are forecasted for non-urban areas in the future. Thus, the analysis of urban tree growth bears the opportunity to project the effect of climate change on forest stands. Against this background, this study analyzed growth reactions of urban trees to climate change and to the Urban Heat Island effect worldwide. To do so, increment cores were taken from urban to rural areas in ten metropolises worldwide, distributed over four climate zones (Brisbane - *Araucaria cunninghamii,* Hanoi - *Khaya senegalensis,* Houston - *Quercus nigra,* Cape Town – *Quercus robur*, Santiago de Chile – *Robinia pseudoacacia*, Paris - *Platanus x hispanica,* Munich -*Aesculus hippocastanum,* Berlin - *Tilia cordata*, Prince George – *Picea glauca*, Sapporo – *Abies sachalinensis*). Based on the tree ring analyses, this article could show that in general, urban trees have undergone accelerated growth since the 1960s. Thereby, urban trees within the city centers showed more rapid growth than those within the rural periphery of the cities. However, concerning the effect of climate change, the present analysis revealed that the environmental conditions induced by the changing climate seem to benefit the growth of rural trees more than that of urban trees. The accelerated growth of urban trees was found to be related to increased carbon storage and provision of many ecosystem services, but also to faster tree aging and thus a shortened lifetime. As such, the changed dynamics of urban tree growth imply new challenges for urban planners to secure the ecosystem services and functions provided by urban trees.

Author Contributions

Jens Dahlhausen performed large parts of the data collection and data preparation, supported the analyses and contributed to writing. Hans Pretzsch initialized the study, contributed to data collection, conceptualized the manuscript and contributed to writing. Peter Biber developed the methodological approach of the analysis and contributed to writing. Enno Uhl conceptualized the study and contributed to data collection and to writing. Gerhard Schütze conducted tree ring analyses. Diana Perkins contributed to tree ring analyses, to data quality, and to writing. Thomas Rötzer revised the manuscript. Juan Caldentey, Takayoshi Koike, Tran van Con, Aurélia Chavanne, Ben du Toit, Keith Foster, Barry Lefer contributed to developing the city specific sampling designs, and supported the manuscript writing process with their local expert knowledge.

II. Thesis

1. Introduction

Trees have manifold functions within forest ecosystems, as they produce biomass, store carbon or provide habitats and dead wood (Escobedo et al. 2011; Gamfeldt et al. 2013; Dobbs et al. 2014; Moser et al. 2015; Mullaney et al. 2015). Biomass production and carbon storage represent a highly important service not only in forest, but also in the urban environment. Within urban environments trees provide further services as cooling the ambient environment, filtering air pollutants and fulfilling aesthetical and structural functions (Escobedo et al. 2011; Mullaney et al. 2015). Thus, trees have unique selling points in and to its environment. The performance of the mentioned functions in turn is mainly dependent on the growing rate of a tree. On the other site, specifically in urban areas, trees also cause disservices, as damage to foot paths, litter fall and fallen branches, causing additional costs and endangering public's safety (McPherson et al. 2005; Escobedo et al. 2011; Livesley et al. 2016). Thus, it is highly important to investigate trees' growth and structural development under its ambient environmental conditions.

Time series of tree stem growth provide valuable information about growth trends in relation to environmental changes (Schweingruber 1996). In forestry, this kind of data has been used for a long time to measure site quality (Skovsgaard and Vanclay 2008), or the effects of silvicultural treatment such as pruning, thinning, or fertilization (Assmann 1970) and last but not least, to analyze human impact, as well as the impact of the changing climate, on forest ecosystems (Pretzsch 1989; Cherubini et al. 2004; Briffa et al. 2004; Uhl et al. 2013; Pretzsch et al. 2014). However, in the context of urban trees the potential of time series data of tree stem growth was hardly used so far (Cook and Kairiukstis 1992), excepting some studies focusing on damage or dieback (Eckstein et al. 1981; Helama et al. 2012; Gillner et al. 2014). Forest trees might be influenced by factors such as inter-tree competition, browsing or thinning, whereas open-grown urban trees might be influenced e.g. by building measurements. Thus, findings from forest trees cannot be directly transferred to urban trees and vice versa.

Several factors are found to influence tree growth. These factors can be divided into biotic and abitotic factors. Important biotic factors affecting tree growth are competition (Pretzsch and Biber 2010), species composition (Gamfeldt et al. 2013) and stand density (Xue et al. 2012) or stand type (pure or mixed) (Pretzsch 2014). The most relevant abiotic factors are site conditions, such as soil type, especially soil nutrients (Lévesque et al. 2016), soil compaction (Day et al. 2000; Quigley 2004), latitude, or altitude (Jochner et al. 2012). For urban environments additional anthropogenic impacts are reported: paving, going in line with reduced pervious surface area under tree crown (Sanders and Grabosky 2014), shade (Akbari 2002; McPherson et al. 2005; Berry et al. 2013), and air and water pollutants (Shepherd 2005; Wittig et al. 2009). First and foremost, however, tree growth is influenced by the availability of the essential resources: light, water and nutrients. According to the optimal partitioning theory (McCarthy and Enquist 2007), the shape of the tree crown, root system, and the relationship between these depends highly on the resource supply of the plant (Pretzsch et al. 2012b, a). Further, the influencing factors interact (e.g. the higher the plant density, the higher the competition for ressources) and vary over space and time (Cienciala et al. 2016).

The resource availability, especially water availability, in turn depends mainly on climatic conditions. Climate controls of forest production and its change over time (last 55 years) are reported by Boisvenue and Running (2006). In their review they state that air temperature, solar radiation and water availability are the main factors controlling tree primary production, as an increase in air temperature may cause higher transpiration rate and a reduced growth. Further it is reported that the temperature – growth response is related to trees' functional group. In other words the growth strategy of a species impacts the response to changing climate conditions (Way and Oren 2010).

The urban climate can be defined as an anthropogenic climate modification, which is induced by the interaction with development and heat release as well as admixtures of air. The schematic representation of the typical air temperature course from the rural surroundings to the center of an urban area is shown in Figure 1. The boundary between rural and urban is characterized by a steep temperature gradient to the prevailing urban heat island effect (UHI). In urban areas, natural land surfaces are replaced by artificial surfaces, which are characterized by different thermal properties as heat capacity and thermal inertia. These differences lead to a higher capacity of storing solar energy and converting it to sensible heat. Additionally the influences in surface albedo and anthropogenic heat release are the main factors for UHI (Shepherd 2005).

Higher air temperatures in the center of urban areas can be observed worldwide (Peng et al. 2012), but the variation between rural and urban is city-specific. Findings for the air temperature difference differ from 10 °C to an average of 1.5 ± 1.2 °C at daytime and respectively 1.1 ± 0.5 °C at nighttime when looking at 419 global big cities (Shepherd 2005;

Peng et al. 2012). Besides city characteristics in terms of building architecture, the temperature difference is further dependent on factors such as clouds and wind speed. The strongest differences occur at clear and windless conditions and during nighttime (Kim and Baik 2002).

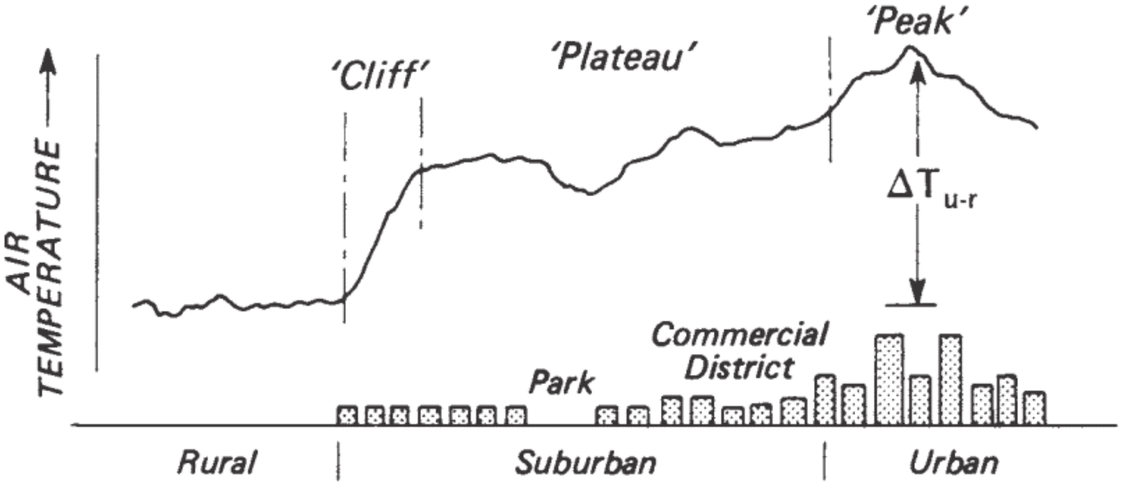


Fig. 1 Generalized cross-section of a typical urban heat island (Oke 1987)

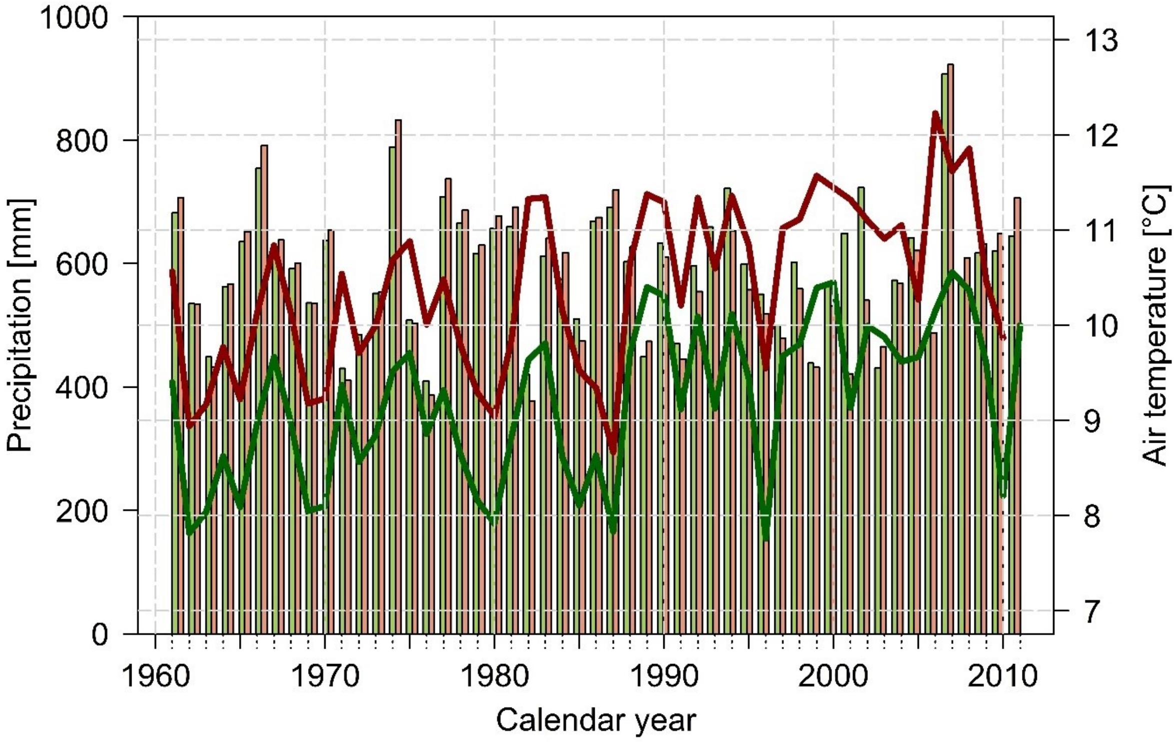
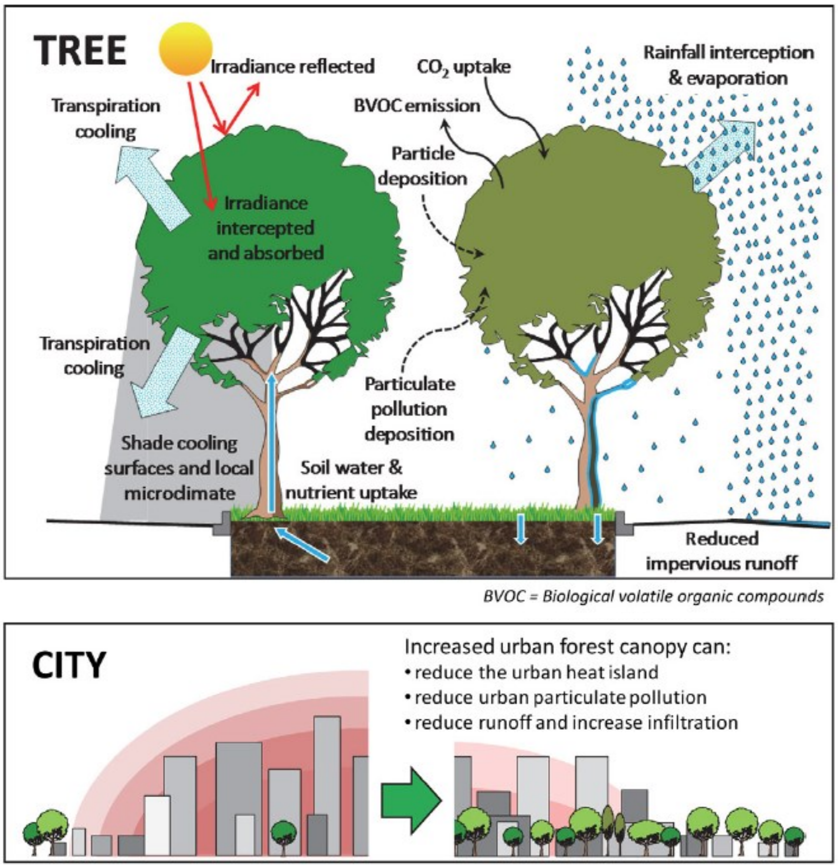


Fig. 2 Air temperature (annual mean; solid line) and precipitation (annual sum, bars) from the climate station "Alexanderplatz" in the city center (red) and from the peripheral station "Dahlem" (green) in Berlin for the period 1961 – 2011.

Looking at an urban and a rural climate station in the city of Berlin (Berlin-Alexanderplatz and Berlin-Dahlem) Figure 2 shows the annual air temperature and precipitation from 1961 to 2011. The data confirms the before explained phenomenon, with consistently higher air temperature values for the urban station, which implies warmer conditions in the more densely build up areas of the city than in the outskirts. Regarding precipitation the findings are not as clear. Before 1990 precipitation is mostly higher at the urban station, whereas after 1990 precipitation is higher at the rural station for most of the years.



BVOC = Biological volatile organic compounds

Fig. 3 Urban tree ecosystem services and functions at different scales (tree, street and city) after Livesley et al. 2016.

The warmer conditions in urban areas cause changes in life conditions for living organisms. One main aspect is the extension of the growing season, which can amount up to 8.8 days (Dallimer et al. 2016). But not only positive effects come along with the phenomenon of UHI. It is reported that the higher air temperatures cause heat stress and increase the human mortality rate in high-dense areas (Scherer et al. 2014). As Figure 3 shows, urban trees play a key role in cooling and mitigating heat stress in high-dense city areas. This was already reported decades ago, where the importance of urban trees due to their function of modifying the urban climate was already stated (Oke et al. 1989). Still, urban stress factors on the trees, as water shortage, low humidity, head loading and air pollution remained mostly unstudied (Oke et al. 1989). In line with an ongoing urbanization, the relevance of this research field has largely increased and within the last decade several studies have been conducted for closing this knowledge gap (Nowak and Crane 2000; McPherson et al. 2005; Morgenroth 2011; Escobedo et al. 2011; Gillner 2012). Also, the present thesis addresses this topic.

Projections for the future development of the climatic conditions are predicted as becoming more extreme, especially in urban areas (McCarthy et al. 2010). Thereby the differences in environmental conditions between urban and rural areas can be large, while the spatial distances are small. Differences in plant phenology between urban and rural areas are reported (Roetzer et al. 2000; Chmielewski and Rötzer 2001; Mimet et al. 2009; Jochner et al. 2012), but the response of plants to climate change is still poorly investigated (Farrell et al. 2015). The setup of analyzing tree growth under urban as well as under rural conditions, gives a unique opportunity to fill this knowledge gap (Farrell et al. 2015; Youngsteadt et al. 2015), as urban trees are already more affected by changing climate conditions, which may result in both positive or negative effects on tree growth.

2. Research objectives

The research objectives of this dissertation are as follows:

1. To analyze the growth behavior of solitary versus stand-grown trees. Thereby the aim is to derive allometric relationships, which can help for management decisions, e.g. planting decisions or tree maintenance and care.

2. To analyze the growth reactions to growing conditions. In specific, two aspects of growing conditions are investigated. First, the influence of resource limitation, in form of the stand density for forest trees or sealed surface for urban trees is investigated. Second, the influence of climatic conditions, e.g. air temperature and precipitation. Thereby differences between urban and rural trees and between recent and past climate conditions are investigated across different climate zones.

3. Based on the consideration of urban trees, an overarching aim of this thesis is to project the effect of climate change on tree growth, as the urban climate (UHI effect) represents today climatic conditions which are forecasted for rural areas due to climate change.

4. Last but not least, the thesis aims at assessing and predicting tree functions and services. In specific, the estimation of biomass and the determination of important biomass predictors, as well as the determination of the corresponding carbon storage capacity of urban trees and forest stands are addressed in this thesis.

To answer the research questions the thesis is primarily based on the three following published papers out of my altogether five publications during the PhD period:

Dahlhausen, J., Uhl, E., Heym, M., Biber, P., Ventura, M., Panzacchi, P., Tonon, G., Horváth, T., Pretzsch, H. (2017). Stand density sensitive biomass functions for young oak trees at four different European sites, Trees, 31(6): 1811-1826.

Dahlhausen, J., Biber, P., Rötzer, T., Uhl, E., Pretzsch, H. (2016). Tree species and their space requirements in six urban environments worldwide, Forests 7(6): 111.

Dahlhausen, J., Rötzer, T., Biber, P., Uhl, E., Pretzsch, H. (2017): Urban climate modifies tree growth in Berlin. International Journal of Biometeorology.

A visualization how the different topics are realized in the three papers is given in Figure 4, which also shows how the three papers complement each other.

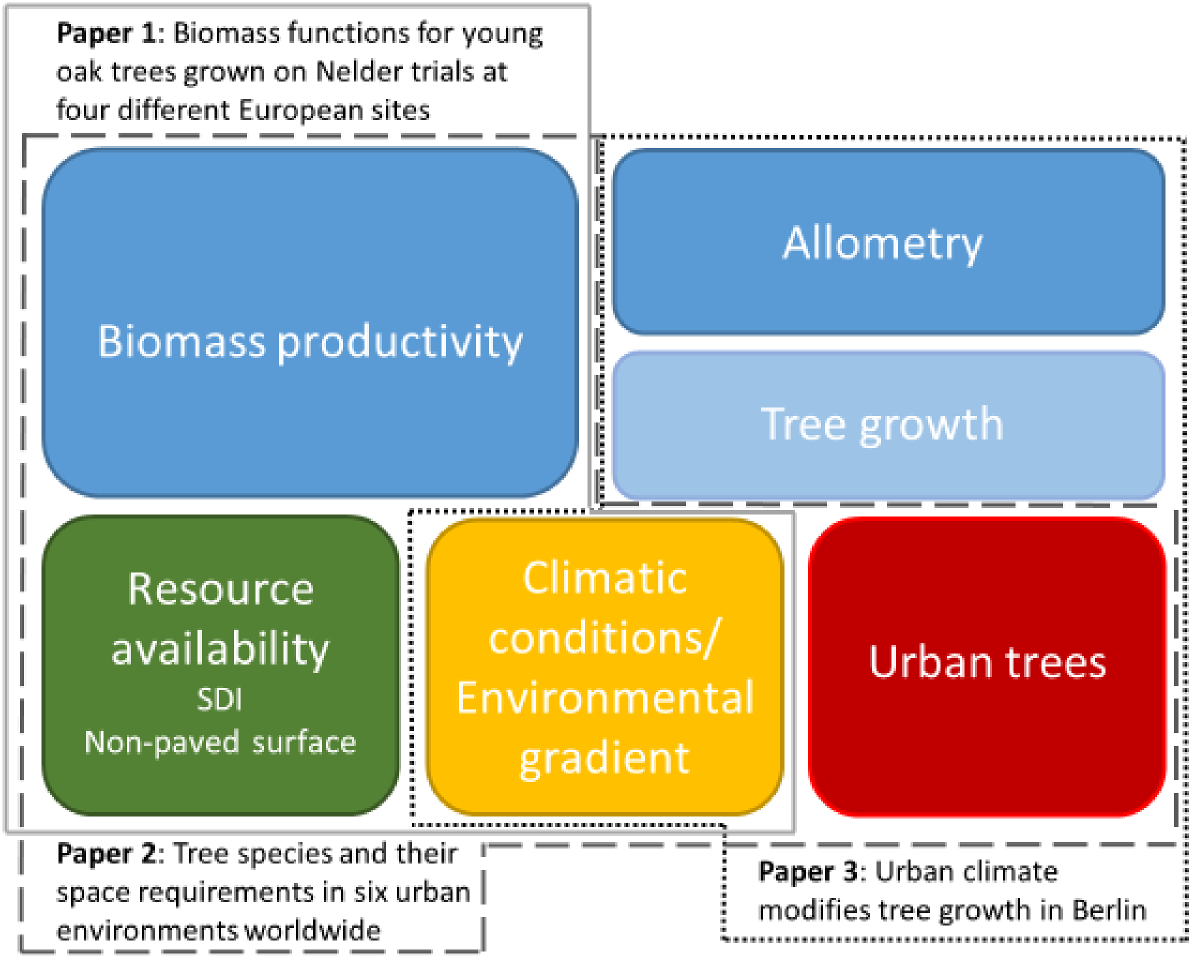


Fig. 4 Overview of the realization of the research topics in the three papers.

3. Material and Methods

3.1 Data collection 1: Nelder project

The first data collection of this thesis was part of the project 'Biodiversity, productivity, and C-sequestration of oak stands', which will be called Nelder project in the following. The Nelder project is founded by the AUDI Environmental Foundation (project term 01/2015 – 12/2019) and investigates the growth of pedunculate oak (*Quercus robur* L.) pure stand at different stand densities on various sites worldwide. The sampled data was the basis for the article 'Stand density sensitive biomass functions for young oak trees at four different European sites', investigating biomass productivity of different tree compartments and in specific the influence of competition level on biomass productivity.

3.1.1 Study design

While the Nelder project has seven investigation sites, for this thesis samples were taken on four sites, which are located close to the following cities in central Europe: Ingolstadt, Germany (ING650); Györ, Hungary (GYO651); Neckarsulm, Germany (NEC652) and Sant'Agata Bolognese, Italy (SAN653) (see Figure 5).

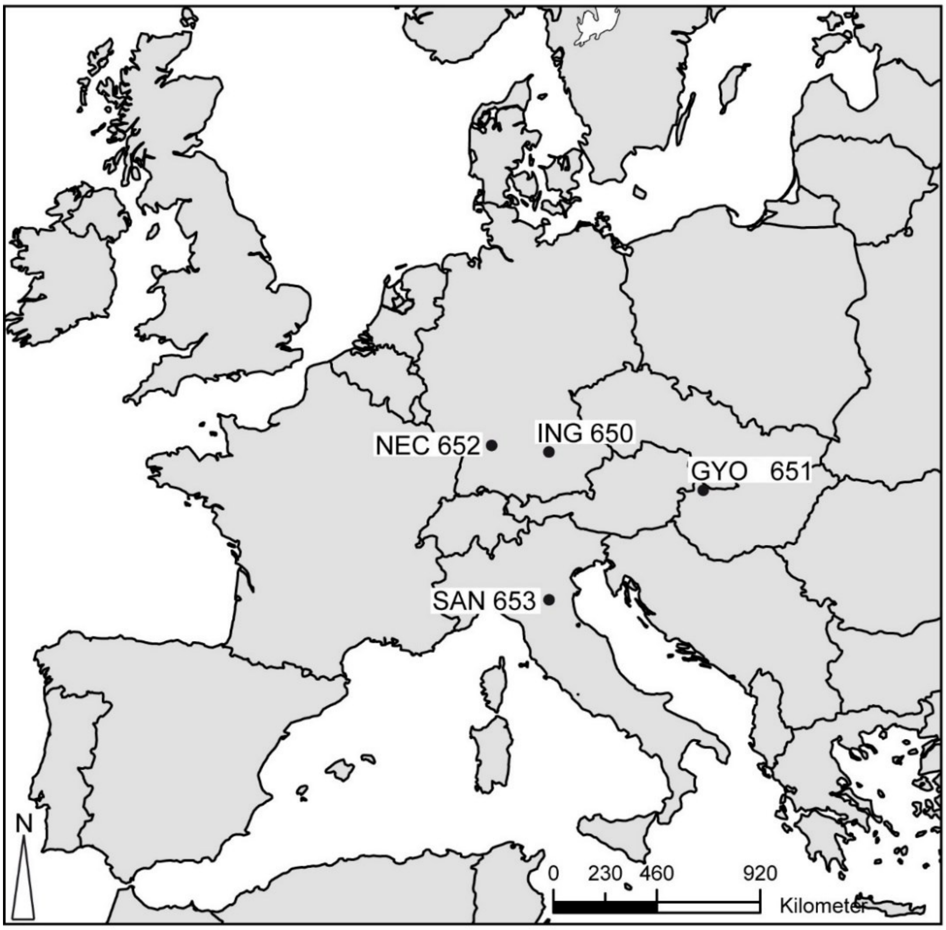


Fig. 5 Map of the sampling locations of this study

The sites were established between 2008 and 2010 as Nelder trials. The spacing trial design by Nelder (1962) can be described as an arrangement of concentric circles and radial spokes in a constant angle distance, which is 20° in the case of the present experimental sites (Figure 6). Thus, the trees in the Nelder design differ in their surrounding stand density, with high density in the center and decreasing density to the outer areas. With this planting design the competitive and facilitative effects, which occur simultaneously, can be analyzed and separated. While each of the investigated sites contains two full Nelder wheels, for this study only plants from surrounding quarter wheels, consisting of 4 (SAN653) or 5 (GYO651, NEC 652) spokes and 11 circles, and half wheels, which have 9 spokes and 11 circles (SAN635) were collected. In the case of ING650 the trees were also planted in quarter wheels but not strictly following the Nelder concept with its constant angle distances.

Looking at the climate conditions of the sampling sites (Table 1), these range from subcontinental (GYO651) to sub mediterranean (SAN653). The mean temperatures vary from 8.2 °C (ING650) to 13.2 °C (SAN653), while the highest mean annual precipitation amounts 760 mm (NEC652) and the lowest 537 mm (GYO651).

Based on the climate data the aridity index after De Martonne (DMI) was calculated as follows (de Martonne 1926):

$$\mathrm{DMI} = \frac{P}{T+10} \quad , \tag{1}$$

with P being the annual precipitation sum of the observation period and T being the mean air temperature for the observation period.

The DMI shows the highest value for NEC652 and the lowest for GYO651. As lower values represent higher aridity, this indicates that GYO651 is the most arid site, followed by SAN653. In comparison, the two German sites ING650 and NEC652 are more humid.

Table 1 Site description including location, longitude (long), latitude (lat), altitude (alt), mean annual temperature (T), mean annual precipitation (P), De Martonne Aridity Index (DMI), planting year (plant yr) and tree age in the year 2016 (age)

Site	Location	long [°E]	lat [°N]	alt [m]	T [°C]	P [mm]	DMI	plant yr	age [yr]
ING650	Ingolstadt (GER)	11.49	48.86	460	8.2	670	36.8	2008	10
GYO651	Györ (HUN)	17.60	47.79	110	11.1	537	25.5	2009	10
NEC652	Neckarsulm (GER)	9.35	49.05	380	9.1	760	39.8	2010	7
SAN653	Sant'Agata (ITA)	11.10	44.46	25	13.2	660	28.4	2010	8

3.1.2 Tree sampling and data preparation

On each investigation site 16 trees were sampled. For the selection of the trees the following criteria were applied: (1) no borderline trees for avoiding edge effects, (2) no neighboring trees and (3) only trees having all eight direct neighbors. Figure 6 visualizes a possible selection of sample trees in the case of a Nelder half wheel.

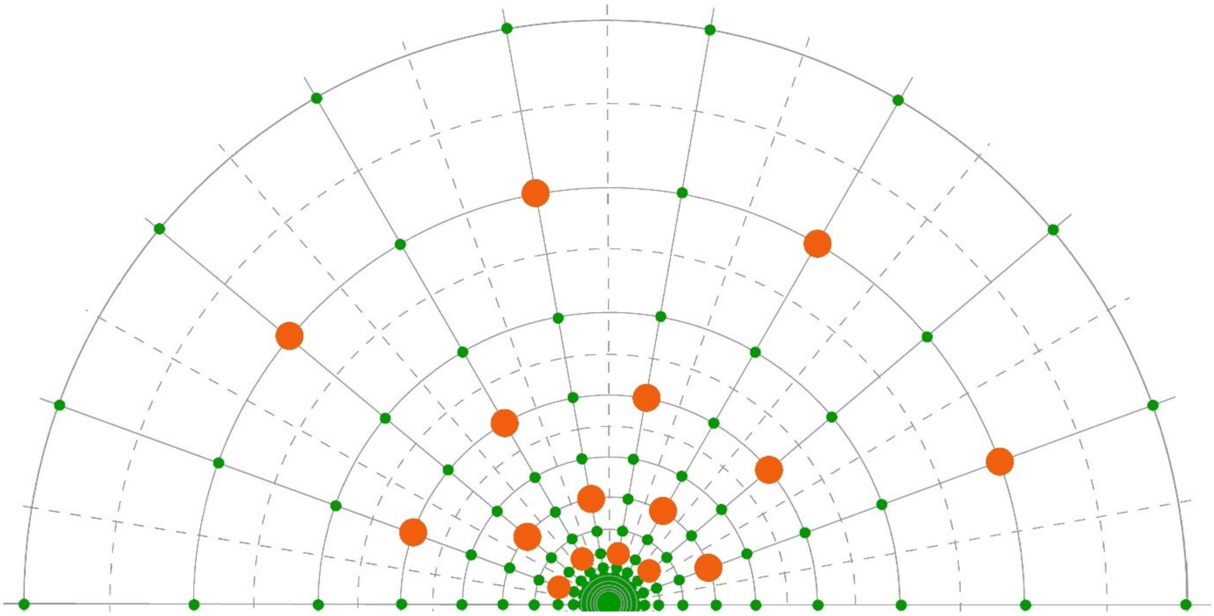


Fig. 6 Schematic representation of a Nelder half wheel (Nelder 1962). Plant positions (green dots) are defined by intersection points of concentric circles and radial spokes. The orange dots show the selected trees for sampling.

For each selected tree the following variables were measured: stem diameter at root collar (d_0), diameter at breast height (*dbh*, at a height of 1.3 m, if already achieved), diameter at crown base (*dcb*), tree height (*h*), height to crown base (*hcb*) and the crown radius (*cr)* in the eight cardinal directions. Hereafter the tree was carefully excavated, including all coarse and fine roots. After excavating the tree was dissected into four compartments: leaves, stem, branches and roots. All compartments per tree were not only directly weighed in the field, but also later in the laboratory after oven-drying for at least 24 hours. The wood density of each tree was determined by the hydrostatic weighing method. To this end, a piece of the stem at a height of 1 m was cut out and freed from bark. The range of the density values for each site are shown in Table 2, together with other tree variables.

As one research aim was to assess the influence of resource limitation, a local stand density index (SDI_l) was calculated for each of the four sites. The SDI_l was calculated by applying a search radius around the position of the tree of interest, whose extension was defined by the mean height of all trees in the quarter or half wheel multiplied by the factor 1.25. The number of trees inside the search radius was then considered as the number of competitors for the tree of interest. According to the following formula the SDI_l normalizes the stem number per hectare to a mean tree size of 25 cm.

$$\mathrm{SDI_l} = \mathrm{N}\left(\frac{25}{dg}\right)^{-1.605} \tag{2}$$

with N representing the stem number per hectare (excluding the tree of interest) derived from the stem number in the search radius, dg representing the quadratic mean diameter of all trees within the search radius and the exponent -1.605 referring to the generic stand density rule (Reineke 1933).

Table 2 Data collection 1 **-** Tree variables (mean values) for each sampling site; minimum and maximum values are given in parenthesis

Site	n	d_0 [mm]	dbh [mm]	h [m]	Density [g/cm³]	SDI_l
ING650	16	44.4 (27 – 63)	20.4 (12 – 39)	2.8 (2.0 – 4.1)	0.82 (0.73 – 0.92)	211 (155.4 – 280.3)
GYO651	16	30.9 (16 – 46)	12.6 (2 – 29)	1.9 (0.9 – 3.5)	0.76 (0.68 – 0.88)	150 (20.9 – 383.0)
NEC652	16	34.3 (20 – 53)	14.7 (5 – 30)	2.1 (1.3 – 2.9)	0.87 (0.76 – 0.94)	168 (4.8 – 688.4)
SAN653	16	44.9 (17 – 90)	13.7 (4 – 27)	2.4 (1.6 – 4.8)	0.79 (0.66 – 0.94)	266 (8.5 – 534.1)
All sites	**64**	**38.6** **(16 – 90)**	**15.5** **(2 – 39)**	**2.3** **(0.9 – 4.8)**	**0.81** **(0.66 – 0.94)**	**199** **(4.8 – 688.5)**

3.1.3 Estimation of tree biomass using linear regressions and Dirichlet regressions

Following data sampling and preparation, biomass was estimated first through the following four linear regression models differing in the predictor variables (d_0, h, SDI_l):

$$\ln W = \beta_1 + \beta_2\, ln\,(d_0) \tag{3}$$

$$\ln W = \beta_1 + \beta_2\, ln\,(d_0) + \beta_3 \ln(h) \tag{4}$$

$$\ln W = \beta_1 + \beta_2\, ln\,(d_0) + \beta_4 \ln(SDI_l) \tag{5}$$

$$\ln W = \beta_1 + \beta_2\, ln\,(d_0) + \beta_3 \ln(h) + \beta_4 \ln(SDI_l) \tag{6}$$

where, W refers to the estimated total biomass weight of a tree. These four models were fitted for total biomass, comprising the single compartments roots, stem, branches and leaves. This single-equation estimate of total biomass (in contrast to summing up separate compartment-wise estimates) has been recommended by previous studies, due to reduced assessment errors and better fitting results (Cienciala et al. 2008; Vejpustková et al. 2015). The normality of the residuals was tested with Q-Q plots.

Secondly the compartments biomass was estimated as the proportions of total biomass using Dirichlet regression. This type of regression is useful for modeling data representing components as percentage of the total (Poudel and Temesgen 2016). For each component c = 1 … C the compartment proportion y_c is given by the compartment biomass divided by the total biomass. These compartment proportions y = (y_1, …, y_C) have to fulfill the follwoing constraints: $y \in (0, 1)$ and $\sum_{c=1}^{C} y_c = 1$.

Under the assumption of Dirichlet distribution, which is a multivariate generalization of the beta distribution, where $\alpha_c > 0, \forall\, c$ are the shape parameters for each compartment,

$$D(y\,|\alpha) = \frac{1}{B(\alpha)} \prod_{c=1}^{C} y_c^{(\alpha_c - 1)} \tag{7}$$

the Dirichlet regression model can be formulated as follows:

$$log(\alpha_c) = \eta_c = X^{[c]}\,\beta^{[c]} \tag{8}$$

Thereby, $X^{[c]}$ represents a matrix of predictors, where the superscript indicates that the model allows for separate predictors in each compartment. This in turn potentially leads to different numbers of regression coefficients per compartment, which are captured in the column vector $\beta^{[c]}$. In the present thesis, however, we assume that all compartments are influenced by common covariates. Concretely, in line with the single equation models, the following equations (9) to (12) were fitted for the four compartments roots, stem, branches, leaves ($c = 1, \dots, 4$):

$$\ln(\alpha_c) = \alpha_{1c} + \alpha_{2c}\ln(d_0) \tag{9}$$

$$\ln(\alpha_c) = \alpha_{1c} + \alpha_{2c}\ln(d_0) + \alpha_{3c}\ln(h) \tag{10}$$

$$\ln(\alpha_c) = \alpha_{1c} + \alpha_{2c}\ln(d_0) + \alpha_{4c}\ln(SDI_l) \tag{11}$$

$$\ln(\alpha_c) = \alpha_{1c} + \alpha_{2c}\ln(d_0) + \alpha_{3c}\ln(h) + \alpha_{4c}\ln(SDI_l) \tag{12}$$

In a last step, the biomass productivity of the whole Nelder wheels at each site was projected. To do so, linear regression models with total biomass (kg) and aboveground biomass (kg) as the dependent variable were estimated. In accordance with the before estimated linear regression models 4 and 6, once d_0 and height, and once d_0, height and SDI_l were chosen as the independent variables. For each of the four investigation sites, the measured data (d_0, height, SDI_l) of all trees in the two full wheels was then inserted into the allometric equations. The estimated biomass was then extrapolated to Mg per hectare. To be able to compare the different locations, the projection calculation was based on data by the tree age of 6 years for each site.

The models for the total biomass were fitted using the software R 3.2.2 (R. Core Team 2015) with the function "lm" of the R package "stats" (R. Core Team 2015) and the compartments biomass was fitted using the R package "DirichReg" (Maier 2014).

3.2 Data collection 2: Metropolis project

The second part of the thesis is based on the project ‘Response of urban trees on climate change’, which was also founded by the AUDI environmental foundation (project term 07/2011 – 06/2014). This project, which is called Metropolis project in the following, focused on the growth and structure of urban tree species in different climate zones (depending on local environmental conditions). The data sampled in this project were the basis for the following articles underlying this thesis: ‘Tree species and their space requirements in six urban environments worldwide’ and ‘Urban climate modifies tree growth in Berlin’, as well as for the co-authored article ‘Climate change accelerates growth of urban trees in metropolises worldwide’. All three articles aimed at investigating the influence of an urban environment on tree growth and respectively biomass productivity.

3.2.1 Study design

Trees in ten different metropolises of the earth’s different climate zones, including the boreal (Sapporo, Japan; Prince George, Canada), temperate (Berlin, Gemany; München, Germany; Paris, France), mediterranean (Cape Town; South Africa; Santiago de Chile, Chile) and the subtropic climate zone (Hanoi, Vietnam; Brisbane, Australia; Houston, USA) were examined (see Figure 7).

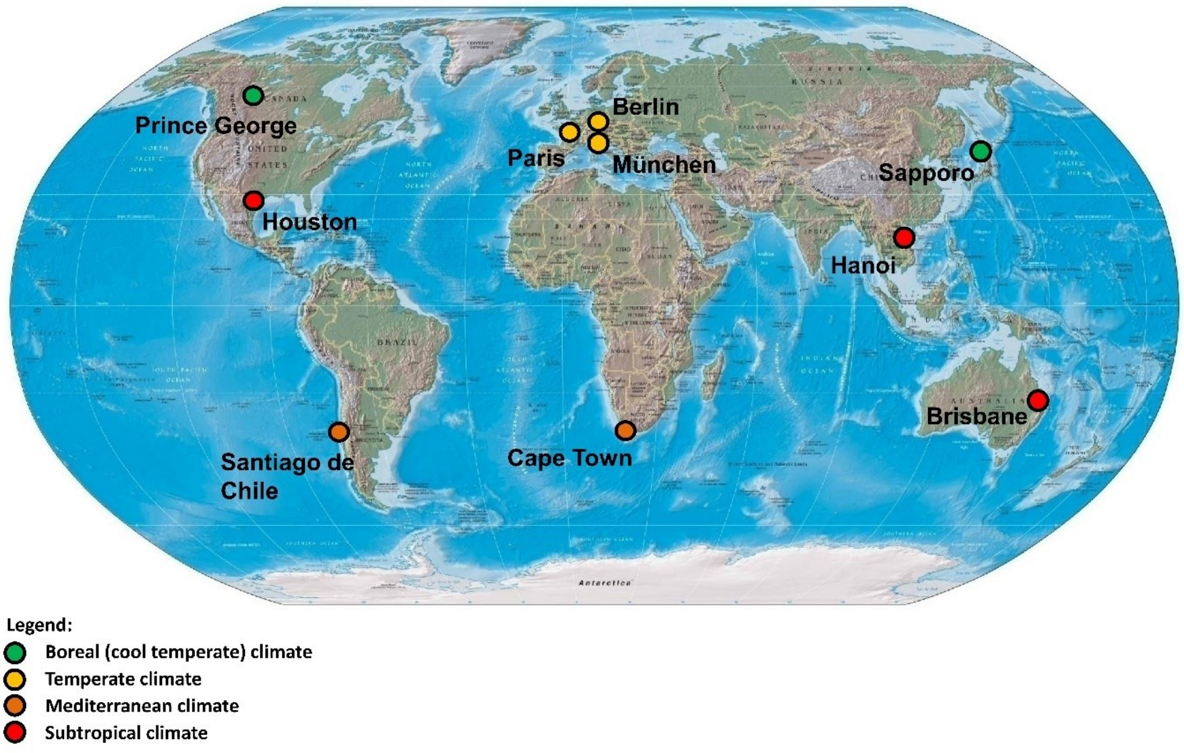


Fig. 7 Map showing the 10 sampling locations of the Metropolis project, distributed over four different climate zones.

To investigate the influence of the urban environment, increment cores were taken from trees along gradients from the city centre to the periphery (see Figure 8). Based on the sampled cores tree growth was analysed and related to environmental conditions, e.g. housing density.

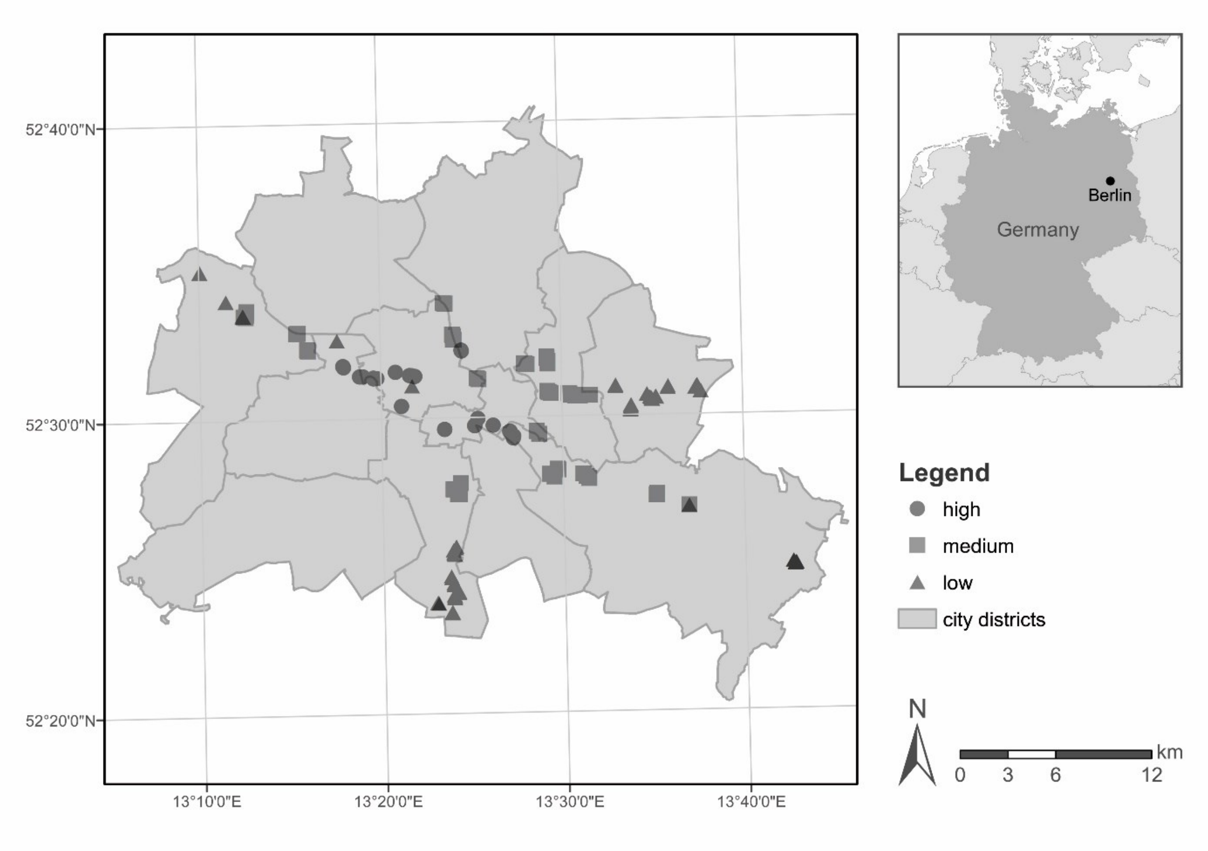


Fig. 8 Map of Berlin showing the distribution of the sample trees within the different districts and the respective housing-density (low, medium, high).

3.2.2 Tree sampling and data preparation

For the articles underlying the present thesis, a subsample of the above-mentioned urban tree data was used, once of six metropolises and once only the sample of Berlin. Looking at these data, the field campaigns took place between October 2010 and June 2014 in the cities of Berlin, Brisbane, Hanoi, Houston, Munich, and Paris. Altogether, the data comprises 1097 trees, with an average of 183 trees per city, a minimum of 126 trees (Brisbane) and a maximum of 252 trees (Berlin). In each city, the most common local urban tree species was chosen. Further selecting criteria for tree sampling were: (1) health, in order to exclude confounding effects caused by tree diseases; and (2) that the trees were not pruned. An overview of the selected cities and species is given in Table 3. The coauthored publication Pretzsch et al. (2017) takes the data of all ten metropolises into account. Further information on this publication and the sampled species can be found in the summary on page 20.

Table 3. Sample description of tree species, within the cities, geography (latitude, longitude), sampling size and time. Only trees in an urban environment are considered.

Species	**Common name**	**City**	**Country**	**Location**	**Number of trees**	**Sampling time**
Aesculus hippocastanum L.	Horse-chestnut	Munich	Germany	48.8°N 11.35°E	231	2013
Araucaria cunninghamii AITON ex. D.DON	Hoop pine	Brisbane	Australia	27.28°S 153.2 E	126	2013
Khaya senegalensis (DESR.) A.JUSS.	African mahogany	Hanoi	Vietnam	21.2°N 105.51°E	163	2012
Platanus x hispanica MÜNCHH.	London plane	Paris	France	48.51°N 2.21°E	171	2013
Quercus nigra L.	Water oak	Houston	USA	29.46°N 95.23°W	166	2014
Tilia cordata MILL.	Small-leaved lime	Berlin	Germany	52.31°N 13.24°E	252*	2010, 2012, 2013

* parts of the analysis (publication Dahlhausen et al. 2016) only included 240 of the 252 sampled trees

For all investigated trees diameter at breast height (*dbh*) was measured with a diameter tape. The crown radii (*r*) in eight cardinal and sub-cardinal directions was measured via the vertical sighting method, as suggested by Preuhsler (1981).The mean crown radius (*cr*) was calculated as the quadratic mean of the eight crown radii, as shown in Equation (13).

$$cr = \sqrt{(r_N^2 + r_{NW}^2 + \ldots + r_{NE}^2)/8} \tag{13}$$

Based on the mean crown radius, the crown projection area was then given by the following Equation (14), ensuring a bias-free transition between crown radius to crown projection area.

$$cpa = cr^2 * \pi \tag{14}$$

Tree height (*h*) and height to crown base (*hcb*) were recorded by using the Vertex IV ultrasonic hypsometer. Furthermore, the unsealed area around the stem base (*npa*) was measured for each tree in four cardinal directions with a measuring tape.

Table 4 gives an overview of the tree characteristics covered by the data. As can be seen, *A. cunninghamii* covers the broadest diameter range (15.7–129.5 cm), while the largest diameter was measured for *P. x hispanica* with 144 cm. The largest maximum *cr* with 14.8 m was also measured for *P. x hispanica*. The tallest tree was of the species *K. senegalensis* with 36 m, and this species also showed the highest range for ring widths. *A. hippocastanum* (232 years) and *P. x hispanica* (234 years) covered the largest age range within the sample.

Npa was largest for *A. cunninghamii* with 410 m^2, and smallest for *T. cordata*, *A. hippocastanum,* and *K. senegalensis* with 0.5 to 100 m^2.

Table 4 Data collection 2 - Mean, minimum and maximum values of tree variables for each species

Species		**dbh (cm)**	**cr (m)**	**h (m)**	**rw[1] (mm)**	**age (yr)**	**npa (m^2)**
Aesculus hippocastanum	Mean	63.6	5.5	16.1	1.61	118	15.1
	Min	27.2	2.9	7.4	0.3	17	1.0
	Max	116.9	9.0	27.2	7.9	249	100.0
Araucaria cunninghamii	Mean	40.7	3.5	17.3	3.6	52	79.8
	Min	15.7	1.6	6.1	0.7	19	3.9
	Max	129.5	11.6	33.5	6.5	182	410.0
Khaya senegalensis	Mean	73.4	6.5	22.6	5.3	53	11.2
	Min	44.1	3.1	14.1	0.6	13	1.0
	Max	123.1	11.7	36.0	18.5	142	100.0
Platanus x hispanica	Mean	64.8	6.6	18.8	2.5	104	33.6
	Min	40.3	2.7	6.8	0.4	20	2.0
	Max	144.0	14.8	34.5	10.9	254	140.0
Quercus nigra	Mean	61.5	7.1	15.9	4.0	52	33.8
	Min	34.2	3.4	10.0	0.8	16	1.5
	Max	98.0	11.9	22.8	12.5	101	150.0
Tilia cordata	Mean	45.5	5.1	16.3	1.6	85	25.3
	Min	25.2	2.5	8.1	0.2	34	0.5
	Max	81.1	9.5	29.1	5.3	194	100.0

[1]rw = ring width

Based on the *npa* the variable *SCON,* which expresses the degree of confinement due to soil sealing like asphalted pavement or concrete surfaces, was calculated as follows in Equation (15):

$$SCON = 1 - \frac{npa}{cpa} \tag{15}$$

where *cpa* is the crown projection area (m^2) and *npa* is the measured non-paved area (m^2).

3.2.3 Increment core collection and Dendrochronology

In addition, two increment cores were taken from each tree at breast height using a 5 mm increment borer. At least two cores at an angle of 90° were taken for minimizing the error rate due to a non-concentric growth. Where possible the coring was done once from North and once from East direction. The cores were polished on a sanding machine. After preparation the tree-ring widths were measured with a Digital Positiometer after Johann (Johann 1977) using the software Lignometer. Information on the ring width for each of the is given in Table 4. Radius was derived by backwards calculation using the year ring width values. Out of this, the basal area was calculated by means of quadratic mean radius of the two cores per tree. Current annual increment was examined by the difference between the basal areas of two consecutive years. In contrast to diameter increment, basal area increment is directly related to a tree's biological production (Assmann 1961) and thus more appropriate for allometric analyses.

Cross-dating was conducted first visually and then by using the dplR library in R (Bunn 2008). Dimensionless ring-width index (RWI) was calculated by fitting a smoothing spline of 0.67 of series length with a 50% frequency cut-off. Strength of the common signal is expressed by the Expressed Population Signal (EPS) value using a 50-year moving window. A resulting EPS value above 0.84 (Wigley et al. 1984) indicates an adequate strength of the common signal for the time series and confirms further use of the data.

3.2.4 Allometry

Plant allometry is a concept used in this thesis to relate tree dimensions to each other as well as to relate plant size variables to increment. Due to its strong theoretical foundation (Enquist and Niklas 2001; Niklas 2004; West et al. 2009) and its mathematical compactness the concept is a powerful tool for applications in science and practice (Pretzsch et al. 2013). Commonly it is used in the double-logarithmic form of the allometric equation (Equation (16)), especially in empirical studies, because it makes the relation between two plant variables x and y, say x = stem diameter, y = height, accessible to linear regression models.

$$\ln y = a + \alpha * \ln x \tag{16}$$

Here, the constant a is the logarithmized allometric scaling coefficient and α is the allometric exponent, which expresses the slope of the curve. Thus, allometry delivers the information how one plant dimension changes, if a second plant dimension changes, whereby the ratio of the two variables stays constant.

In this thesis, the following two allometric models (Equations (17) and (18)) were fitted to link basal area to vertical and horizontal space requirements:

$$\ln h_i = \beta_0 + \beta_1 * \ln dbh_i + \varepsilon_i \tag{17}$$

$$\ln cr_i = \beta_0 + \beta_1 * \ln dbh_i + \varepsilon_i \tag{18}$$

where *h* is tree height, *cr* crown radius, and *dbh* is a tree's diameter at breast height. The latter can be easily obtained if basal area is known by $dbh = \sqrt{ba * 4/\pi}$. Both models were fitted city-wise by ordinary least squares (OLS) regression.

Further a linear mixed effects model (Equation (19)), which describes the allometric relationship between the annual basal area increment *iba* (cm²/yr) and the corresponding basal area *ba* (cm²) at the beginning of the corresponding year was fitted to the retrospective tree growth data of each city.

$$\ln iba_{ij} = \beta_0 + \beta_1 * \ln ba_{ij} + b_i + \varepsilon_{ij} \tag{19}$$

The indexes i and j represent the j^{th} observation of the i^{th} tree, β_0 and β_1 are fixed effect parameters, b_i is a random effect on tree level with $b_i \sim N(0, \tau^2)$, and ε_{ij} are i.i.d. errors.

To estimate the influence of spatial restriction on basal area increment, the variable *SCON* is added to the model (Equation (20)). The variable describes the confinement of a tree's growing area by soil sealing and was assessed in three categories: total absence of non-paved area (0), medium limitation (0.5), and maximum limitation (0.9).

$$\ln iba_{ij} = \beta_0 + \beta_1 * \ln ba_{ij} + \beta_2 * SCON_i + b_i + \varepsilon_{ij} \tag{20}$$

For this model only the tree growth data after 1980 were used, because the non-paved area was only measured once at survey time, and we refrained from assuming it was in effect for four decades or more. Possibly due to the comparably short time series from the restricted data set, we did not obtain plausible estimates for the allometric slope β_1 when fitting Equation (20). We therefore decided to keep the allometric slopes β_1 from the fitted Equation (20), and to use the following model (Equation (21)) for assessing the influence of *SCON*:

$$\ln iba_{ij} - \beta_1 * \ln ba_{ij} = \alpha_0 + \alpha_1 * SCON_i + b_i + \varepsilon_{ij} \tag{21}$$

Here, α_0 and α_1 are the fixed effects parameters to be estimated with the model. Thus, for estimating a tree's basal area increment *iba* from its basal area *ba* under a given spatial confinement *SCON*, without considering tree-specific random effects, the Equation (22) can be used:

$$\widehat{\ln \iota ba} = \alpha_0 + \beta_1 * \ln ba + \alpha_1 * SCON \tag{22}$$

Analogously, if the spatial confinement effect shall not be considered explicitly in the estimation of basal area increment, the fit results of Equation (19) can be applied with Equation (23):

$$\widehat{\ln \iota ba} = \beta_0 + \beta_1 * \ln ba \tag{23}$$

Both equations allow for estimating a tree's temporal basal area development by using them in the following alternative serial calculations (Equations (24) and (25)):

$$ba_{t+1} = ba_t + e^{\alpha_0+\beta_1*\ln ba_t+\alpha_1*SCON} \tag{24}$$

$$ba_{t+1} = ba_t + e^{\beta_0+\beta_1*\ln ba_t} \tag{25}$$

The index *t* represents one point of time, *t* + 1 is the point of time one year later. Starting with a given initial value for basal area ba_{t_0}, basal area development for any reasonable time span can be projected. For the presented study $ba_{t_0} = 78.54$ cm^2 was chosen as a common initial value, which corresponds to a diameter at breast height of 10 cm, a size at which urban trees are often planted, and basal area development was projected for 200 years.

3.2.5 Quantification of general growth trends in urban versus rural areas

The influence of the urban environment on the general growth trend was analyzed for the city of Berlin, based on the 252 sampled trees (*T. cordata*). To do so, first only the growth of the trees in low-dense areas was analyzed, to exclude the urban impacts, and thereafter the growth of trees in high-dense areas was analyzed. For the analysis, the data set was split into the two periods, 1961 - 1990 and 1991 - 2011. One reason for dividing the data set in the year 1990 were the increased urban development measures starting in Berlin after 1990 (Schmelcher 2011). With the data up to 1990 a biologically plausible and thus extrapolatable growth equation was fitted to each tree's basal area development. Comparing the extrapolated model's predictions with the real basal area development after 1990 then reveals growth trends in the second period. For the extrapolation, we chose the Bertalanffy growth function (Zeide 1993), supplemented by an additional additive parameter *c* which covers the uncertainty of tree age estimation.

$$\widehat{ba} = c + a * (1 - e^{-bt})^3 \tag{26}$$

Where $\widehat{ba}$ is the estimated basal area (cm²/yr), t is the tree age, a and b are the parameters of the original Bertalanffy equation and c is an additive parameter covering the uncertainty of tree age estimation. The parameter estimates for each tree were obtained by nonlinear least squares regression.

The annual deviations (Δba) of a tree's actual basal area (ba) from the extrapolated Bertalanffy curve values ($\widehat{ba}$) obtained from Equation (26) were calculated as

$$\Delta ba_{ij} = ba_{ij} - \widehat{ba_{ij}} \qquad (27)$$

with the indices i and j referring to a given tree and a given calendar year, respectively.

For further use the subsequent calculation of the basal area increment (iba) was derived by building the difference of the recent Δba value with the previous year value:

$$\Delta iba_{ij} = \Delta ba_{ijx} - \Delta ba_{ij(x-1)} \qquad (28)$$

with x indicating the current calendar year.

3.2.6 Estimation of tree biomass

This Metropolis project dealt with urban trees, for which it was only possible to measure certain variables, but not to excavate and weigh the trees. Thus, for the biomass estimations of this data set existing biomass equations had to be applied. The following species specific equations for estimating aboveground woody biomass were used: Jenkins et al. (2003) for *A. hippocastanum*, Eamus et al. (2000) for *A. cunninghamii*, Clément (1982) for *K. senegalensis*, Yoon et al. (2013) for *P. x hispanica*, Clark et al. (1985) for *Q. nigra*, and Čihák et al. (2014) for *T. cordata*. Excepting the equation for *P. x hispanica*, which is based on urban tree data, these biomass equations are based on forest tree data, and thus on trees under competition by other trees. Trees in urban areas are mostly solitary grown, which calls the applicability of the above-mentioned equations into question. To account for this a factor of 0.8 (McPherson et al. 1994; Nowak and Crane 2000) was applied to the traditional biomass equations. Based on the estimated aboveground biomass the related carbon storage was determined by multiplying the biomass with 0.5 (Intergovernmental Panel on Climate Change et al. 2003).

4. Results

4.1 Tree growth and tree allometry for solitary grown and stand grown trees

Tree growth and in specific allometric relationships between different tree growth parameters were investigated for urban trees, as well as for trees in forest stands. Starting with the allometric relationships of solitary grown trees, Figure 9 shows the results of a 200-year time series estimated based on measured tree and year ring data for six different tree species in six metropolises. For each metropolis, a widely distributed tree species, well adapted to its environment, was chosen. Thus, the results do not represent a mere species comparison. Even though all chosen tree species are well adapted to their respective urban environment, the results show strong differences between tree species and cities respectively. Concerning the stem diameter, the highest growth over time could be found for *K. senegalensis* in Hanoi, the lowest growth was found for *T. cordata* in Berlin. By the age of 100 years the dbh of *K. senegalensis* amounted 92 cm and for *T. cordata* 42 cm. Also for the relationship between height and diameter the upper level was marked by *K. senegalensis* in Hanoi, while the lowest level was found for *A. hippocastanum* in Munich until an age of 130 years. For the relationship of crown radius to diameter *Q. nigra* from Houston marked the upper limit with 9 m by the age of 100 years whereas the species *A. cunninghamii*, *T. cordata* and *A. hippocastanum* showed a crown radius of about 5 m.

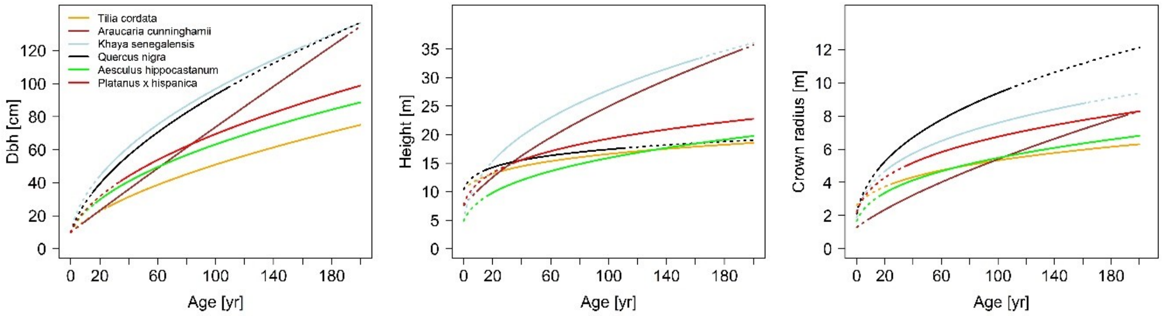


Fig. 9 Allometric relationships for (left) diameter at breast height; (middle) tree height; and (right) crown radius based on allometric model parametrizations for six tree species. Dotted lines show projections which are not covered by measured data.

To be able to analyze whether the allometric relationships are different for open grown trees versus trees in (urban) forests, three quantile regressions were run on the urban tree data. Concretely, the allometric relationship between crown radius and diameter was fitted (1) for the 95% quantile, representing open-grown trees which typically show a broad crown, (2) for the 50% quantile, representing the average tree and (3) for the 5% quantile, representing suppressed trees. The analysis was run for five of the six species mentioned above. The *Q. nigra* trees in Houston could not be considered for this analysis, as the data collection took part at a later point. Instead the results of *Q. robur* will be shown. This subsample is based on the data collection of the Metropolis project in Cape town. Further for *Q. robur* and *T. cordata* stand-grown trees, from long term research plots in Southern Germany were considered. For the other species only the data gathered in the Metropolis project from street trees, trees in parks and trees in urban forests were analyzed. The results of the quantile regressions are shown in Figure 10.

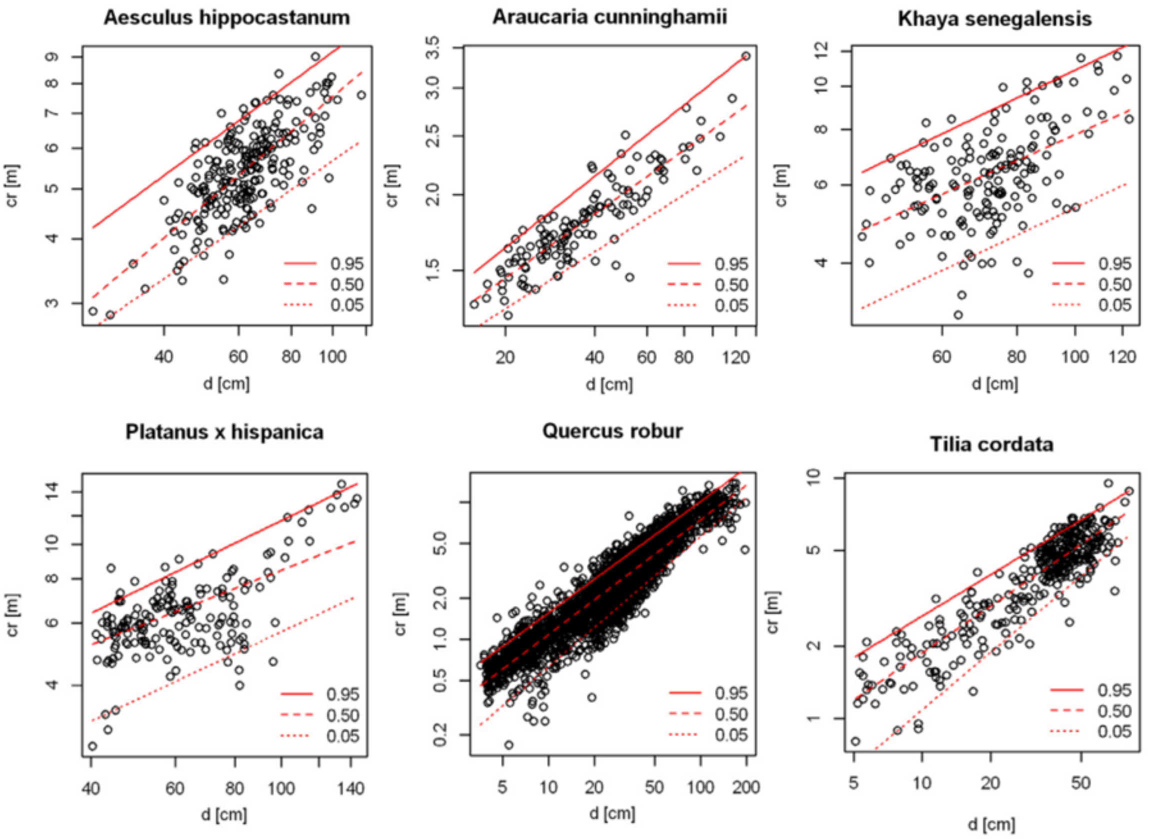


Fig. 10 Quantile regression results (95%, 50%, and 5% quantiles) for the allometric relationship ln(cr) = a + α * ln(d) for six species (in alphabetical order).

The analysis reveals different information. First, looking at the allometric relationship, differences between the tree species in their respective environment can be observed. While *A. hippocastanum, K. senegalensis, P. x hispanica* and *T. cordata* show a rather large crown radius and a moderate slope, *A. cunninghamii* shows a small crown radius and flat slope. For the *Q. robur* trees a medium crown radius, but steep slope can be reported.

Second, the quantile regression reveals that the differences between stand grown and solitary grown trees is also dependent on the species or the environment respectively. Smallest difference is found for *Q. robur*, which might be explained by the fact that this subsample consists of mainly stand-grown trees. For *Q. robur* and *T. cordata* the difference between open grown and forest grown trees further decreases with increasing diameter. On contrast, the difference increases for *A. cunninghamii*, or stays constant for the other three species.

Summing up, differences in tree growth over time were identified between species. These differences might be explained by differences in the growth behavior between the species, but also by differences in the environmental conditions. Results of three quantile regressions supports the assumption that it is a combination of both, as the tree species differed in the allometric relationship between crown radius and diameter, as well as in their growth behavior related to the environmental conditions (stand-grown versus open-grown). The following chapter looks in detail at possible influence factors on tree growth.

4.2 Influences on tree growth

4.2.1 Resource availability

The resource supply of a plant is highly dependent on the level of competition. In the case of forest stands this competition is mainly determined by the neighboring trees. As outlined earlier, the Nelder design allows to investigate productivity of forest trees under different competition levels.

The results of the linear regression models (Equations 3-6) revealed the expected negative influence of stand density on biomass. The higher the stand density, the lower the biomass productivity. This can also be seen in Figure 11a, which illustrates the projected biomass productivity ((1) total biomass predicted by d_0 and height, (2) total biomass predicted by d_0, height, and SDI_l and (3) aboveground biomass predicted by d_0 and height) for each of the four investigated sites in dependency on the stand area per plant.

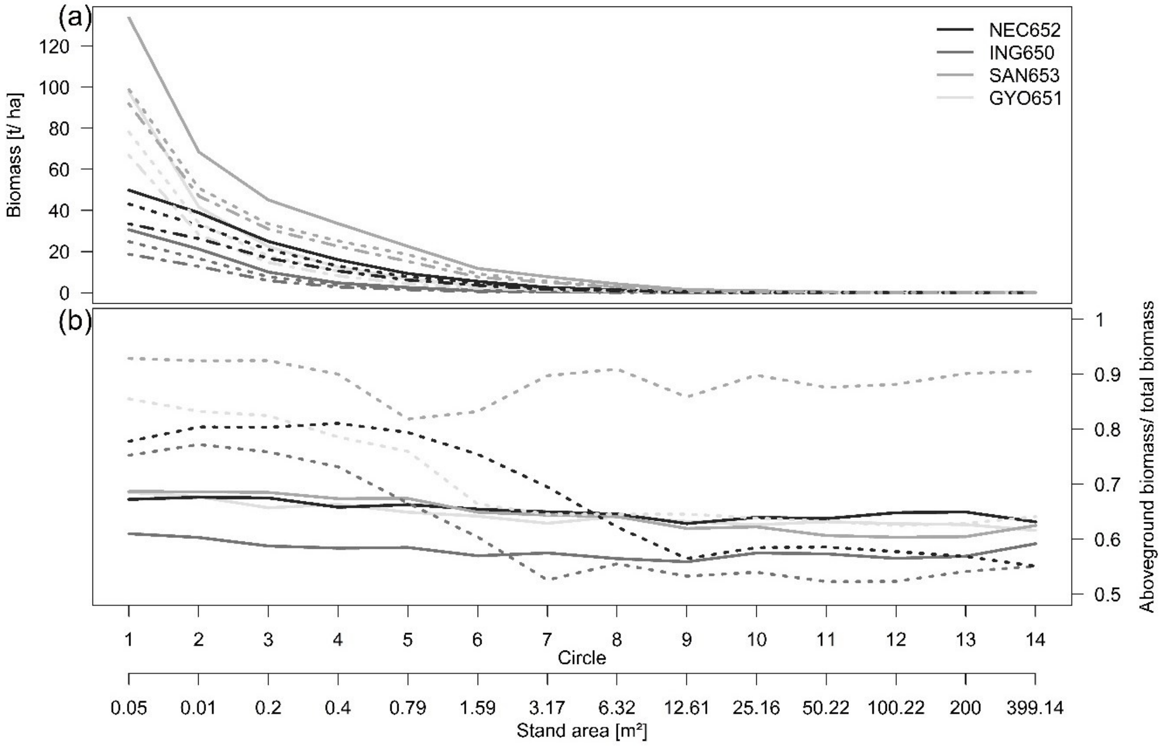


Fig. 11 Projected biomass productivity per site (a) and relation of aboveground to total biomass (b). Solid lines represent biomass productivity estimations using d_0 and height as predictors (Equation 10), dashed lines represent total biomass productivity estimations using d_0, height, and SDI_l as predictors (Equation 12) dash-dotted lines represent aboveground biomass productivity estimations using d_0 and height as predictors (Equation 10).

The course of the projected biomass is the same for all sites and the three estimations per site show a parallel course. Thereby the graph for the estimated aboveground biomass is logically on a lower level than the graphs visualizing the projected total biomass. Comparing however the estimations with and without the SDI_l, it is remarkable that for all sites the projected biomass productivity is on a lower level when considering the SDI_l. Thereby the differences between the two models (with SDI_l and without SDI_l) decrease with decreasing plant density. At stand densities realized from circle eight (= 1582 N/ha) upwards productivity related to area seems almost neglectable.

Looking at the ratio of aboveground biomass to total biomass (Figure 11b) allows to analyze the effects of inter-tree competition in more detail, concretely to analyze the effect on the proportion of above- and belowground biomass. In the model with d_0 and tree height as predictors, the aboveground biomass, accounted for 50 - 70% of total biomass and respectively belowground biomass accounted for 30 to 50% of total biomass independent of the different stand areas. In difference, when considering the SDI_l as an additional predictor for biomass, the ratio remained constant only for the site SAN653, with aboveground biomass accounting for 80 – 90 % and belowground biomass respectively for 10 – 20%. For the other three sites (NEC652, ING 650, GYO651) aboveground biomass accounted for about 80% when the stand density is high. From stand densities realized from circle four (= 25000 N/ha) upwards, however, the ratio shifted to 30 – 50% belowground biomass and only 50 – 70% aboveground biomass.

The results show that the consideration of the plant density is important when projecting biomass productivity, as it shows a strong and significant influence. Thereby the findings in Figure 11b indicate that resource competition induced by high stand densities has a stronger effect on belowground biomass than on aboveground biomass. The findings in Figure 11a further indicate an overestimation of biomass when not considering the factor stand density.

In the case of solitary grown urban trees the resource supply is limited by surrounding buildings as well as by the sealed surface, leading to a reduced belowground resource availability, e.g. water supply. Considering three different levels of confinement (no limitation (SCON = 0), 50 % limitation (SCON = 0.5) and high limitation (SCON = 0.9)), the limitation of belowground resource availability on tree growth was statistically tested for six metropolises (see Tab. 5). Looking at the results shows that, besides for *Q. nigra* in Houston, a higher level of confinement led as expected to a lower tree growth. The effect of SCON on tree growth however was only significant for *K. senegalensis* in Hanoi, *A. hippocastanum* in Munich and *Q. nigra* in Houston. The not-plausible positive coefficient for the effect of sealed surface on tree growth in Houston can be explained by little variation in the level of confinement within this subsample. Focusing thus on the cities Hanoi (*K. senegalensis*) and Munich *(A. hippocastanum*), Figure 12 shows the effect of SCON on the allometric growth relationships for the tree parameters *dbh*, *h* and *cr*. As can be seen, a much stronger effect was found for *K. senegalensis* in Hanoi than for *A. hippocastanum* in Munich. For *A. hippocastanum* the differences between the three confinement classes were very small for all three analyzed tree parameters. In opposite, the differences for *K. senegalensis* were much higher between SCON = 0.5 and SCON = 0.9. The third class, no limitation did not exist in Hanoi.

Table 5 Linear regression results for Equation (21) for the basal area—basal area increment allometry and the influence of SCON (α_1) for all six species (ordered according to latitude)

Species	α_0	**SE** (α_0)	p (α_0)	α_1	**SE** (α_1)	p (α_1)	τ^2
A. cunninghamii	−4.6109	0.0769	0.0000	−0.0005	0.1116	0.9964	0.0765
K. senegalensis	−3.4053	0.3660	0.0000	−1.4998	0.3928	0.0002	0.2249
Q. nigra	−5.5567	0.1794	0.0000	0.7648	0.2221	0.0007	0.2222
P. x hispanica	−4.9857	0.2699	0.0000	−0.5632	0.3251	0.0856	0.3752
A. hippocastanum	−5.3079	0.0997	0.0000	−0.4056	0.1306	0.0022	0.2028
T. cordata	−5.7364	0.1721	0.0000	−0.1285	0.1954	0.5119	0.1868

Parameter estimates (α_0, α_1) with standard errors (SE), significances (p), and the variance of the random effect (τ^2).

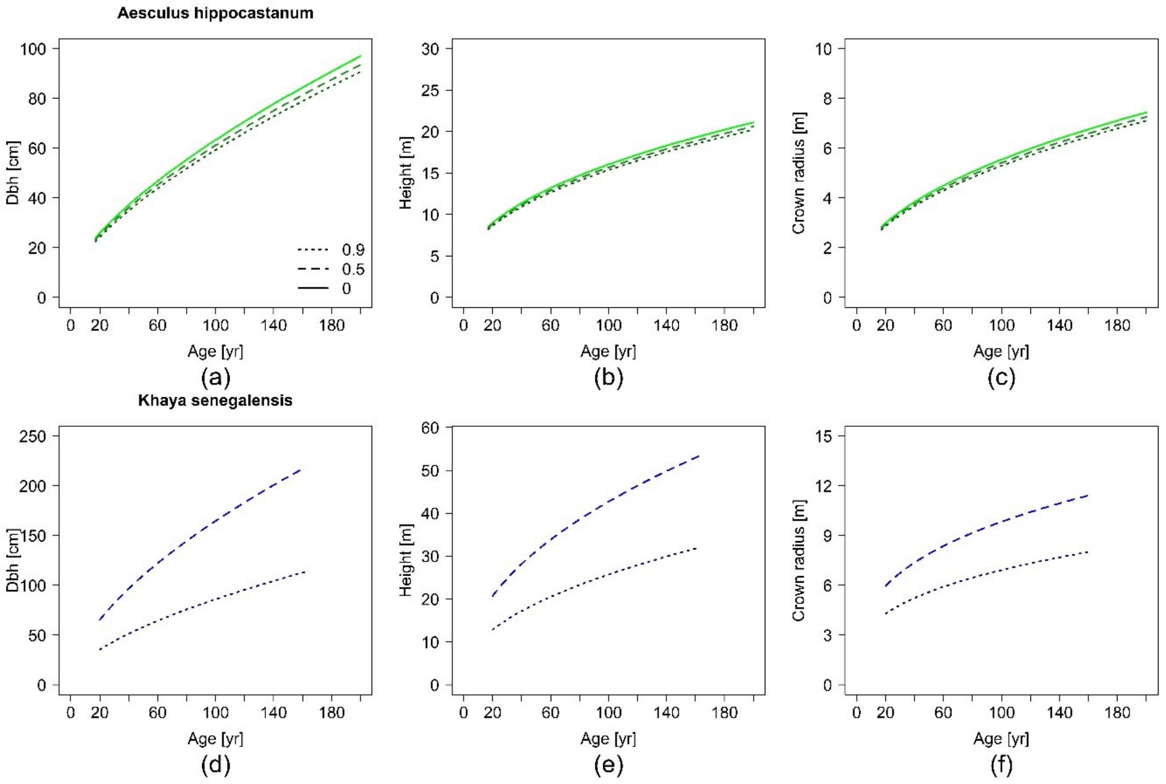


Fig. 12 Effect of SCON on allometric growth relationships for diameter at breast height, tree height, and crown radius depending on age for the species *Aesculus hippocastanum* (panels a–c) and for *Khaya senegalensis* (panels d–f); solid line: no limitation, dashed line: 50% limited, and dotted line: highly limited (90%).

Summing up, the results show that for both, stand-grown and solitary grown trees, higher competition or inhibition respectively leads to reduced growth and thus reduced biomass. Even though the environments are contrary and the kind of inhibition (inter-tree competition versus sealed surface) is contrary, both leads to a reduced resource availability, which is likely to be the reason for the reduced growth. The findings are of high interest, as especially the level of confinement in urban areas, is an anthropogenic modification. In other words, the level of confinement seems to be a possibility to take influence on tree growth.

4.2.2 Climate impact

Besides the influence of competition and thus resource availability on tree growth, this thesis aimed at investigating the effect of climatic conditions on tree growth.

In the first data collection, investigating biomass on Nelder trials, four sites differing in their environmental conditions were compared. The results show that SAN652 is the most productive site, followed by GYO651, NEC653 and finally ING650 (Figure 11). This order indicates a trend related to the site conditions, as SAN652 and GYO651 represent the more arid sites. However, a causal effect cannot be stated based on the available data and performed analyses.

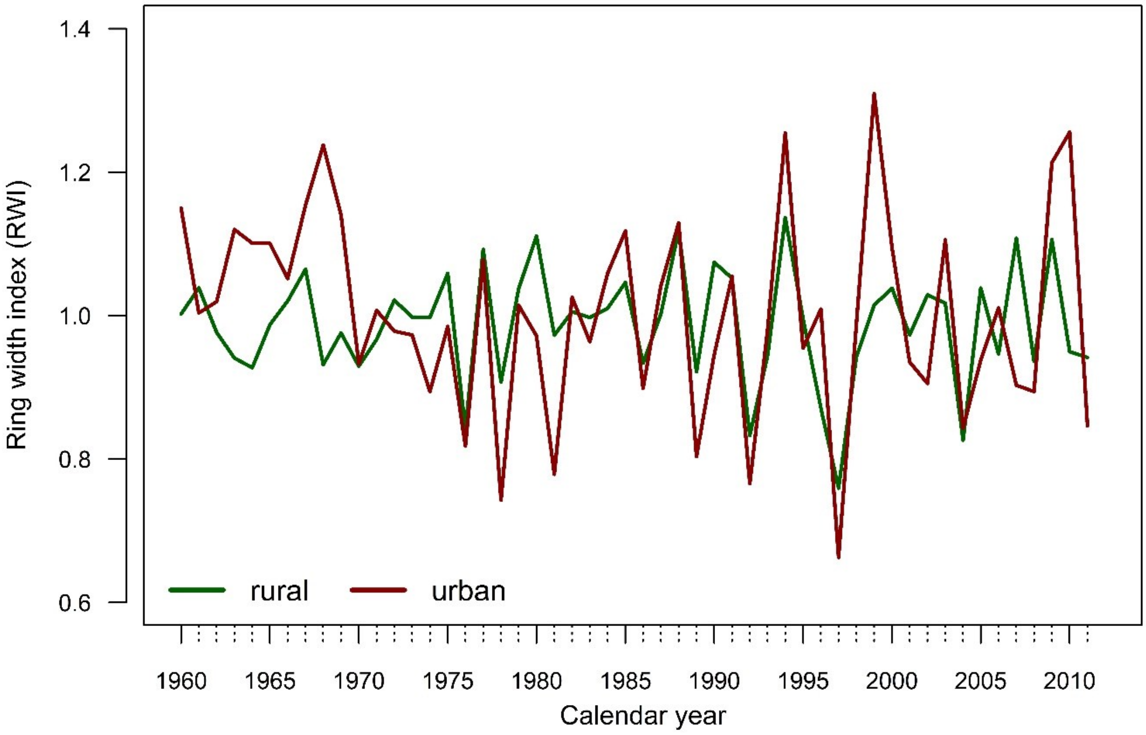


Fig. 13 Annual growth course (RWI) from the trees grown in the city center (red) and in the peripheral surroundings (green) of Berlin for the period 1961 – 2011.

Due to the fact that the urban environment is already today characterized by changing climate conditions the analysis of the influence of the urban environment on tree growth was of specific interest. Comparing the annual growth rates from trees in the city center versus in the outskirts of the city of Berlin, Figure 13 illustrates that, at least after 1990, the growth of the urban *T. cordata* trees was higher than in the rural areas of the city. A possible explanation for this finding are the warmer conditions in the city center, as well as the lower precipitation after 1990 (Figure 2). Thereby it is conspicuous that the urban trees show a higher variation in growth.

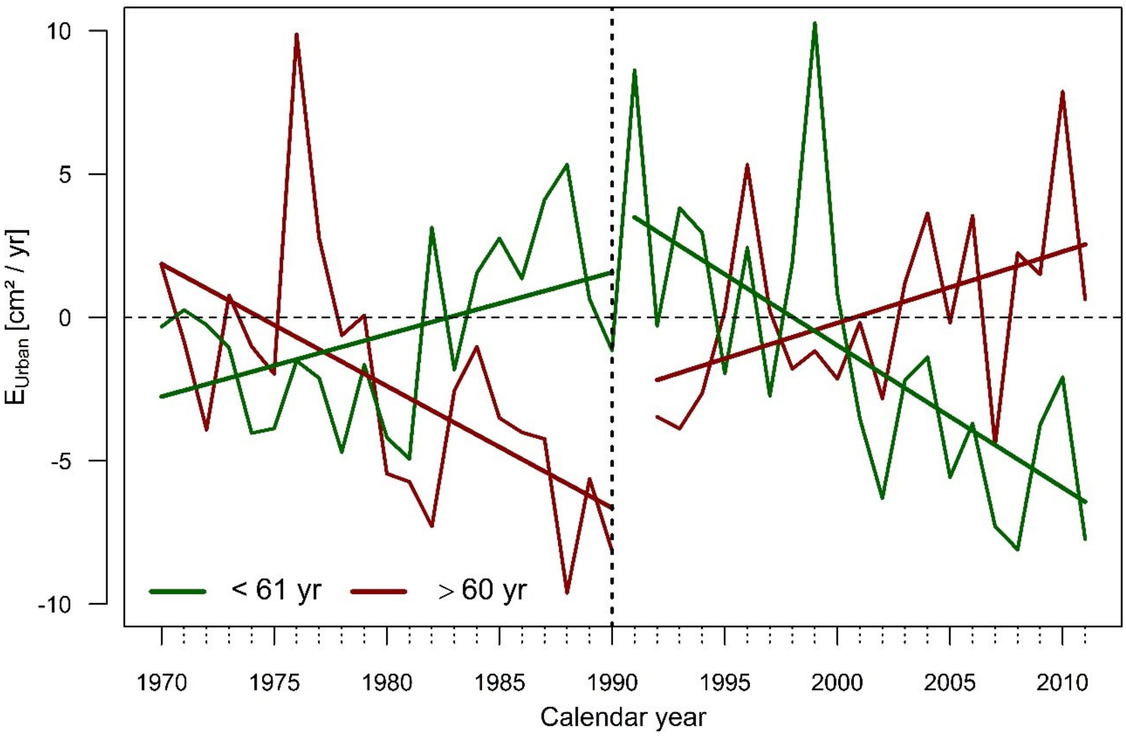


Fig. 14 Effect of urban climate on tree growth ($E_{\text{Uurban}} = \overline{\imath ba}_{\text{hd}} - \overline{\imath ba}_{\text{ld}}$) shown for two age classes < 61 years (green) and ≥ 61 years (red), with the bold lines indicating the linear trend for the respective age classes and observation periods.

Figure 14 visualizes the growth of *T. cordata* in areas with high versus low building density in the city of Berlin or in other words the effect of the urban environment on tree growth. Thereby the increment growth of trees younger 60 years was compared to the growth of trees older 61 years. Further the periods before and past 1990 were regarded separately.

Interestingly the results for the two periods, as well as the results of the younger and the older trees, are almost inverse. Before 1983 and after 2000 the young trees showed higher growth rates in the rural areas, whereas in the period between 1983 and 2000 the growth of the young trees was higher in the city center. Contrarily the trees older 61 years showed higher growth rates in the urban areas before 1979 and after 2003, whereas in between the growth rates of these older trees were higher in the peripheral areas.

Results of a mixed linear regression model further showed that, after 1990, in high-dense areas higher air temperature and less precipitation led to higher growth rates. In contrast, in low-dense areas no significant relationship between air temperature, precipitation and tree growth could be found.

Summing up, the results show that the urban environment leads to higher growth rates. In specific the higher growth rates seem to be a result of higher air temperatures and less precipitation. A comparison of different forest sampling sites leads to the same impression, that warmer and drier climatic conditions lead to higher tree growth and biomass productivity respectively.

4.3 Biomass productivity and carbon storage

As part of this thesis biomass productivity of urban as well as of forest grown trees was estimated. The biomass productivity is of special interest as it is directly related to the carbon storage capacity of a tree.

Starting with the solitary grown, urban trees, Figure 15 shows the amounts of produced aboveground biomass (estimated based on species-specific equations from literature) over age for the six tree species investigated under urban environmental conditions.

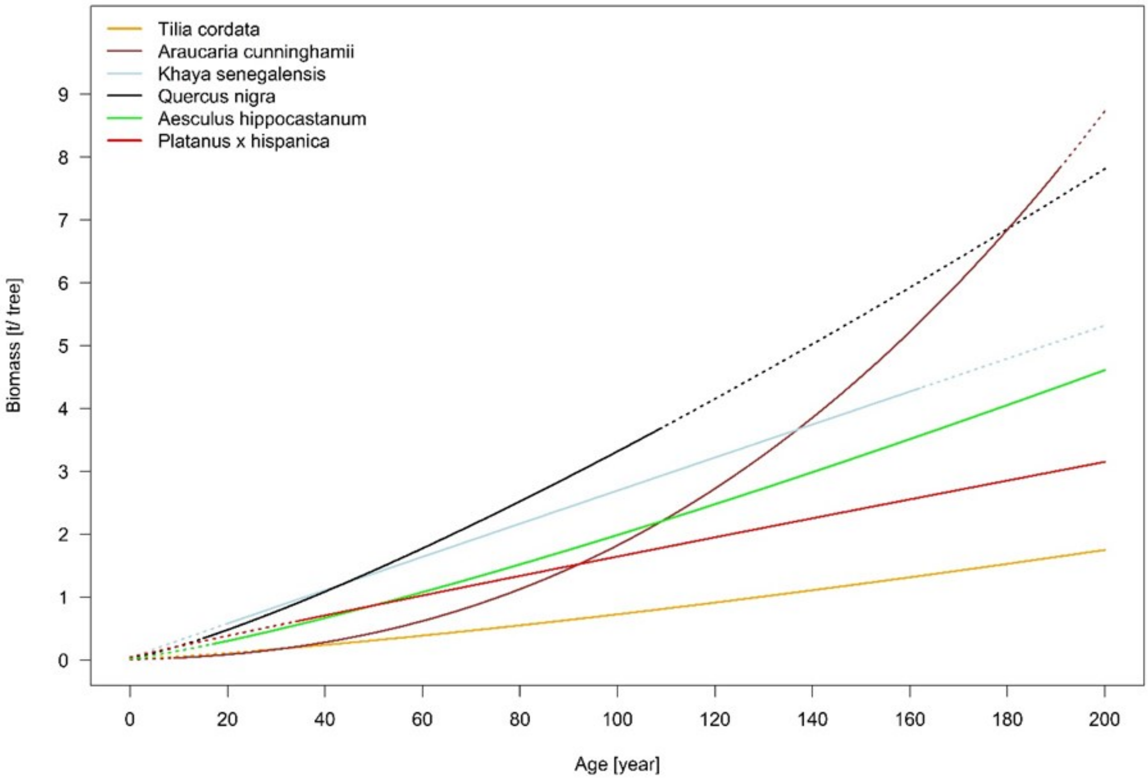


Fig. 15 Estimated aboveground woody biomass for six tree species in urban environments, based on allometric equations. The data include the correction factor of 0.8 for transferring a stand biomass equation to urban trees. Dotted lines show projections which are not covered by measured data.

As can be seen, the species differ in their biomass productivity and differences increase with increasing tree age. Comparing the biomass productivity by the age of 160 years, *T. cordata* in Berlin and *P. x hispanica* in Paris showed the lowest biomass productivity with 1.3 t and 2.5 t per tree respectively. For the same age, *A. hippocastanum* and *K. senegalensis* showed a higher biomass productivity with 3.5 and 4.2 t, respectively and the highest values were achieved by *A. cunninghamii* and *Q. nigra* with 5.2 and 5.9 t biomass per tree. Interestingly all species, besides *A. cunninghamii* in Brisbane, showed an almost linear increase in biomass productivity with increasing age. In difference *A. cunninghamii* in Brisbane showed an exponential increase in biomass productivity with increasing age.

Based on the same data, Figure 16 visualizes the carbon storage capacity per tree, independent of the tree age. As can be seen, the range of the capacity is similar for *K. senegalensis* in Hanoi, *P. x hispanica* in Paris and *Q. nigra* in Houston with 500 kg to 1000 kg carbon storage. Meanwhile a higher capacity and a higher range was found for *A. hippocastanum* in Munich with 600 kg to 1300 kg. On contrary for *T. cordata* in Berlin the carbon storage capacity was between 300 kg and 500 kg and for the coniferous species *A. cunninghamii* in Brisbane it was only between 100 kg and 400 kg.

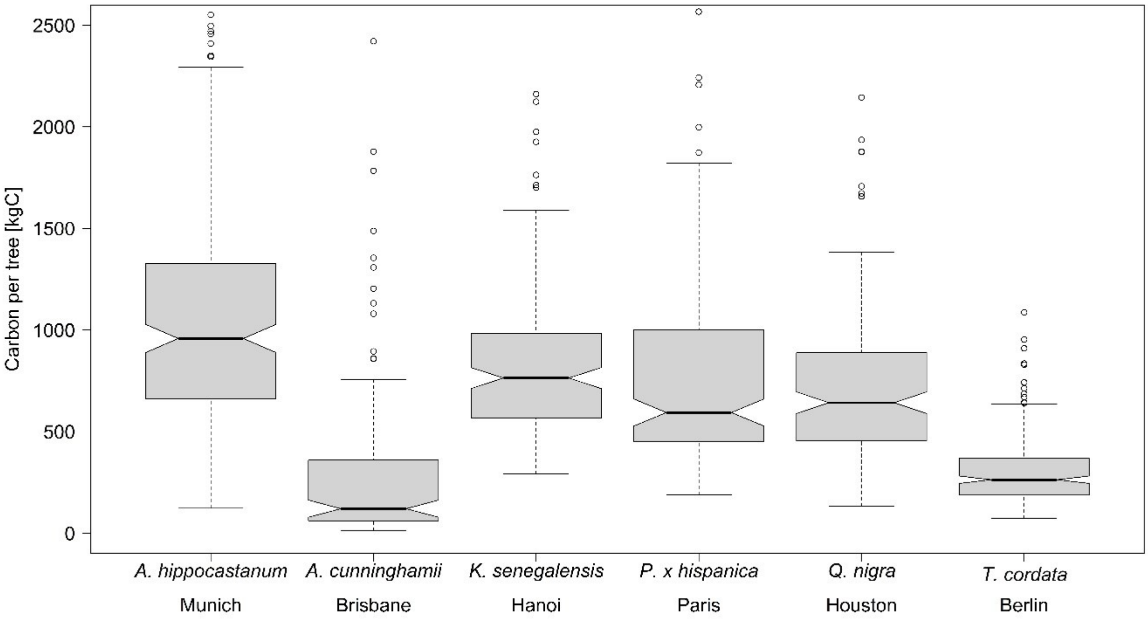


Fig. 16 Carbon storage capacity of six tree species in six metropolises, estimated based on species-specific equations from literature. The data include the correction factor of 0.8 for transferring the biomass equations to urban trees.

Looking at these results it has to be noted that the subsamples differed in their age distribution, as well as in other tree variables (see Table 4). As Figure 15 showed, biomass productivity and as such the carbon storage capacity was related to tree age. However, a look at the age distribution of the subsamples reveals that the differences in tree age are not the main factor for the found differences in carbon storage capacity. To give an example, the *T. cordata* trees in Berlin are older than the *Q. nigra* in Houston or the *K. senegalensis* in Hanoi, still the carbon storage capacity is clearly higher for the later ones.

The carbon storage capacity of *Q. robur* trees, grown in forests, is visualized in Figure 17. Again, the subsamples differed in their age distribution, as well as in other tree variables (see Table 1 and Table 2). However, due to the fact that on all four investigation sites the same species was sampled and that only young trees were sampled, the differences in age as well as in other tree variables between the subsamples was fairly small. Still the results revealed differences, with ING650 showing the lowest carbon storage capacity and the smallest range (0.5 kg – 1 kg). GYO651 and NEC652 showed comparable results with a carbon storage capacity between 1 kg and 2 kg, while the highest capacity and the highest variation were found in SAN653 with 1.5 kg to 5 kg. Due to the fact that the age of the trees was highest in ING650 and GYO651 (10 years) and lowest in SAN653 (7 years), these results cannot be explained by the differences in tree age.

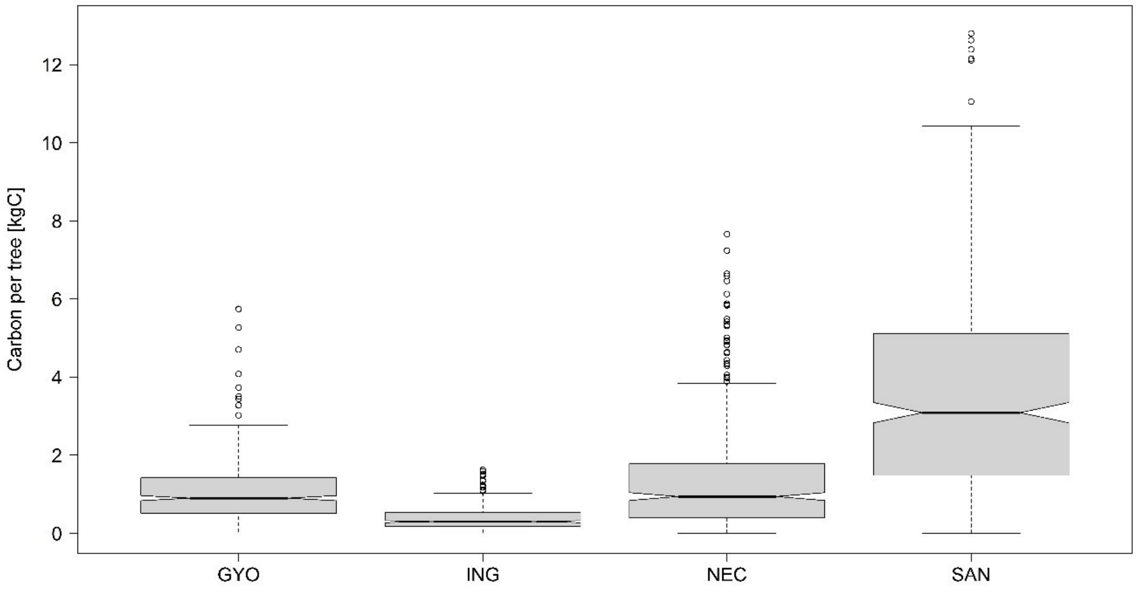


Fig. 17 Carbon storage capacity of *Q. robur* on four forest investigation plots, estimated based on the measured data tree diameter and tree height.

For the forest grown trees different linear regression models were additionally estimated to identify the predictor variables for biomass productivity. As can be seen in Table 6, all three tested variables (d_0, h, SDI_l) were found to significantly predict tree biomass.

Table 6 Linear regression models for total biomass predicted by d_0, h, SDI_l (Eq. 3 - 6)

Model	**ß$_1$**	**ß$_2$**	**ß$_3$**	**ß$_4$**	**SE**	**R^2_{adj}**	**RMSE**
W_{total}	-0.9858*	2.2526***			0.3605	0.8298	0.3549
	-2.6591***	1.9543***	0.5096**		0.342	0.8468	0.3339
	-0.7405	2.2286***		-0.0330	0.3615	0.8289	0.3529
	-2.6963***	1.7132***	0.7791***	-0.1139**	0.3251	0.8616	0.3147

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

The influence of these predictor variables on the proportions of the different tree compartments was then further tested using Dirichlet regression. In difference to the results for total biomass, tree height did not show a significant effect on the proportions of the tree compartments roots, stem, branches and leaves, while the other two predictor variables (d_0, SDI_l) did so.

Table 7 Alpha coefficients for Dirichlet regression for estimating relative biomass volume per compartment predicted by d_0, h, SDI_l (Eq. 9 - 12)

Model (Eq.)	**Compartment**	α_{1c}	α_{2c}	α_{3c}	α_{4c}
(9)	Leaves	1.9256***	-0.0114		
	Branches	1.6099***	0.0029		
	Stem	3.0992***	-0.0172*		
	Roots	3.1055***	-0.0192		
(10)	Leaves	0.7599	0.0236	-0.0001	
	Branches	0.4781	0.0291*	0.0014	
	Stem	1.4185**	0.0080	0.0039	
	Roots	1.8122***	0.0289	-0.0017	
(11)	Leaves	3.3600***	-0.0211*		-0.0042***
	Branches	2.4207***	-0.0015		-0.0021**
	Stem	3.8380***	-0.0214*		-0.0018*
	Roots	4.1206***	-0.0240*		-0.0030***
(12)	Leaves	1.9813***	0.0138	0.0005	-0.0039***
	Branches	1.2295**	0.0269*	0.0010	-0.0020*
	Stem	2.2364***	0.0075	0.0027	-0.0017*
	Roots	2.6885***	0.0261	-0.0021	-0.0024**

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

The Dirichlet regression model with d_0 and SDI_l as predictor variables (Equation 11) seems to fit the data best and is therefore visualized in Figure 18. As can be seen, with increasing d_0 the proportions of roots and stem decreased, while the proportion of the leaves stayed almost unaffected and the proportion of the branches clearly increased. These findings are valid for high, as well as low stand density levels. Comparing the two stand density levels, it can be observed that a lower stand density led to higher root and leaves proportions and lower proportions of stem and branches.

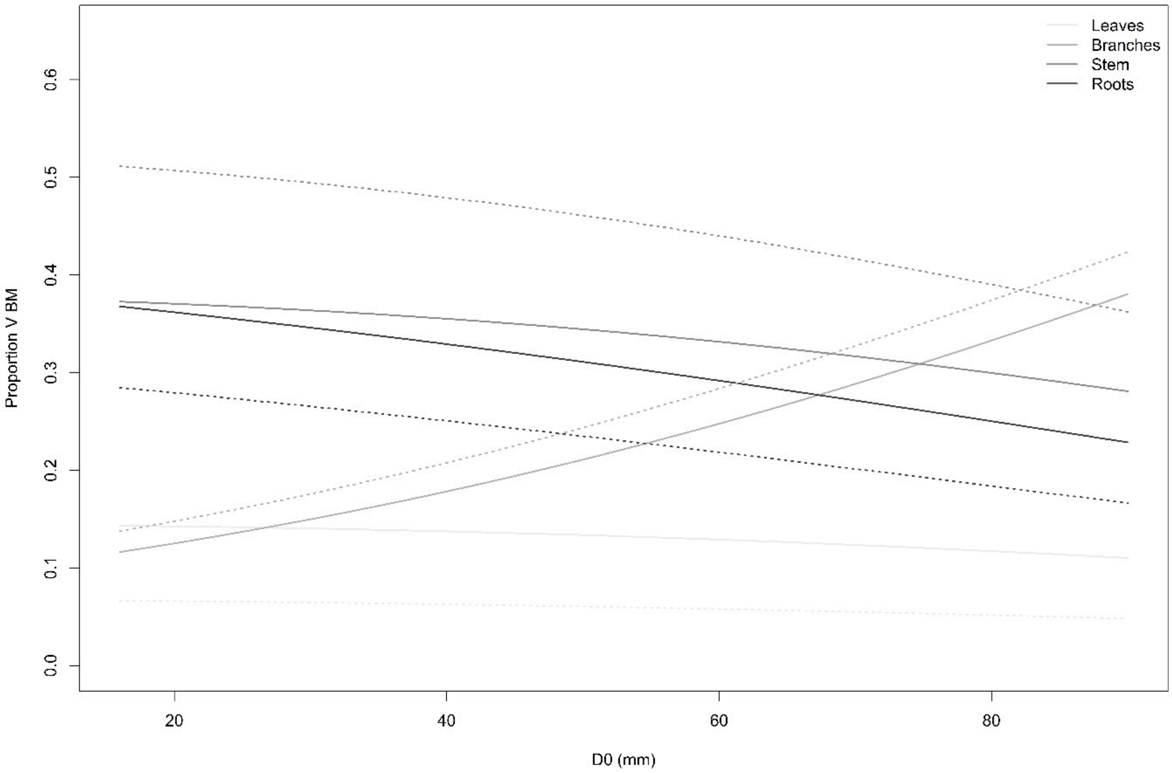


Fig. 18 Fitted values of the Dirichlet regression model $(ln(\alpha_c) = \alpha_{1c} + \alpha_{2c}\, ln(d_0) + \alpha_{4c}\, ln(SDI_l))$ considering the single biomass compartments. Dashed line: SDI_l value fixed at 650, solid line: SDI_l value fixed at 200.

Summing up, the results showed that tree diameter and tree height are predictors for total biomass. These tree variables are also the ones which are used in equations from literature, like done for the urban trees in this thesis. However, in the estimated linear regression models all three tested predictor variables showed a significant effect, further variables were not tested. Thus, it is conceivable that there are further predictors for biomass, which might also be site- or species-specific and which are not considered in existing equations in literature.

5. Discussion

In the following discussion, the previously shown results will be brought together to show how the ambient conditions differ between forest stands and urban trees, what we can learn from the combination of urban and forest tree investigations and to examine whether the urban trees anticipate the changing climate.

5.1 Trees in urban and forested areas

Within the present thesis two types of tree environments were examined, forest stands versus urban areas. In these two environments, trees grow under heterogenous conditions. This makes the combined investigation of forest trees and urban trees challenging and the consideration of the essential differences between both important for discussing the findings.

Urban and forest trees are unequally distributed. In quantity terms, forest trees amount much more than urban trees. For humans, the value of a single mature tree however might be higher in urban areas. This is due to the diverse functions they fulfill within their ecosystem.

The primary services of forest trees are the production of biomass, the provision of habitats and dead wood as well as the carbon and nitrogen storage (Escobedo et al. 2011; Gamfeldt et al. 2013; Dobbs et al. 2014; Moser et al. 2015; Mullaney et al. 2015). Besides these functions the value of a tree in forests is given by the economic value for the respective timber (Rais et al. 2014; Ramage et al. 2017).

The services and functions of urban trees are different. McPherson et al. (2016) report storage of carbon dioxide, uptake of air pollutants, rainfall interception and energy saving due to shading as functions and values for street trees in California. Further urban trees have an aesthetical function in urban areas (Mullaney et al. 2015). Thereby, the amount of the given service is higher by older trees, e.g. the amount of surface water storage capacity. This service was investigated by Xiao and McPherson (2016), who conclude that, due to a wider crown extension, older trees have a higher storage capacity. Further they report a higher surface water storage capacity for the coniferous species compared to the broad-leaved species.

Especially in urban areas, the functions and services of trees are offset by costs for tree maintenance, as well as by the replacement value. Based on a big data set on urban trees in the United States McPherson et al. (2016) investigated the values of trees within cities. They quantify the value of services like shading by reduced energy consumption, reduction of runoffs through the interception of rainfall, or the sequestration of carbon dioxide minimizing the carbon dioxide emissions. The amount of the listed costs for the benefits compared to the costs of their maintenance revealed a clear positive account, which means that the monetized value of services of urban trees outweigh their costs.

As different as the services and functions are also the environmental conditions for forest trees and urban trees. While forest environments are regarded as natural environments, urban environments are characterized by artificial modification. On the second view however, forest environments have also undergone strong changes due to anthropogenic interference. In both environments, these interferences lead to specific growth conditions which have been analyzed in this thesis and which will be discussed in the following.

5.2 Higher competition or inhibition decelerates tree growth

In the case of forest stands the trees compete with each other for resources (e.g. water, light, nutrients). Thus, the resource availability largely depends on the surrounding plants and the prevailing stand density. In urban areas trees are often solitary grown, which means they do not have to compete for resources with other trees. In this case, the competition is induced by the artificial conditions e.g. sealed surfaces and surrounding buildings.

The results showed that space limitation has similar impacts on tree growth within forests (Nelder trials) and urban environments (urban trees). Concretely it could be shown that the available stand area in forests influences biomass productivity and that the degree of sealed surface influences the growth of trees in urban areas. The extent of growth reduction is thereby species-specific.

It is assumed that in both cases the reduced growth is a result of reduced resource availability, especially water availability. Previous studies have reported a reduced root growth as a consequence of water stress induced by rising air temperatures and reduced rooting space (Way and Oren 2010; Pretzsch et al. 2017). Less root growth in turn further hampers the water uptake. In this context further a shift in the distribution of biomass (above- in relation to belowground) is reported for forest trees (Way and Oren 2010). This finding can be confirmed with the findings of this dissertation, where on three of the four forest sites the amount of belowground biomass in relation to aboveground biomass was found to decrease with increasing stand density (Figure 11b). The lower degree of belowground biomass then also leads to a reduced water uptake like explained before. The higher degree of aboveground biomass in turn leads to higher wood production but also to higher projection area and thus less light availability for smaller plants.

In the case of the urban trees, such a shift in biomass allocation might have costly consequences. Considering the safety aspect of trees in urban environments, which has to be guaranteed in the context of public safety, the changes in allocation might negatively influence the stability of a tree. The slenderness ratio, expressed as the ratio between *h* and *dbh*, can be used to identify whether a tree is still stable or not (Rust 2014).

The results of this dissertation could show changes in tree allometry due to competition, when jointly considering forests and urban trees. Thereby, for all investigated species, solitary grown trees showed a wider crown radius in relation to diameter, compared to forest trees. These results however do not consider the degree of inhibition due to sealed surface.

When looking at the response of urban trees on limited non-paved area, the results do not indicate a shift in biomass allocation. A reduction in non-paved area around the stem was found to lead to reduced aboveground growth, concretely reduced diameter, height and crown radius. Only the results of Houston, which looked implausible on the first view as they indicated a reduced growth with an increasing degree of sealed surface, might indicate such a shift in biomass allocation. Unfortunately, in none of the metropolises information on the root growth could be gathered, due to the difficulties of such an investigation in urban areas. Thus, no definite conclusion can be drawn, leaving room for further research.

5.3 Urban conditions accelerate tree growth

Besides the anthropogenically induced resource competition in urban areas, also the climatic conditions in urban areas are anthropogenically influenced and thus different to rural areas. While climate change is a universal phenomenon, the climate conditions in urban areas are additionally intensified by the specific effects of urban climate, as the Urban Heat Island effect. Together with increasing building measures, going in line with increased sealing, as well as other anthropogenic interventions, this results in a much faster elevation of temperature in urban areas, which consequently leads to higher stress for urban trees.

Against this background an overarching aim of this thesis was to determine whether urban trees anticipate the changing climate, for being able to forecast the influence of climate change on forests. The study design of studying urban trees to investigate the growth behavior to warmer and drier climatic conditions is supported by other studies (Farrell et al. 2015; Calfapietra et al. 2015). The urban environments thus serve as ‘living laboratories’ (Farrell et al. 2015).

The results of the analysis of urban trees showed that warmer conditions in urban areas led to accelerated tree growth. This finding can be found for *Tilia cordata* in the city of Berlin. The related study by Pretzsch et al. (2017) shows a worldwide trend of a faster growing of urban trees. Based on these results it can be assumed that urban trees do anticipate the changing climate.

Besides the general finding that the changing climate accelerates tree growth worldwide, differences in tree growth between the investigated species in their respective urban environment were found. Thereby the results of Pretzsch et al. (2017) indicate that urban trees within boreal climates cope better with the warmer temperatures in the city center compared to trees sampled in two Mediterranean metropolises. This finding can be confirmed by Way and Oren (2010), who report that boreal and temperate species are less vulnerable to rising temperatures than tropical species. For these results, it has to be discussed whether the differences in tree growth are induced by species selection or by environmental conditions. In the Metropolis project a common tree species was chosen in each investigated city. This study design has the advantage that the chosen species are well adapted to their (natural) environment, which is important, as the range of environmental conditions a species can cope with is limited, species-specific and sometimes difficult to identify (Farrell et al. 2015). Meanwhile it has the disadvantage that no causal effect between tree species and growth or environmental conditions and growth can be analyzed.

The influence of tree species on its performance in growth has been shown in different studies, which identify ‘functional groups’ of tree species differing in their growth behavior as the response to changing climate (Boisvenue and Running 2006; Way and Oren 2010; Farrell et al. 2015). Thereby the review of Way and Oren (2010) find that growth of deciduous species is more enhanced by elevated temperatures than for evergreen species. Based on these studies it can be assumed that the observed increased growth results out of an interplay of species and climatic conditions.

Independent of species differences the positive influence of higher air temperatures on tree growth can further be confirmed with the results of the forest tree investigations in this thesis, where the species remained the same, while the climatic conditions differed. For forest trees, Pretzsch et al. (2014) further report this relationship, with an increase in tree growth within forest stands over the last century going in line with rising temperatures.

In contrast, Boisvenue and Running (2006) report for forest trees that an increase in air temperature may cause higher transpiration rates leading to a decelerated growth. One reason for the different findings might be how growth is determined. Like explained before, higher temperatures might lead to water stress, which in turn might lead to shift in biomass allocation between the compartments. Concretely, under the warmer conditions biomass is primarily allocated to leaves and less to roots and stem (Way and Oren 2010). This biomass allocation might also be the reason for the questionable finding that less precipitation had a positive influence on aboveground tree growth.

Another explanation for the contrary findings regarding the influence of air temperature on tree growth might be the age of the respective trees. This could be shown for the city of Berlin, where trees older than 60 years showed an inverse growth behavior compared to trees younger than 60 years. Especially in the period after 1990 a faster growth of the younger trees could be observed. A possible explanation is that the younger trees already grew up under the warm conditions induced by the high-dense areas and might thus be better adapted to these conditions. Further, young trees might have less resource requirements compared to older trees, which seem to be stressed more by the increased air temperature. Especially in urban areas impacts of heats and droughts, as well as mechanical impacts leading to higher soil compaction rates with reduced gas diffusion potential within the rhizosphere result in limited water supply, which might hamper tree growth (Day et al. 2010; Viswanathan et al. 2011; Savi et al. 2015).

This already addresses an important consideration, namely that besides air temperature and precipitation, the urban climate, as well as climate change lead to further differences in growth conditions.

The results for Berlin revealed a relation between housing density and tree growth. This might be explained by the Urban Heat Island effect. However, when looking at the results, it can also be observed that there is no linear growth trend in relation to housing density, but rather an up and down. An explanation for this could be the influence of heats and droughts, as well as the fact that the urban environment is very complex and that growth impacting factors as light and temperature can be strongly related to each other. For example, a change in building measures, e.g. an elimination of tree surrounding high buildings can cause an increase in light and also temperature over daytime (Berry et al. 2013). Meanwhile, at nighttime, the temperature can be cooler due to less emissions of long-wave radiation.

The highest sensitivity of tree growth for the subsample of *Tilia cordata* trees in Berlin was found within the mid-dense areas, which leads to the conclusion that in these areas the most extreme conditions prevail. These areas can be assumed as those districts within the city, having the biggest changes regarding urban development measures and infrastructure. This assumption can be supported by Oke (1988) who also states that in suburban areas, e.g. industrial areas outside the city center, the climatic conditions might be even more extreme compared to the city centers characterized by houses and parks. As sensitivity is an indication for vulnerability (Schweingruber 1996; Gillner et al. 2013, 2014) this finding is of high importance. A closer examination of the trees' response to housing, industry and related climatic variables would be an interesting field for future research.

Further, besides higher air temperatures, higher amounts of air contaminants within densely build up urban areas probably also have an influence on tree growth. In their study within New York City, Gregg et al. (2003) found that ozone has a strong influence on tree growth within urban areas. However, the ozone concentration might be even higher in the rural or suburban districts compared to the city centers. The review of Wittig et al. (2009) studied the impact of ozone on tree biomass of forest grown trees in northern-hemisphere forests (boreal to temperate forests). Findings showed a significant reduction of biomass growth by 7% and consequently decreased carbon storage due to increased ozone concentrations compared to the pre-industrial conditions. For the future, a biomass reduction of 11% or 17% is predicted for 2050 or 2100. Thereby the authors reviewed that especially for root biomass a high sensitivity to ozone can be found.

Last but not least, it should be acknowledged that besides changes in tree growth, the changing climate leads to further growing responses. In this context higher air temperatures leading to higher transpiration rates, are reported to lead to a higher amount of carbon allocation, due to the fact that respiration acclimates more quickly than photosynthesis (Way and Oren 2010). Further it is reported that climatic change leads to prolonged growing seasons (Dallimer et al. 2016) and diverse changes in phenological characteristics (Roetzer et al. 2000; Chmielewski and Rötzer 2001; Jochner et al. 2012). It is assumed that the changing conditions will cause adaption strategies for plants and species. However, it is also already reported that the changing urban conditions can cause diebacks (Helama et al. 2012).

5.4 Limitations

Before drawing a final conclusion, some limitations of the underlying studies shall be reflected.

One aim of this thesis was to determine the influence of the climatic conditions on tree growth and respectively on biomass productivity. In the case of the forest trees the sampling size at each site was small, resulting in the fact that a statistical analysis of the differences between the sites was not possible. Further, detailed information on the climatic differences between the four sampling sites were not available. Thus, tracing back differences in biomass productivity between the four sites to the environmental conditions is only an assumption, which can be underlined by previous findings but not be proven with the gathered data. In the case of the Metropolis project, climate data for each metropolis was available. However, only information on air temperature and precipitation from one or few climate stations per city were available. Despite the analyzed and discussed factors, it has to be acknowledged that especially within the urban environment there are additional factors which can be expected to influence tree growth. These unknown factors might not be as obvious, but might affect tree growth directly or in interaction with the mentioned factors air temperature and precipitation. Already in the case of reduced tree growth in response to sealed surface around the stem it has to be questioned whether the found effect is a result of reduced water availability, compacted soil or of some other unknown factor. However, an exclusion of these confounding variables would only be possible under laboratory conditions. These laboratory conditions in turn would not reflect real growing conditions and it would have to be questioned whether results obtained under these conditions are also valid for the trees' common environments. Thus, the advantages of the analysis of tree growth under real conditions, in 'living laboratories', seems to outweigh the uncertainties about the causality of the results found. Still, the quality of the analysis would be higher if more climatic and site-specific variables were considered, possibly even on a microclimatic level.

Further, the study designs of the two projects were very different to each other. While in the Nelder project only young *Quercus robur* trees were sampled, resulting in a quite homogenous sample with low variation in age and size, the subsamples in the Metropolis project not only differed in species, but also showed a broad age and size variation and were distributed over four climate zones.

In the case of the rather homogeneous sample in the Nelder project, the low variation in age and sizes of the sampled trees might be the reason why an analysis of the dependency of wood density on tree size and competition revealed no significant results.

The disadvantages of the study design of the Metropolis project have been named and discussed previously, first and foremost no inter-species growth effects to environmental conditions could be analyzed. However, this was also not the aim of the study and sampling the same tree species in all metropolises was obviously impossible, as (1) a certain number of trees needed to be available for achieving an adequate sampling size and (2) the trees needed to be well adapted to their environment for achieving useful results. Thus, while one might argue that the cross-city analyses were not meaningful, one could also argue that the analysis of the growth of common tree species in urban environments worldwide allows generalizability of the found results.

Independent of the pro and cons, the differences in study designs made it difficult to relate the studies to each other. An ongoing question is whether results obtained in forest environments can be transferred to urban areas and vice versa. Due to the differences in study design this question cannot be answered. Using the same study design in urban and forest areas would allow to better analyze similarities and differences in the growth behavior, as well as to e.g. verify the application of a correction factor of 0.8 for the estimation of biomass productivity in urban areas. Further perspectives for future research will be given in the following paragraph.

5.5 Perspective

The present thesis provides new knowledge on the growth of urban and forest trees, but still also shows that more research is needed, especially in the field of urban tree growth. In the following several aspects for future research will be presented.

Taking up the before mentioned limitations, a study investigating the same tree species at different urban or also rural sites within one climate zone would allow cross-city analyses or the analysis of the effect of the urban environment on tree growth. For example, the investigation of the growth behavior of *Tilia cordata* or *Platanus x hispanica* trees within different cities in the temperate climate zone would be conceivable. Another approach could be to focus on one or few cities, but investigate the growth behavior of more than one species per city. Doing so, a species comparison could be conducted, which explores growth differences between species under the same urban conditions. Both approaches could deliver important information for urban planners and arborists, which help in the planning, e.g. regarding species choice or space requirements and maintenance of trees in urban environments. The first approach would allow to more adequately investigate the influence of the urban environment on tree growth and could thus help to a more precise characterization of a trees optimal conditions within an urban environment. The later approach would allow to determine the suitability of certain common tree species to a given environment and as such could especially support the initial choice of a tree species. In both cases, detailed information, characterizing the tree environment, e.g. surrounding building density, should be sampled together with the data on tree growth.

Further, in future studies the ambient climatic conditions should be investigated in more detail. In the thesis at hand, climate data was only available from one or few climate stations per city. Thus, the distance of the climate stations to the sampled trees was in most cases several kilometers, which did not allow an adequate characterization of the (micro-) climatic conditions of a sampling trees´ environment. A denser network of the climate measurements, or the conduction of own climatic measurements nearby the sampled trees, would give important information of the trees' immediate climatic conditions. This information combined with the growth data would deliver important information to quantify the Urban Heat Island effect and analyze the growth response within the different zones of a city.

In line with this, the analysis of tree growth in relation to air quality data would be an interesting field of research, particularly against the currently much discussed background of fine particulate air pollution in urban areas. Thereby not only research on the growth response to air parameters is missing, but also the other way around the trees' function to filter air particulates in dependence on tree and crown size is so far scarcely investigated. The quantification of trees' services and functions in urban areas in turn is of high interest, as they determine the value of trees in urban environments.

Finally, further research is needed in the field of belowground growth in response to rooting space, especially for urban trees. Still little is known about the space requirements roots have in urban areas, where they are contrasted with impervious surfaces, compacted soils, pipelines and other building measures. Highly correlated with this point is the availability of water and the water storage capacity of urban soils. For this, more knowledge about the belowground conditions, including soil properties are needed. Possibly due to the difficulties for sampling information on roots and soil in urban areas, research in this area is scarce. Not only for the root investigations, in the long view the planting of sampling trees in urban areas could help to overcome the difficulties of sampling urban trees.

Summing up, while especially the data of the Metropolis project constitute a so far unique worldwide data set, a more qualitative follow-up study could help to gain additional and more detailed knowledge on urban tree growth and the influence of climate and environmental conditions on it.

6. Conclusion

The combination of growth behavior investigation on urban and forest trees under specific environmental conditions shows that in both cases growth is decelerated, when growing space is restricted. Further it can be found that the growth itself under warmer and drier conditions in the city is accelerated. Based on these results it can be concluded that urban trees anticipate the changing climate, and respond with faster growth and alteration. This finding is at least true for young trees, which seem to better cope with the changing climate. It can be expected that these young trees have developed adaption strategies in response to the changing conditions. However, it cannot be forecasted whether these adaption strategies also help the trees to respond to the increasing number of extreme weather events.

The thesis also shows that further research is needed. While it seems reasonable to assume that above mentioned aspects are relevant factors influencing tree growth, several other factors that possibly influence tree growth could not be analyzed. Concretely, further climatic indicators like e.g. ozone should be considered. Further, the inhibition of tree growth due to impervious surface could be identified as an important aspect. Due to the fact that this is a field of potential conflict between arborists and highway engineers and possibly leads to high maintenance costs, the influence of impervious surface, as well as of soil compaction on tree growth should be further studied.

Related to this, a biomass allocation from belowground to aboveground has been found for forest trees. Such a biomass allocation could not yet be confirmed for urban trees, as the data, especially on root growth are missing and are difficult to gather. However, such a shift in biomass allocation, resulting out of higher temperatures, less water availability or compacted soil, possibly leads to higher biomass allocation in leaves and less in roots and stem. This in turn would again lead to higher maintenance costs, for removal of foliage, as well as for tree care or replacement resulting out of higher slenderness leading to higher instability.

Last but not least, also the reported acceleration in tree growth poses the tree managers to new challenges. The faster growth goes along with the fact that trees' extensions are achieved in a shorter time period than before. In cases where the expansion area of the tree is limited or the tree maintenance becomes too expensive this might lead to tree replacement within a shorter time period. To avoid these conflicts, it is important to know a tree's expected allometry over age, to which this dissertation contributes.

„Wir müssen danach streben, Natur, Gebäude und Menschen in einer höheren Einheit zusammenzubringen.“

Le Corbusier

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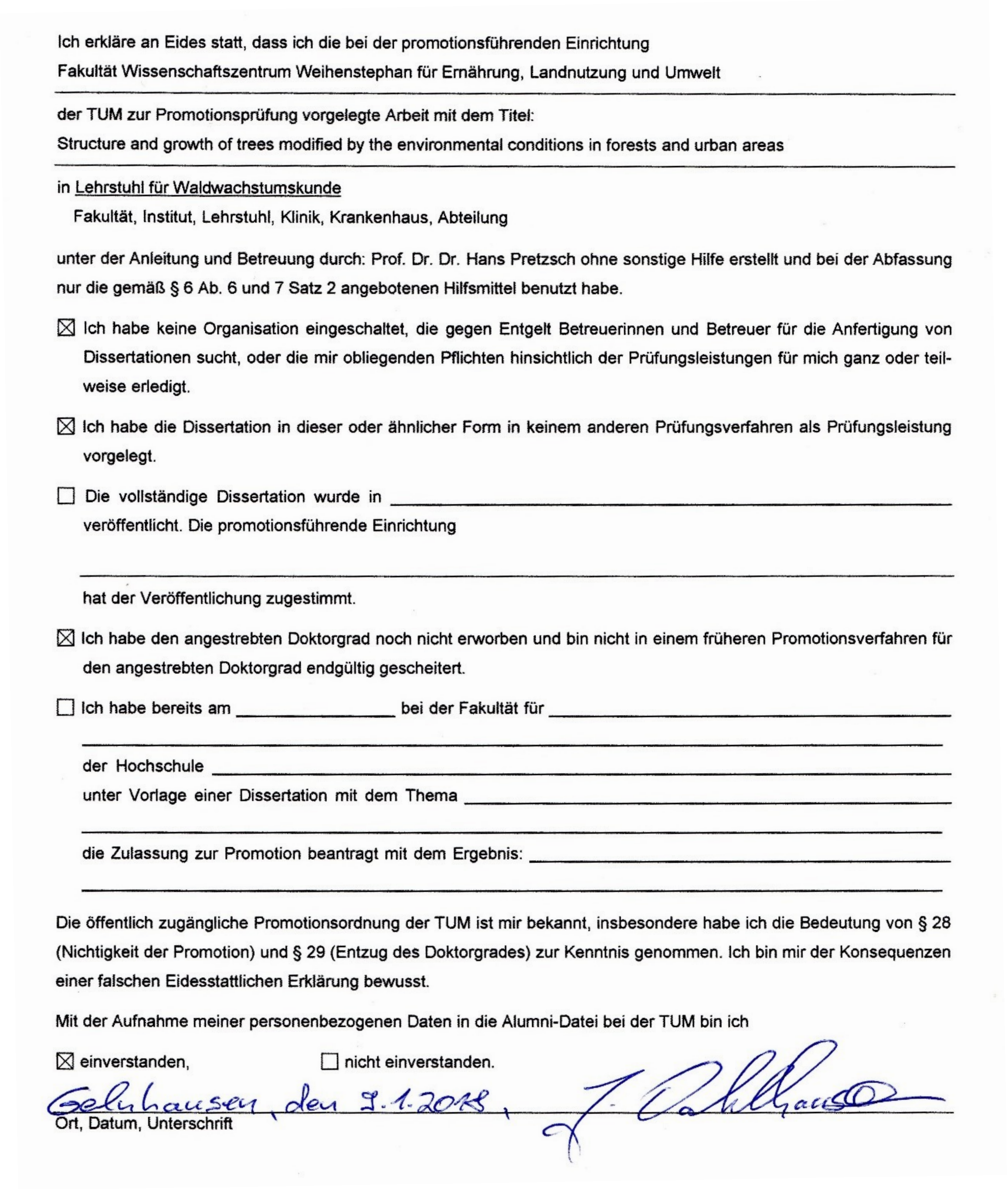

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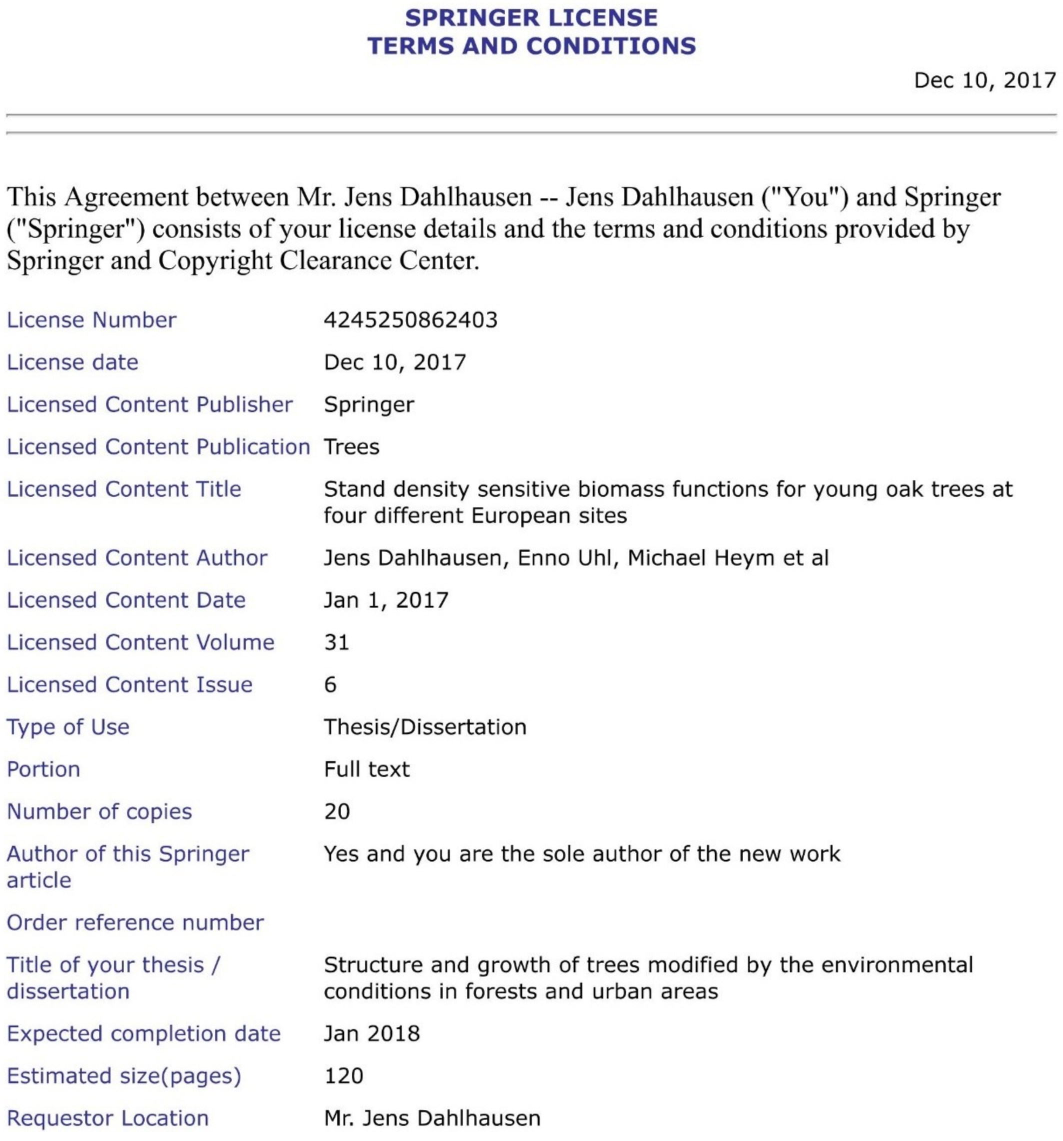
Appendix

Dahlhausen, J., Uhl, E., Heym, M., Biber, P., Ventura, M., Panzacchi, P., Tonon, G., Horváth, T., Pretzsch, H. (2017). Stand density sensitive biomass functions for young oak trees at four different European sites, Trees, 31(6): 1811-1826;



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ORIGINAL ARTICLE

Stand density sensitive biomass functions for young oak trees at four different European sites

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Abstract

Key message **Relative biomass of tree compartments is dependent on plant size and stand density, with stand density being an important predictor, especially for belowground biomass and at high stand densities.**

Abstract Estimation of biomass production is an important issue against the background of climate change and carbon storage. Even though many studies investigated the biomass productivity of trees or single compartments, only few considered the belowground biomass. Further, there is a lack of studies focusing on young trees and considering further influencing factors such as the prevailing stand density. In the present study, young *Quercus robur* trees were sampled on Nelder trials, which comprise different stand densities, on four European sites differing in climatic conditions. Besides the estimation of logarithmically transformed power equations, Dirichlet regressions were applied for deriving biomass functions for the single compartments leaves, branches, stem and roots. Thereby, the dependence of total and compartment biomass allocation on diameter at root collar (d_0), tree height and stand density is tested. The results show that besides d_0, the local Stand Density Index ($\mathrm{SDI_l}$) is an important predictor for biomass. Especially, the belowground biomass shows a significant relation to the $\mathrm{SDI_l}$, which is less the case for the aboveground biomass. Not considering the $\mathrm{SDI_l}$ leads to an overestimation of the biomass productivity, especially when the stand density is high. Furthermore, the results show that the belowground biomass is lower than the aboveground biomass, but with 50–80% of the aboveground biomass still of considerable size. This indicates the importance of including stand characteristics when estimating above- and belowground tree biomass in future studies.

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spruce, Scots pine, and Sessile oak). Their results reveal that under the same competition index diameter growth is more strongly reduced on light-limited fertile sites than on poor sites. Thus, they conclude that the competition effect is stronger on good compared to poor sites. This shows that biomass investigations are likely to be dependent on the competition level, as well as on site characteristics. Looking also into site characteristics, the investigation of Cienciala et al. (2008) parameterize total aboveground biomass functions in forests of the Czech Republic. They sampled oak trees (*Quercus robur*, *Q. petraea*) from six different sites, representing important regions of oak forest management. In their study, diameter at breast height (dbh) was found to be the strongest predictor for aboveground biomass, tree height and crown parameters could improve the model fits for the biomass estimation of single compartments. Site characteristics in the form of the altitude as an additional predictor did not show an improvement of the fitted models. Further studies support the finding that the inclusion of height parameters, conveying information about the competitive status of the tree, can improve the accuracy of biomass estimations (Wirth et al. 2004; Ruiz-Peinado et al. 2011). Another study (Vejpustková et al. 2015) also conducted in Czech Republic, but covering a broader range of site and stand conditions showed in some points different results. For beech trees, they also found tree diameter to be the main predictor for aboveground biomass. However, in their study tree height could not significantly improve the model fit. Further, they found a better fit for total aboveground biomass by including the altitude. The inclusion of altitude and site index, representing the site productivity and tree height by the age of 100 years, improved the results for stem and branch biomass.

Furthermore, several studies have shown that tree growth is influenced by climatic conditions (Lu et al. 2002; Lindner et al. 2010). In this context, Lindner et al. (2010) report for the Mediterranean zone that biomass growth is expected to decline in future due to droughts caused by rising temperatures and decreasing precipitation. If, however, the climatic conditions have an influence on the biomass productivity, it might be misleading to apply existing biomass equations to tree data due to climate differences between the sample sites.

Addressing the above mentioned research gap, in the present study, 64 juvenile oak trees (dbh <5 cm), grown on Nelder trials in pure stands on four different sites in central Europe, were sampled. Biomass of four tree compartments (leaves, branches, stem, and roots) was quantified and biomass equations for these compartments were derived. In addition, different competition levels were considered and taken into account for the analysis of biomass productivity. Last but not least, the same tree species was sampled at four climatically different sampling sites, which allows us to analyze the climatic influence on biomass productivity. Doing so we address the following research questions:

1. Which variables (diameter, height, stand density) determine total biomass production and compartment biomass production (leaves, branches, stem and roots) of juvenile oak trees?
2. How does above- and belowground biomass depend on diameter, height and stand density?
3. Is the wood density dependent on plant size and stand density?
4. How much is the total biomass productivity per hectare of juvenile oak trees depending on stand density and climatic conditions?

Summing up, this study addresses the research gap of an investigation focusing on young oak trees and the impact of stand density and environmental conditions on biomass production. Further, this study uses a holistic approach, by considering not only aboveground biomass, like most studies do, but also belowground biomass.

Materials and methods

Experimental design

This study is designed as a comparison of trees grown on four different pedunculate oak (*Q. robur* L.) pure stand sites. The sites were established between 2008 and 2010 as Nelder trials and are located close to the following cities in central Europe: Ingolstadt, Germany (ING650); Györ, Hungary (GYO651); Neckarsulm, Germany (NEC652) and Sant'Agata Bolognese, Italy (SAN653). Table 1 shows information about the sample sites, their locations are visualized in Fig. 1. A detailed description of the sites can be found in Uhl et al. (2015).

As shown in Table 1 the four sites differ in their climate conditions. The climate ranges from subcontinental (GYO651) to sub Mediterranean (SAN653). The long-term mean annual temperatures vary from 8.2 °C (ING650) to 13.2 °C (SAN653), while the highest mean annual precipitation amounts 760 mm (NEC652) and the lowest 537 mm (GYO651). Based on these climate data, the aridity index after De Martonne (DMI) was calculated as follows (de Martonne 1926):

$$\mathrm{DMI} = \frac{P}{T + 10}, \tag{1}$$

with P being the annual precipitation sum of the observation period and T being the mean air temperature for the

Table 1 Site description including location, longitude (long), latitude (lat), altitude (alt), long-term mean annual temperature (MAT), long-term mean annual precipitation (MAP), De Martonne Aridity Index (DMI), planting year (plant year) and tree age in the year 2016 (age)

Site	Location	Long (°E)	Lat (°N)	Alt (m)	MAT (°C)	MAP (°C)	DMI	Plant year	Age (years)
ING650	Ingolstadt (GER)	11.49	48.86	460	8.2	670	36.8	2008	10
GYO651	Györ (HUN)	17.60	47.79	110	11.1	537	25.5	2009	10
NEC652	Neckarsulm (GER)	9.35	49.05	380	9.1	760	39.8	2010	7
SAN653	Sant'Agata (ITA)	11.10	44.46	25	13.2	660	28.4	2010	8

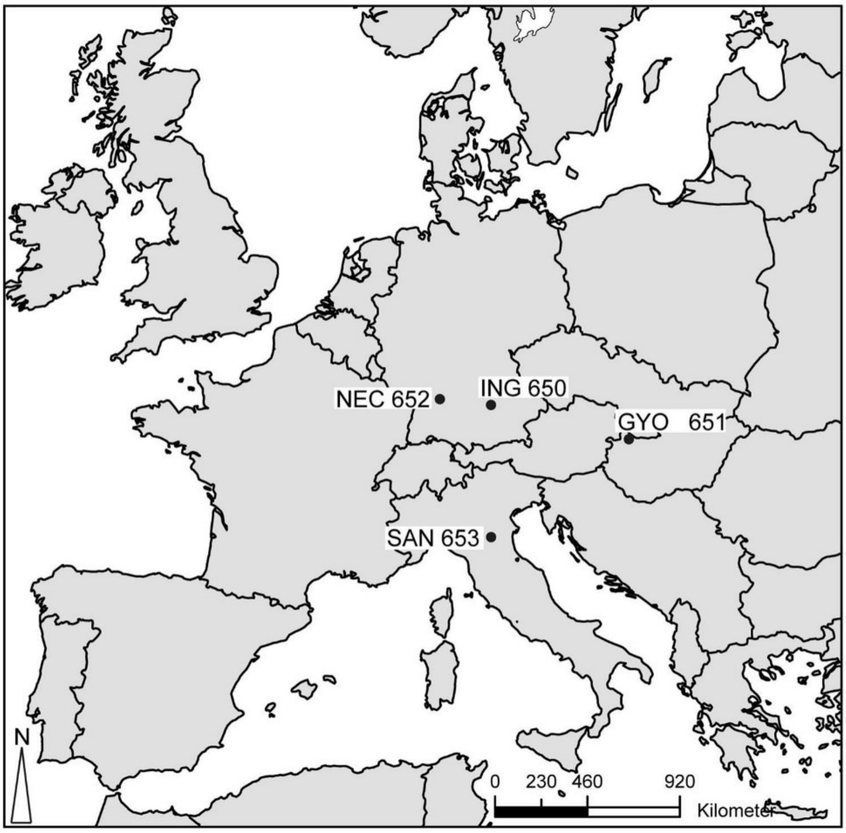

Fig. 1 Map of the sampling locations of this study

observation period. The DMI (Table 1) shows the highest value for NEC652 and the lowest for GYO651. As lower values represent higher aridity, this indicates that GYO651 is the most arid site, followed by SAN653. In comparison, the two German sites ING650 and NEC652 are more humid.

On all sites local provenances were used, and plant ages at establishment were between 1 and 3 years with heights between 30 and 70 cm. The site ING650 was established 2008 on clear-cuts within forests. In difference, the sites NEC652 (planted in 2010), GYO651 (planted in 2009) and SAN653 (planted in 2010) were established on former agriculturally used areas, within forests (NEC652 and GYO651) or outside forests (SAN653). At all sites long-term yield trials using a Nelder design were established (Uhl et al. 2015). The spacing trial design by Nelder (1962) can be described as an arrangement of concentric circles and radial spokes in a constant angle distance, which is in the case of our experimental sites 20° (Fig. 2). Thus, the trees in the Nelder design differ in their surrounding stand density, with high density in the center and decreasing density to the outer areas. With this planting design the competitive and facilitative effects, which occur simultaneously, can be analyzed and separated. In particular, the transition level of density, where the negative and positive effects are in balance can be identified (Uhl et al. 2015). Each of the investigated sites

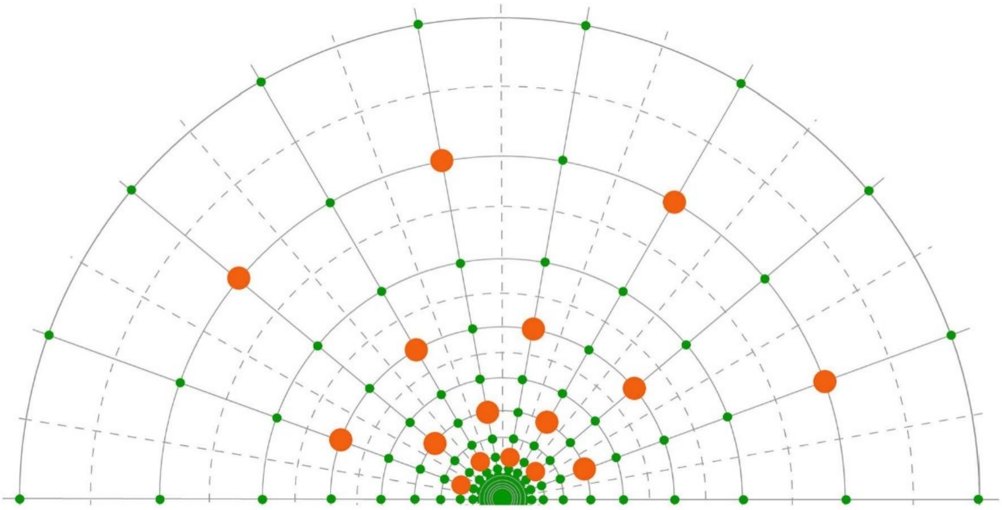

Fig. 2 Schematic representation of half Nelder wheel (Nelder 1962). Plant positions (*green dots*) are defined by intersection points of concentric circles and radial spokes. The *orange dots* show the concept of the tree selection for sampling

comprises two full Nelder wheels reflecting an initial stand density range from 100.000 to 50 trees per hectare. At most sites (GYO651, NEC652 and SAN653), additional semi and even smaller wheels following the same design were established. For this study, we collected only plants from surrounding half and quarter wheels, which were established for this purpose at the same time as the full wheels. These half and quarter wheels follow the same structure as the full wheels. Thereby the quarter wheels consist of 4 (SAN653) or 5 (GYO651, NEC 652) spokes and 11 circles. The half wheels have 9 spokes and 11 circles (SAN635). This results in a total amount of 55 plants per quarter wheel in GYO651 and NEC652 and 44 plants per quarter wheel for SAN653 plus 99 plants per half wheel. In the case of ING650, the trees were also planted in quarter wheels but not strictly following the Nelder concept with its constant angle distances.

Tree sampling

Samples were taken during June and July 2016 at the four different sites. At each investigation site, 16 trees of the species pedunculate oak (*Quercus robur* L.) were sampled. For the selection of trees in the Nelder design, the following criteria were applied: (1) no borderline trees for avoiding edge effects, (2) no neighboring trees and (3) only trees having all eight direct neighbors. Figure 2 visualizes a possible selection of sample trees in the case of a Nelder half wheel.

Before excavating a sample tree, the following variables were measured: stem diameter at root collar (d_0), diameter at breast height (dbh, at a height of 1.3 m, if already achieved), diameter at crown base (dcb), tree height (h), height to crown base (hcb) and the crown radius (cr) in the eight cardinal directions. After carefully excavating the trees, including all coarse and fine roots, the tree was dissected into four compartments: leaves, stem, branches and roots. All compartments per tree were not only directly weighed in the field, but also later in the laboratory after oven-drying for at least 24 h. The wood density of each tree was determined by the hydrostatic weighing method. To this end, a piece of the stem at a height of 1 m was cut out and freed from bark. The range of the density values for each site is shown in Table 2, together with other tree parameters.

A local stand density index ($\mathrm{SDI_l}$) was chosen for comparing the competition levels between the four sites. Following Uhl et al. (2015), the $\mathrm{SDI_l}$ was calculated by applying a search radius around the position of the tree of interest, whose extension was defined by the mean height of all trees in the quarter or half wheel multiplied by the factor 1.25. The number of trees inside the search radius was then considered as the number of competitors for the tree of interest. According to the following formula, the $\mathrm{SDI_l}$ normalizes the stem number per hectare to a mean tree size of 25 cm. Equation (2) gives the formula for calculating the $\mathrm{SDI_l}$, with N representing the stem number per hectare (excluding the tree of interest) derived from the stem number in the search radius and dg representing the quadratic mean diameter of all trees within the search radius. The value of the exponent −1.605 was used according to the generic stand density rule (Reineke 1933).

$$\mathrm{SDI_l} = N\left(\frac{25}{\mathrm{dg}}\right)^{-1.605}. \tag{2}$$

In ING650 (and partly in GYO651) trees were sampled, which were planted at the same time as the Nelder wheel,

Table 2 Tree characteristics (mean values) for each sampling site; minimum and maximum values are given in parenthesis

Site	n	d_0 (mm)	dbh (mm)	Tree height (m)	Density (g/cm^3)	SDI$_l$
ING650	16	44.4 (27–63)	20.4 (12–39)	2.8 (2.0–4.1)	0.82 (0.73–0.92)	211 (155.4–280.3)
GYO651	16	30.9 (16–46)	12.6 (2–29)	1.9 (0.9–3.5)	0.76 (0.68–0.88)	150 (20.9–383.0)
NEC652	16	34.3 (20–53)	14.7 (5–30)	2.1 (1.3–2.9)	0.87 (0.76–0.94)	168 (4.8–688.4)
SAN653	16	44.9 (17–90)	13.7 (4–27)	2.4 (1.6–4.8)	0.79 (0.66–0.94)	266 (8.5–534.1)
All sites	64	38.6 (16–90)	15.5 (2–39)	2.3 (0.9–4.8)	0.81 (0.66–0.94)	199 (4.8–688.5)

using same planting material, but which were not planted with the constant angle distance which is characteristic for Nelder trials. In these cases, for each of the sample trees the competition status was similarly evaluated as for trees from Nelder design. Precisely, the SDI$_l$ for each of those trees was determined by taking the 14 surrounding trees and its distance to the sampling tree as well as its dimensions into account.

Results of the SDI$_l$ calculation shown in Table 2 indicate on average the highest stand density in SAN653 and by far the lowest stand density in GYO651. The very narrow value range for ING650 can be explained by the before mentioned planting design, which is different compared to the other three sites.

Biomass equations

Commonly, biomass is predicted using Snell's (1892) power equation $y = \beta_1 x^{\beta_2}$ (Annighöfer et al. 2016), where y denotes biomass and x denotes the predictors. Due to heteroscedasticity, this equation is often logarithmically transformed before fitting into $\ln y = \ln \beta_1 + \beta_2 \ln x$. Doing so a linear regression can be applied to the data (Pilli et al. 2006). For the biomass estimations in the present study, we follow the described procedure, using the logarithmically transformed data. As shown in Eqs. (3)–(6), we estimate four models for biomass weight, differing in the predictor variables (d_0, h, SDI$_l$). While the dbh is commonly used for biomass estimations of larger trees, the diameter at root collar has been found to be more appropriate for young trees (Wirth et al. 2004; Pajtík et al. 2008; Annighöfer et al. 2016; Cotillas et al. 2016) (and for trees $h < 1.3$ m there is evidently no choice at all). For all trees with a minimum height of 1.3 m, we fitted all models shown below alternatively with dbh and with d_0 as predictor variable. Thereby d_0 consistently yielded better model fits. Thus, only the results considering d_0 are presented in the further text. The following models were fitted:

$$\ln W = \beta_1 + \beta_2 \ln(d_0) \quad (3)$$

$$\ln W = \beta_1 + \beta_2 \ln(d_0) + \beta_3 \ln(h) \quad (4)$$

$$\ln W = \beta_1 + \beta_2 \ln(d_0) + \beta_4 \ln(\mathrm{SDI_l}) \quad (5)$$

$$\ln W = \beta_1 + \beta_2 \ln(d_0) + \beta_3 \ln(h) + \beta_4 \ln(\mathrm{SDI_l}). \quad (6)$$

Thereby, W refers to the estimated total biomass weight of a tree. The four models are fitted for total biomass, comprising the single compartments roots, stem, branches and leaves. This single equation estimate of total biomass (in contrast to summing up separate compartment-wise estimates) has been recommended by previous studies, due to reduced assessment errors and better fitting results (Cienciala et al. 2008; Vejpustková et al. 2015). The normality of the residuals was tested with Q–Q plots.

In addition, however, also the compartments biomass shall be estimated as the proportions of total biomass in a way that they can be applied to a previously estimated total biomass, adding always up to 1. To do so, we used a Dirichlet regression. This type of regression is useful for modeling data representing components as percentage of the total (Poudel and Temesgen 2016). In other words, for each component $c = 1 \ldots C$ the compartment proportion y_c is given by the compartment biomass divided by the total biomass. These compartment proportions $y = (y_1, \ldots, y_C)$ have to fulfill the following constraints: $y \in (0, 1)$ and $\sum_{c=1}^{C} y_c = 1$.

We then assume that the compartments follow the Dirichlet distribution, which is a multivariate generalization of the beta distribution, where $\alpha_c > 0, \forall c$ are the shape parameters for each compartment.

$$D(y|\alpha) = \frac{1}{B(\alpha)} \prod_{c=1}^{C} y_c^{(\alpha_c - 1)}. \quad (7)$$

The Dirichlet regression model can be formulated as follows:

$$\log(\alpha_c) = \eta_c = X^{[c]} \beta^{[c]}. \quad (8)$$

Thereby, $X^{[c]}$ represents a matrix of predictors, where the superscript indicates that the model allows for separate predictors in each compartment. This in turn potentially leads to different numbers of regression coefficients per compartment, which are captured in the column vector $\beta^{[c]}$.

In the study at hand, however, we assume that all compartments are influenced by common covariates [d_0 (mm), h (cm)]. Concretely, in line with the single equation models, the following Eqs. (9)–(12) were fitted for the four compartments roots, stem, branches, leaves ($c = 1, \ldots, 4$):

$$\ln(\alpha_c) = \alpha_{1c} + \alpha_{2c}\ln(d_0) \quad (9)$$

$$\ln(\alpha_c) = \alpha_{1c} + \alpha_{2c}\ln(d_0) + \alpha_{3c}\ln(h) \quad (10)$$

$$\ln(\alpha_c) = \alpha_{1c} + \alpha_{2c}\ln(d_0) + \alpha_{4c}\ln(\mathrm{SDI_l}) \quad (11)$$

$$\ln(\alpha_c) = \alpha_{1c} + \alpha_{2c}\ln(d_0) + \alpha_{3c}\ln(h) + \alpha_{4c}\ln(\mathrm{SDI_l}). \quad (12)$$

With the common parametrization, the expected values are then defined as $E[y_c] = \alpha_c/\alpha_0$, where α_0 is the sum of all α_c (see Maier 2014 for more information).

In a last step, the biomass productivity of the whole Nelder wheels at each site was projected. To do so, linear regression models with total biomass (kg) and aboveground biomass as the dependent variable were estimated. In accordance with before estimated linear regression models 4 and 6, once d_0 and height, and once d_0, height and $\mathrm{SDI_l}$ were chosen as the independent variables. For each of the four investigation sites, data from inventory measurements (d_0, height, $\mathrm{SDI_l}$) of all trees in the two full wheels was then inserted into the allometric equations. The estimated biomass was than extrapolated to Mg per hectare. To be able to compare the different locations, the projection calculation was based on data by the tree age of 6 years for each site.

The models for the total biomass were fitted using the software R 3.2.2 (R Core Team 2015) with the function "lm" of the R package "stats" (R Core Team 2015) and the compartments biomass was fitted using the R package "DirichReg" (Maier 2014).

Results

The sampled trees showed a dbh between 2 and 39 mm and a height between 0.9 to 4.8 m. $\mathrm{SDI_l}$ values vary between 4.8 and 688.4 reflecting different competition status of single plants (see Table 2). Although, in general, diameter-height relationship is in a narrow range, site-specific variations are observable. Competition status of single plants seems to effect allometric behavior. Plants from ING650 show minimum variation in $\mathrm{SDI_l}$ values as they were sampled from nearly constant spacing areas. Considering trees from all sample sites, the relationship between height and dbh remains within a narrow range (Fig. 3).

On all four sites, most trees have a dbh between 10 and 30 mm with a tree height between 170 and 350 cm. While on the other sites dbh values below 10 mm can be found, all trees in ING650 have a dbh greater than 10 mm. This might be due to the fact that ING650 is the oldest site, or due to the narrow $\mathrm{SDI_l}$ range in ING650. The climate

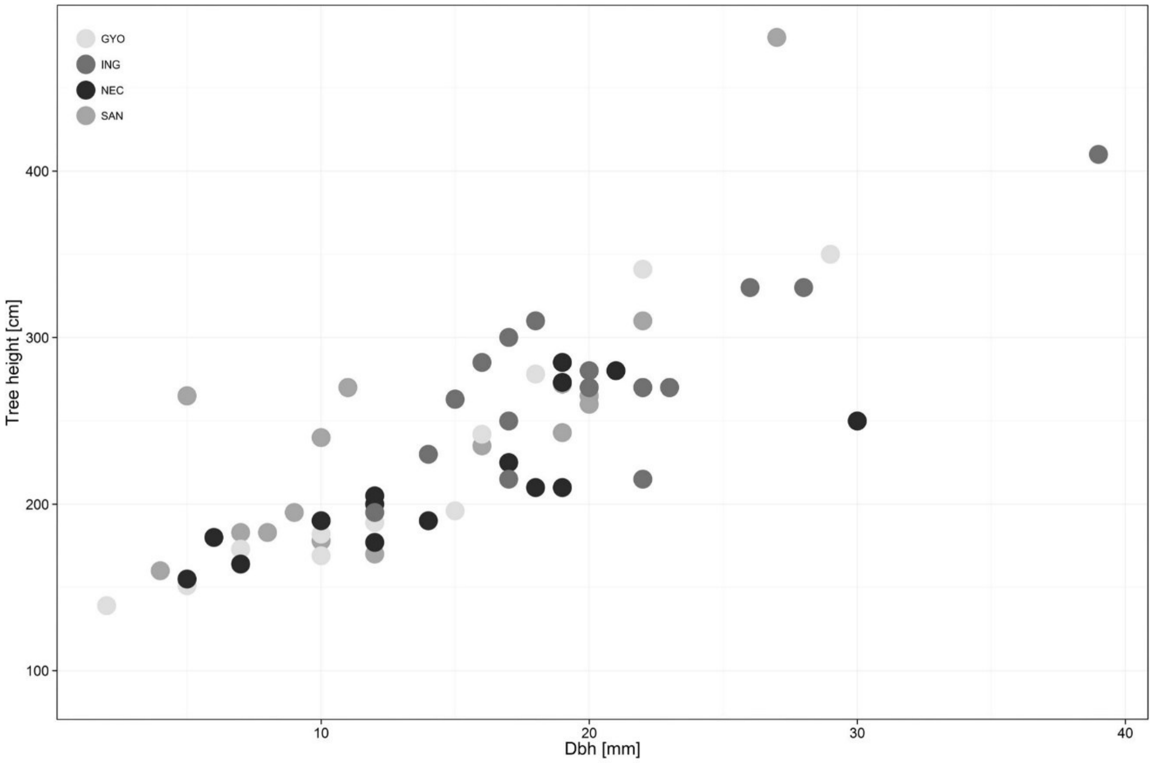

Fig. 3 Tree diameter at breast height (dbh) in relation to tree height ($n = 59$) classified by site characteristics, with *dark color* indicating humidity to *bright color* indicating aridity

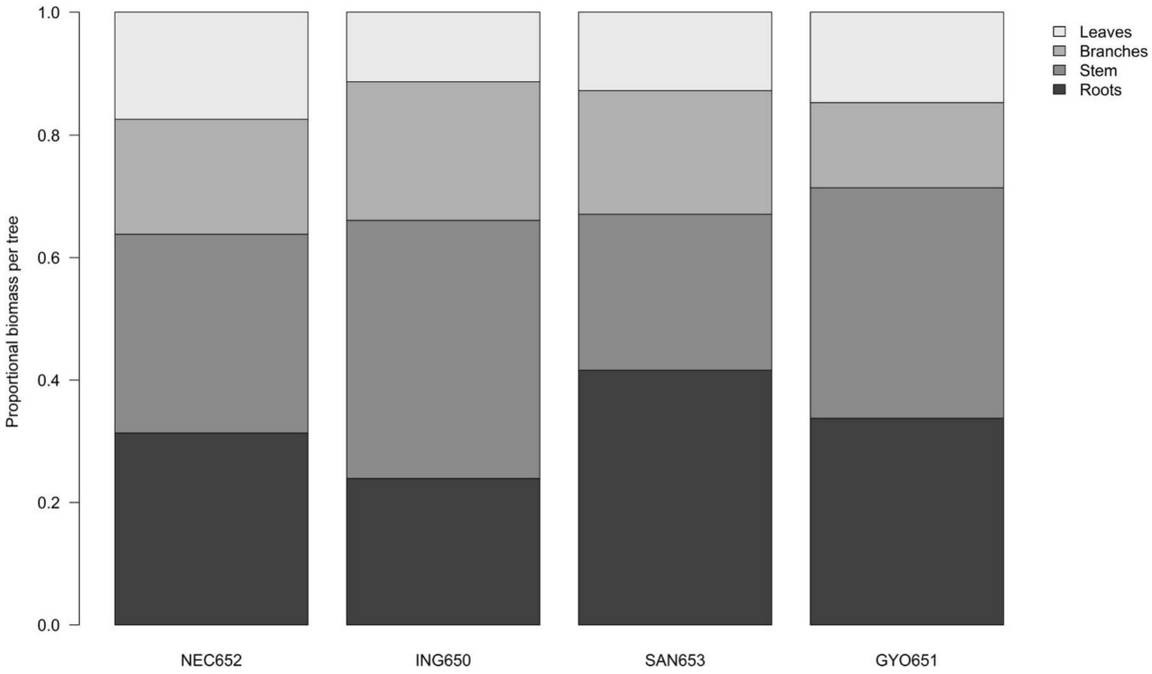

Fig. 4 Relative compartment biomass composition per site based on dry weight

Table 3 Average absolute compartment biomass and total biomass per tree

Site	Root biomass (kg)	Stem biomass (kg)	Branch biomass (kg)	Leaf biomass (kg)	Total biomass (kg)
ING650	0.52 (0.13–1.03)	0.92 (0.21–3.00)	0.49 (0.11–1.07)	0.25 (0.07–0.57)	2.18 (0.52–5.66)
GYO651	0.28 (0.08–0.63)	0.32 (0.07–1.01)	0.12 (0.01–0.33)	0.12 (0.02–0.27)	0.84 (0.18–2.22)
NEC652	0.34 (0.07–0.90)	0.36 (0.08–0.98)	0.21 (0.02–0.91)	0.19 (0.03–0.63)	1.10 (0.26–3.41)
SAN653	0.61 (0.05–2.26)	0.37 (0.07–1.20)	0.29 (0.01–0.88)	0.19 (0.01–0.61)	1.46 (0.14–4.45)

conditions of the sites, indicated by a bright (arid) versus dark (humid) color in Fig. 3, seem to have no influence on the relation between dbh and height.

Differentiating plants' total biomass into the compartments leaves, branches, stem and roots, mean values of site-specific sample trees reveal substantial differences between the relative compartments' amounts (Fig. 4). Leave and branch biomass show for all four sites the smallest and second smallest relative compartment amount. But relative stem and root biomass, respectively, vary between the sites. Moreover, the second highest absolute mean plant stem biomass is found in SAN653 (Table 3); the relative mean stem biomass is smallest on this site.

It is remarkable that although at same age, plants in GYO651 indicate a higher relative root biomass than in ING650. One possible explanation might be climatic differences between the sites, with GYO651 showing higher long-term mean annual temperature and lower long-term mean annual precipitation values (see Table 1). The same pattern is valid for the nearly same aged tress at NEC652 having moister soil conditions and SAN653 being dryer. Comparing relative above- and belowground biomass, plants from SAN653 and GYO651 show a share of 40% of aboveground biomass, plants from NEC652 have 50% and plants from ING650 have 60% (Fig. 5).

Relating the biomass of the different compartments to the SDI_l, as depicted in Fig. 6, differences between the sites can be observed.

For the sites NEC652 and SAN653, the biomass of all four compartments decreases with increasing SDI_l. For the site GYO651, a similar trend can be observed. However, the relation is not as clear, due to a high variation in biomass at low SDI_l values. For the site ING650, no trend in the relation can be found, which might be due to a small SDI_l range. Despite this small SDI_l range, high variation regarding the biomass can be found for the trees in ING650.

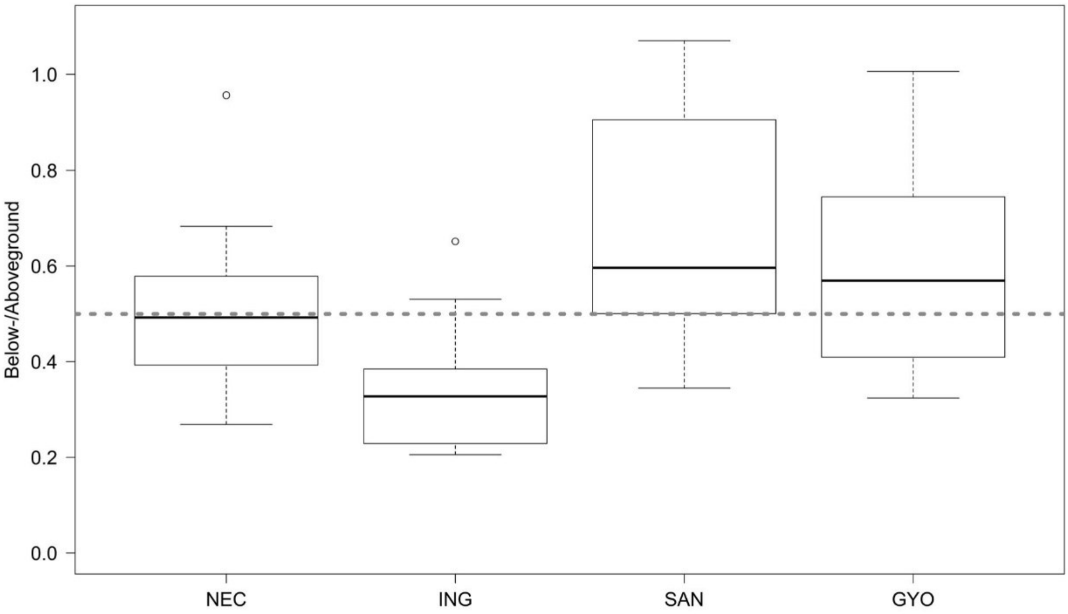

Fig. 5 Below-/aboveground biomass relation of the four sites ordered from humid location (NEC652) to more arid location (GYO651)

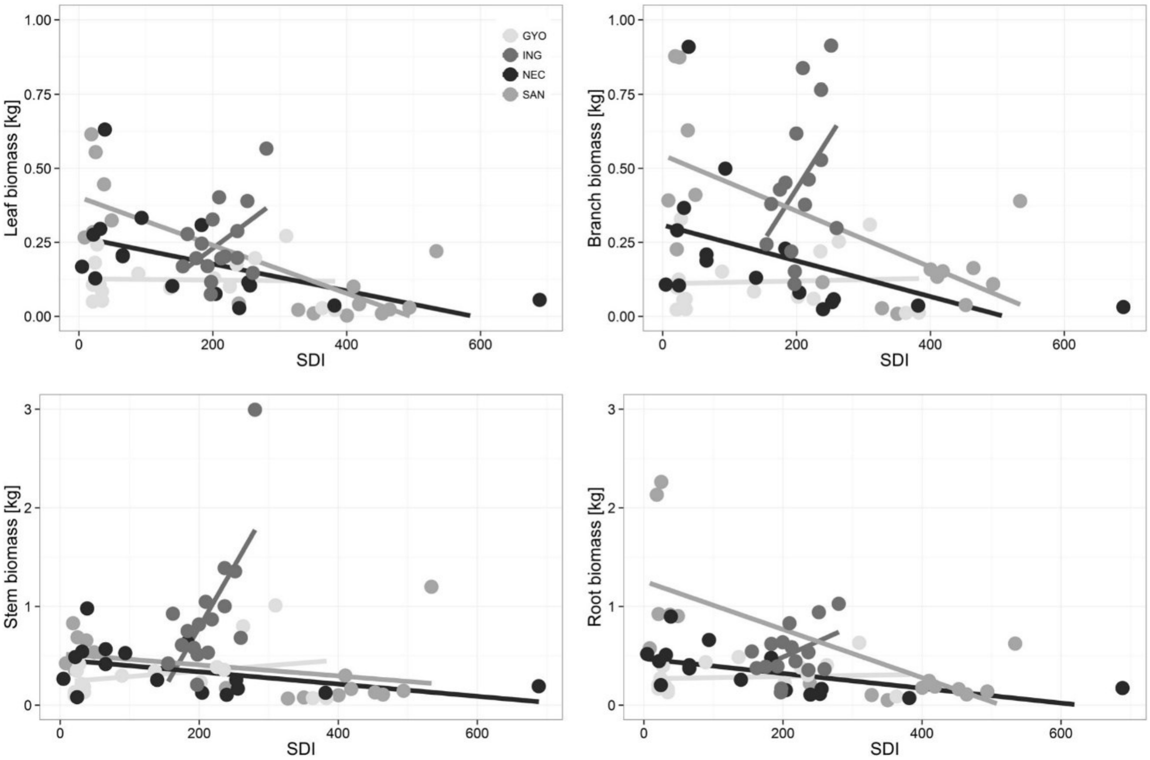

Fig. 6 Relation of biomass to stand density index (SDI$_l$), shown for all four compartments (leaf, branch, stem, root). *Darker* points indicate the more humid sites; *solid lines* symbolize the linear trendline

Table 4 Linear regression models for total (W_{total}), below (W_{below}), above (W_{above}) and the ratio of below to aboveground ($W_{\text{below/above}}$) biomass weight (Eqs. 3–6)

Model	β_1	β_2	β_3	β_4	SE	R^2_{adj}	RMSE
W_{total}	−0.9858*	2.2526***			0.3605	0.8298	0.3549
	−2.6591***	1.9543***	0.5096**		0.342	0.8468	0.3339
	−0.7405	2.2286***		−0.0330	0.3615	0.8289	0.3529
	−2.6963***	1.7132***	0.7791***	−0.1139**	0.3251	0.8616	0.3147
W_{below}	−1.4297**	2.0600***			0.3527	0.8098	0.3471
	−1.4898	2.0492***	0.0183		0.3555	0.8067	0.3471
	−0.48714	1.96741***		−0.12660***	0.3242	0.8393	0.3165
	−1.54540*	1.68858***	0.42154*	−0.17038***	0.3144	0.8488	0.3045
W_{above}	−1.673**	2.329***			0.4326	0.7832	0.4258
	−4.1390***	1.8889***	0.7509***		0.3966	0.8178	0.3872
	−1.77941**	2.33901***		0.01426	0.4359	0.78	0.4255
	−4.16654***	1.71006***	0.95087***	−0.08451	0.3907	0.8232	0.3783
$W_{\text{below/above}}$	0.2435	−0.2686			0.408	0.037	0.4016
	2.6492**	0.1603	−0.7326***		0.3713	0.2026	0.3625
	1.29226*	−0.37160**		−0.14086**	0.3779	0.174	0.3689
	2.62114**	−0.02148	−0.52933*	−0.08588	0.3641	0.2329	0.3526

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Biomass equations

We tested the dependencies of total above- and belowground plant biomass, as well as of the ratio of below- to aboveground biomass, from plant size parameters (d_0, h) and competition situation (SDI_l) (Eqs. 3–6). The results of the linear regression models are summarized in Table 4. For estimating total biomass, Eq. (6) provides the best fitting indicated by the level of significance of the parameters and adjusted R^2. This is also valid for belowground biomass. In case of aboveground biomass, sufficient fitting quality seems to be achieved using diameter at root collar and height as predictors, only. The relation between below- and aboveground biomass appears to be assessable by the parameters d_0 and SDI_l.

In a second step, the Dirichlet regression was used for analyzing the impact of the independent variables (d_0, h, SDI_l) on the relative biomass of the single compartments. The results of the four estimated models (Eqs. 9–12) are given in Table 5.

While plant height shows no significant effect on the relative compartments' biomass at all, tree diameter and competitive situation modify biomass allocation between compartments. Equation (11) presents best fitting results. Running the model without the variable tree diameter, which is not significant for the compartment branches, does not reveal a better model fit. This means, dropping d_0, lowers the explanatory power of the SDI_l for at least one of the other compartments. Therefore, we continue with the results of Eq. (11). Based on the α coefficients, the expected values of the biomass proportions (E(compartment)) can be estimated as follows:

$$\alpha_0 = 28.789 d_0^{-0.0211}\text{SDI}_\text{l}^{-0.0042} + 11.254 d_0^{-0.0015}\text{SDI}_\text{l}^{-0.0021} + 46.433 d_0^{-0.0214}\text{SDI}_\text{l}^{-0.0018} + 61.596 d_0^{-0.0240}\text{SDI}_\text{l}^{-0.0030}$$

$$E(\text{leaves}) = 28.789 d_0^{-0.0211}\text{SDI}_\text{l}^{-0.0042}/\alpha_0$$

$$E(\text{branches}) = 11.254 d_0^{-0.0015}\text{SDI}_\text{l}^{-0.0021}/\alpha_0$$

$$E(\text{stem}) = 46.433 d_0^{-0.0214}\text{SDI}_\text{l}^{-0.0018}/\alpha_0$$

$$E(\text{roots}) = 61.596 d_0^{-0.0240}\text{SDI}_\text{l}^{-0.0030}/\alpha_0.$$

A visualization of the estimates of Eq. (11) is captured in Fig. 7. Proportional compartments' biomass is plotted against d_0. To consider the effect of stand density, the curves' progression is illustrated for two different SDI_l values. SDI_l 650 (dashed lines in Fig. 7) is used to reflect dense stand situations and SDI_l 200 (solid lines in Fig. 7) to represent low competition.

In general, with increasing plant size the relative biomass of stem, roots and leaves is decreasing. Conversely, relative branch biomass is increasing during plant's development. At high stand densities, relative root biomass and relative leaf biomass are substantially smaller than at low densities. Concerning relative stem biomass and relative branch biomass, the opposite pattern is true, having higher relative biomass at higher stand densities, indicating stronger biomass allocation into stem and branches.

Besides the analysis regarding the total and the compartment biomass, it was also tested whether the wood density is dependent on plant size, SDI_l or climatic conditions. In difference to the before shown results, however, no significant influences of these variables on wood density could be found. A possible explanation for this might be little variation in wood density, due to the small age variation within the sample.

Biomass productivity projection for the Nelder wheels

Inserting the tree data of the Nelder full wheels into different allometric equations, Fig. 8a illustrates the projected

Table 5 Alpha coefficients for different variables from Dirichlet regression of the models referring to Eqs. 9–12 for estimating relative biomass weight per compartment

Model (Eq.)	Compartment	α_{1c}	α_{2c}	α_{3c}	α_{4c}
(9)	Leaves	1.9256***	−0.0114		
	Branches	1.6099***	0.0029		
	Stem	3.0992***	−0.0172*		
	Roots	3.1055***	−0.0192		
(10)	Leaves	0.7599	0.0236	−0.0001	
	Branches	0.4781	0.0291*	0.0014	
	Stem	1.4185**	0.0080	0.0039	
	Roots	1.8122***	0.0289	−0.0017	
(11)	Leaves	3.3600***	−0.0211*		−0.0042***
	Branches	2.4207***	−0.0015		−0.0021**
	Stem	3.8380***	−0.0214*		−0.0018*
	Roots	4.1206***	−0.0240*		−0.0030***
(12)	Leaves	1.9813***	0.0138	0.0005	−0.0039***
	Branches	1.2295**	0.0269*	0.0010	−0.0020*
	Stem	2.2364***	0.0075	0.0027	−0.0017*
	Roots	2.6885***	0.0261	−0.0021	−0.0024**

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

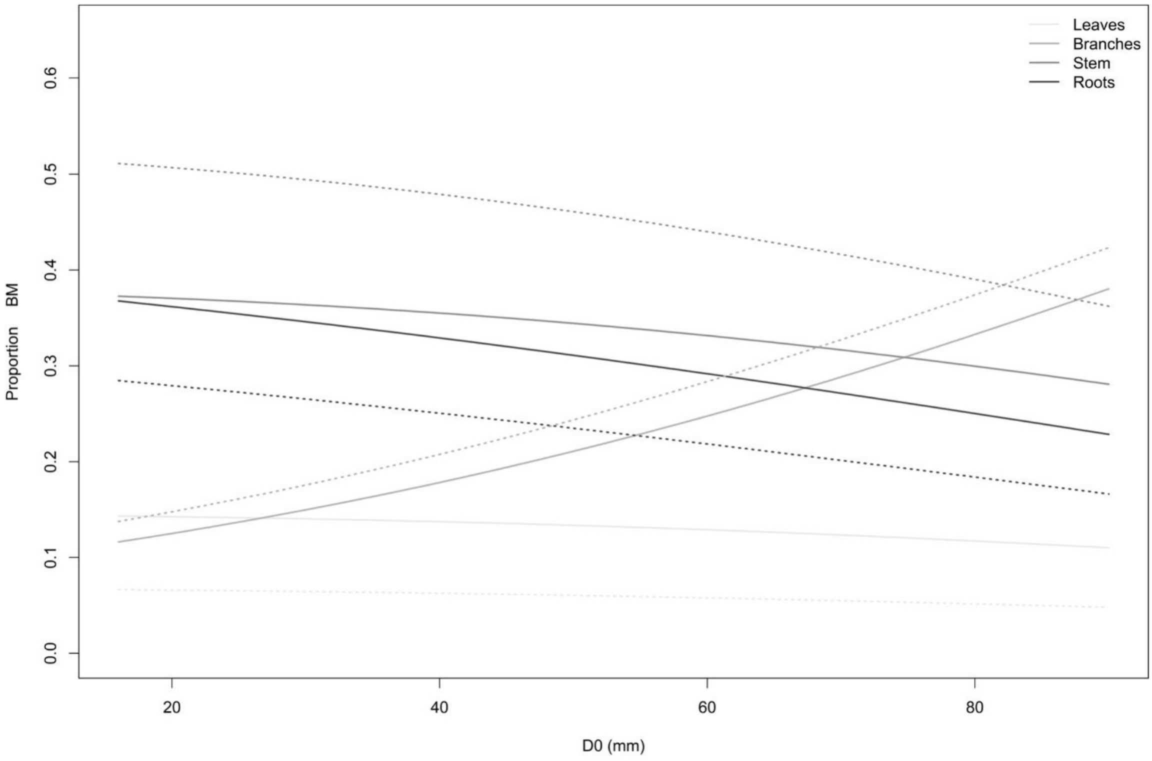

Fig. 7 Fitted values of the Dirichlet regression model (Eq. 11) considering the single biomass compartments. *Dashed line* SDI_l value fixed at 650, *solid line* SDI_l value fixed at 200

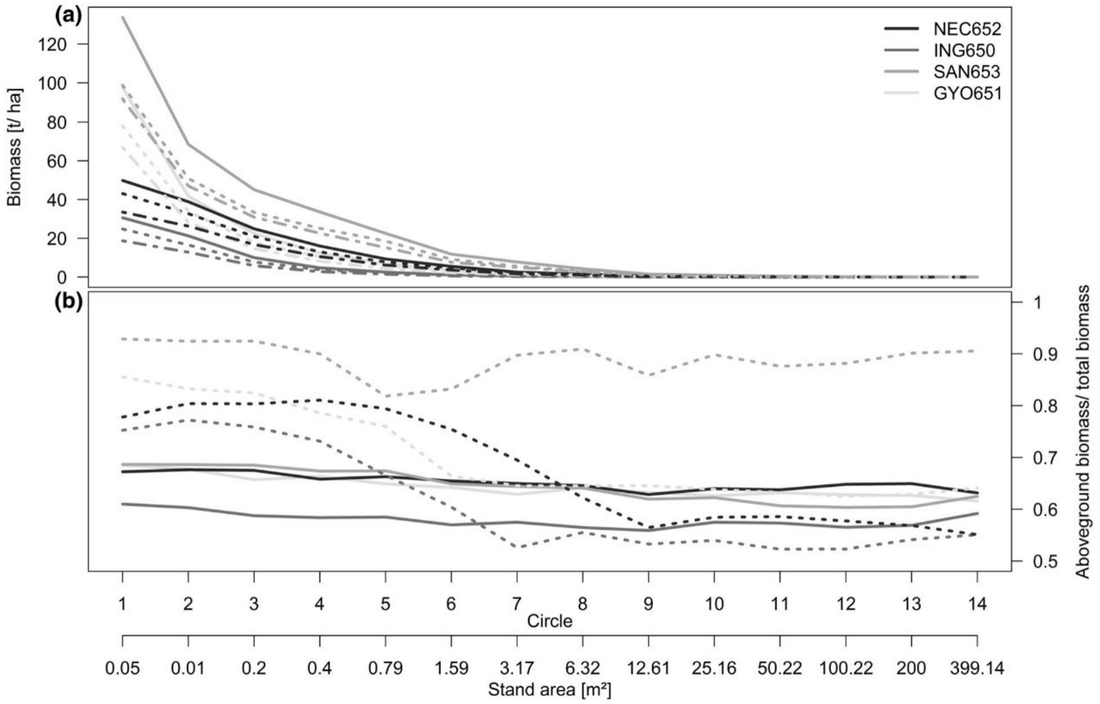

Fig. 8 Projected biomass productivity per site (**a**) and relation of aboveground to total biomass (**b**). *Solid lines* represent biomass productivity estimations using d_0 and height as predictors (model 4), *dashed lines* represent total biomass productivity estimations using d_0, height, and SDI_l as predictors (model 6) *dash-dotted lines* represent aboveground biomass productivity estimations using d_0 and height as predictors (model 4)

biomass productivity per site. The *x*-axis follows a stand density gradient using both circle number and stand area per plant as units. The most productive site is SAN652, followed by GYO651, NEC653 and finally ING650. This order indicates a trend related to the site conditions, as SAN652 and GYO651 represent the more arid sites. However, at stand densities realized from circle eight (=1582 N/ha) upwards productivity related to area is almost neglectable. Focusing on the estimation with the SDI_l, it is remarkable that for all sites the projected biomass productivity is on a lower level compared to the estimation without SDI_l. Again, the differences between the two models decrease with decreasing plant density. This might indicate an overestimation of biomass for sites with high plant density, when not considering the factor stand density. Looking at the aboveground biomass, the graph is logically on a lower level then the graphs visualizing the projected total biomass. Thereby, all three graphs seem to have a parallel course.

In more detail, the ratio of aboveground biomass to total biomass, as well as to SDI_l dependent total biomass, is depicted in Fig. 8b. Looking first at the model with d_0 and tree height, the aboveground biomass, accounts for 50–70% of total biomass. and respectively, belowground biomass accounts for 30–50% of total biomass independent of the different stand areas. This relativizes the finding of Fig. 8a, where differences in biomass decreased with decreasing plant density. While total biomass decreases with decreasing plant density, the ratio of aboveground and belowground biomass remains constant. Considering also the SDI_l as an additional predictor for biomass, for three sites (NEC652, ING 650, GYO651) a decline can be observed after circle 4. While with little stand area per tree the belowground biomass accounts only for 10–30% of total biomass, it increases to 30–50% when the stand area per tree enlarges. Only for the site SAN653 the ratio remains constantly between 10 and 20% independent of the stand area. A visualization of the proportion of total biomass to aboveground biomass is added in the appendix (Fig. 9). Like Fig. 8b it shows that especially at low stand densities the consideration of belowground biomass is important.

Summing up, these results highlight that (1) the consideration of the root compartment is important, as it accounts for a considerable amount of total biomass, and that (2) the consideration of the plant density is important when projecting biomass productivity, as it shows a strong influence.

Discussion

Biomass equations are essential for inventory, analysis, and modeling of forest trees and stands. They allow the prediction of total plant biomass or various fractions of it (leaves, branches, roots) depending on easy-to-measure tree variables such as stem diameter or height. They mostly assume species specific but age and competition invariant allometric relationships between latter stem attributes and biomass. However, many recently published studies show that beyond species identity (Zianis et al. 2005; Pretzsch 2014) allometry can be determined by age (Genet et al. 2011), and by the spatial constellation of a tree within the stand (Bayer et al. 2013; Pretzsch 2014).

The introduced biomass equations for common oak in the early tree development phase and their derivation for a broad range of spatial constellations consider both, the dependency of intra-individual growth partitioning on size and the competitive status of trees. Our equations represent very well the age of 7–10 years. They are based on a wide range of competition status, from solitary growth (growing space of 399.14 m^2 per tree) to extremely dense stocking (0.05 m^2 per tree). To our knowledge, no existing biomass equations cover such a broad range of competitive constellations. So, their applicability goes beyond so far available equations by Zianis et al. (2005) which are mainly based on older trees and neglect the effect of neighborhood on tree allometry, which is particularly strong in case of common oak due to its phenotypic plasticity (Pretzsch 2014).

The share of the root biomass of the total tree biomass continuously decreases with increasing tree size (Pretzsch 2010). So, any constant ratios or expansion factors as applied by Burschel et al. (1993) for scaling from the aboveground to total biomass will be flawed. According to the optimal partitioning theory (McCarthy and Enquist 2007), the shape of the tree crown, root system, and the relationship between these depends highly on the resource supply of the plant (Pretzsch et al. 2012a, b). Part of the large variation in the root–shoot relationship of plants can be explained by this theory. It predicts that the limitation of a resource leads to the promotion of growth of the plant organ responsible for supplying that critical resource (Keyes and Grier 1981; Comeau and Kimmins 1989).

Our biomass functions consider these dependencies as they estimate total plant and root biomass as a function of size, growing space, and site conditions. And the statistical characteristics when deriving these relationships showed that all factors have a significant effect on the relationship between root biomass and shoot biomass even in the early phase of tree and stand development.

Predictors for biomass functions

As indicated above, most studies chose dbh and tree height as predictors for biomass. Doing so, Pajtík et al. (2008) investigated biomass estimations of young Norway spruce trees and found stem diameter as the main independent variable. The additional variable height did not show an improvement on the overall scale. We find tree height to have a significant influence on total biomass and aboveground biomass, but not on the relative compartment biomass. Regarding the dbh, Annighöfer et al. (2016) proposed to use d_0 instead of dbh in the case of young trees. In the present article, both variables were tested and it can be confirmed that d_0 is the better predictor in the case of young trees. In their study, on seedlings and saplings of European tree species, Annighöfer et al. (2016) found the best model fit for a combination of d_0 and tree height as independent variables.

In addition to these commonly chosen predictors, our approach considered the stand density and found that neglecting this factor leads to an overestimation of biomass. The results show that the SDI_l has a negative influence on biomass. This result holds for total biomass and belowground biomass, as well as for the single compartments. The finding can be confirmed by Xue et al. (2012), who also found for aboveground biomass a decrease with increasing stand density. This result is in accordance with the optimal partitioning theory, as the higher the plant density, the higher the competition for resources. Anyhow, most studies neglect this factor.

The finding that wood density is not dependent on d_0, tree height or SDI_l, can be confirmed by Bergès et al. (2000). In their study on oak trees, they came to a similar finding, concluding that wood density has only a marginal effect on biomass production change, whereas ring widths shows a strong effect. In difference, Zhao et al. (2016) reported for Loblolly pine trees an increase of wood density by raising dbh. We conclude that the small and similar-aged sampling set underlying the present article might not be useful for detecting a tendency. A greater variation in ages and sizes would be needed to accurately test the dependency of wood density on size and competition.

Dirichlet regression

Recently, several studies have used Dirichlet regression models for estimating compartment biomass (Zhao et al. 2016; Poudel and Temesgen 2016). However, these studies primarily have a methodological focus, comparing different methods for biomass estimation, while this article represents an application. Nonetheless, the usability of this method shall shortly be discussed. In general, it can be stated that for compositional data, like in the case of biomass compartments, Dirichlet regressions are superior to usual multivariate statistical methods. The main reason for this is the fact that Dirichlet regression allows simultaneous fitting of the compartment proportions, wherefore the predicted proportions add to 1 (Hijazi and Jernigan 2009; Maier 2014; Zhao et al. 2016; Poudel and Temesgen 2016). Poudel and Temesgen (2016) assume the capability to capture the variance in proportions that sum to a constant, exhibiting skewness and heteroscedasticity, to be the reason why Dirichlet regression models outperform other methods. In their study on estimating aboveground biomass for Douglas-fir and lodgepole pine trees, they found that Dirichlet and beta regressions are the superior methods for modeling compartment biomass, compared to multinomial log-linear regressions. Zhao et al. (2016) also compared different methods which guarantee the unit sum. Using Dirichlet regression, fractional multinomial logit and log ratio regressions to model aboveground compartment biomass for loblolly pine trees, they found the Dirichlet regression to be the most adequate method. These results confirm earlier works which found that Dirichlet modeling was as successful as log ratio methods, when components have common predictors (Hijazi and Jernigan 2009). This is certainly the case for biomass estimations, where most studies assume all compartments to be primarily influenced by dbh and tree height. The results presented in this study confirm the assumption of common predictors, in our case d_0 and $\mathrm{SDI_l}$. However, the main advantage of the Dirichlet regression is that, through the simultaneous fitting of the compartment proportions, it also reveals how these predictors influence the proportions of the compartments' biomass.

Author contribution statement HP initiated the study and contributed to the manuscript. JD conducted the field and laboratory work, and data analysis and wrote the manuscript. EU conceptualized the study design and revised the manuscript. MV, PP and TH contributed to the development of the study design and supported data acquisition and revised the manuscript. MH supported data analysis. PB supported statistical analysis and revised the manuscript. GT revised the manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest. The founding sponsors had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, and in the decision to publish the results.

Appendix

See Figs. 9, 10.

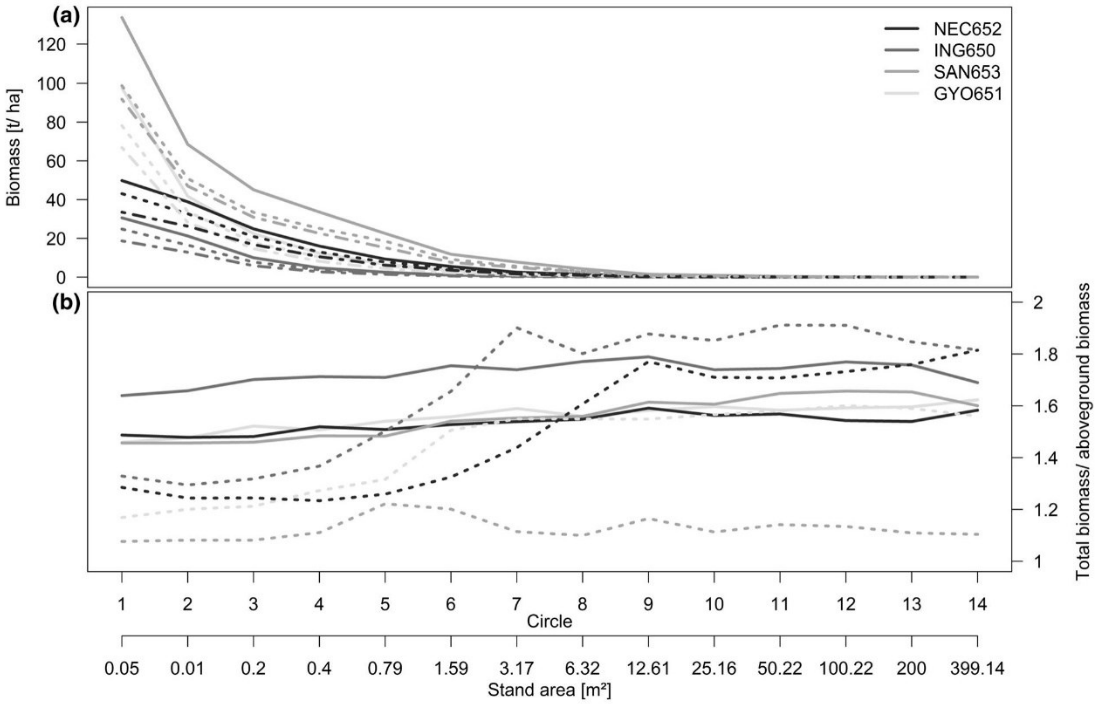

Fig. 9 Projected biomass productivity per site (**a**) and relation of total to aboveground biomass (**b**). *Solid lines* represent biomass productivity estimations using d_0 and height as predictors (model 4), *dashed lines* represent total biomass productivity estimations using d_0, height, and $\mathrm{SDI_l}$ as predictors (model 6) *dash-dotted lines* represent aboveground biomass productivity estimations using d_0 and height as predictors (model 4)

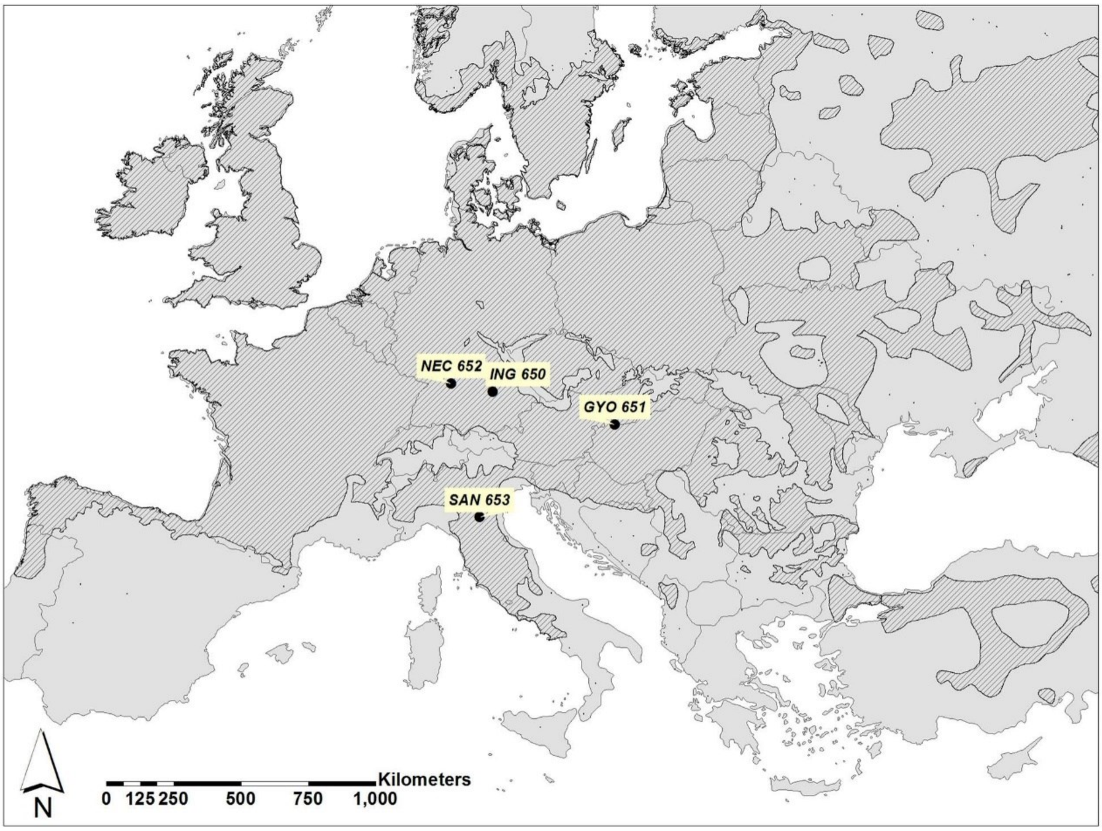

Fig. 10 Distribution of the study locations across Europe and distribution of *Q. robur* according EUFORGEN (http://www.euforgen.org)

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Tree Species and Their Space Requirements in Six Urban Environments Worldwide

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Abstract: Urban trees have gained in importance during recent decades, but little is known about the temporal dynamic of tree growth in urban areas. The present study investigated the allometric relationships of stem diameter, tree height, and crown radius for six different tree species in six metropolises worldwide. Increment cores of the trees were used for identifying the relationship of basal area and basal area increment and for extrapolating the temporal dynamics for each species in relation to the allometric parameters and growth extensions. Space limitation and its direct influence on growth were quantified, as well as the aboveground woody biomass and the carbon storage capacity. The results show that, among the investigated species, *Quercus nigra* and *Khaya senegalensis* have the highest growth rates for stem diameter and crown radius, whereas *Tilia cordata* and *Aesculus hippocastanum* remain on a lower level. A significant reduction of tree growth due to restricted non-paved area was found for *Aesculus hippocastanum* and *Khaya senegalensis*. Estimations of aboveground biomass were highest for *Quercus nigra* and lowest for *Tilia cordata.* These results show the species-specific allometries of urban trees over a projected time period. Thus, the data set is highly relevant for planners and urban green managers.

Keywords: growing space requirements; metropolises; tree allometry; tree growth dynamics; urban trees; biomass

1. Introduction

Along with urban greening the interest in tree growth rapidly increased during recent decades. On the one hand, it can be explained by the fact that trees provide many ecosystem services and functions, like cooling the environment, filtering harmful particulate matter from the air, and having aesthetical and structural functions within build-up areas [1,2]. On the other hand, several disservices of urban trees exist, like litter fall, damage to foot paths, and fallen branches which cause additional costs [1,3,4] and can endanger the public's safety.

Due to the benefits and disadvantages, the growth of urban trees and its space requirements are of high interest for urban planners and managers, as well as for arborculturists. First, it is important to know the future space requirements for the existing trees at a certain age. Second, for future planning the growing space requirements can be crucial for the choice of tree species before planting at a certain place [5]. Lastly, information on allometric relationships of urban trees is essential for the treatment measures of arborculturists for ensuring public safety. While there are several studies on forest trees, the space development of urban trees (solitary and open grown trees) is rarely known. Only a few studies [6,7] have investigated the differences in allometry and biomass between forest and urban trees. Our study aims at generating knowledge for urban trees by analyzing the space requirements, growth dynamics, and allometry of urban trees.

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Taking a deeper look at the benefits, one major benefit of urban trees is their carbon sequestration. The carbon storage capacity in turn is species-specific as Moser *et al.* [8], for example, showed for *Robinia pseudoacacia* and *Tilia cordata* in two German cities. They found a storage capacity of 461 kg C per tree for *Robinia pseudoacacia* (mean age: 39 years) and with 196 kg C a remarkable lower storage capacity for *Tilia cordata* (mean age: 41 years). Yoon *et al.* [9] estimated 24.9 t of total average C storage for the tree species *Acer buergerianum, Ginkgo biloba, Prunus yedoensis,* and *Zelkova serrata* in Daegu, Korea, and 69.7 t C ha^{-1} for *Platanus orientalis*.

A key variable for space occupation is the crown size. Species-specific crown projection areas were found by Pretzsch *et al.* [10] while analyzing the growing space requirements of 22 tree species worldwide. They focused on crown size parameters and determined five different crown extension types. Large crown expansions, crown sizes, and tree heights result in higher service functions such as shading and filtering particulates. The dimensions of the crown are responsible for shading and cooling, two of the most important ecosystem services of trees in urban areas. They play an important role not only on a tree scale, cooling down the microclimate, but also on a street scale. This means that through shading, trees can increase human thermal comfort [11]. Further, on the city scale this service can reduce the urban heat island effect [4]. Additionally, the shading of street trees can reduce the maintenance costs for streets by protecting the asphalt from solar radiation. McPherson and Muchnick [3] report an extended lifetime of 10 to 25 years for road and pavement surfaces in California that are highly shaded in comparison to those that are not shaded.

A further benefit at all three aforementioned scales is the reduction of water runoff. Besides tree number, increasing tree and crown dimension also reduces water runoff due to higher evapotranspiration and interception rates. This reduction in the amount of runoff is species-specific [4,12,13] and might also reduce stormwater runoff [14,15].

While the studies mentioned above show that trees have many benefits, the related space requirements of urban trees are a potential conflict. On the one hand, space in urban areas is limited and therefore expensive. On the other hand, open space is essential for housing prices, especially close to the city center [16]. Thus, knowing the space requirements of certain tree species is of high interest for urban planning. As tree growth is species-specific, the growth rate and the spatial dimensions of different tree species in dependence on tree age could be essential information for urban planning. While the growth behavior (*i.e.*, the crown radius, diameter at breast height or tree height) is well known for forest stands, little is known for solitary urban trees [17]. Studies have shown that information about growth dynamics of trees from forest stands cannot be directly transferred to urban trees [6]. This is due to the fact that in urban areas mainly mechanical stresses outweigh effects in forest stands, such as competition between trees or forest management measures [18].

The discussion about space requirements of trees in urban areas is not only relevant for the aboveground tree structure, but also for the rooting zone. The root growth is influenced by the available soil fraction, soil compaction, and the volume of root-penetrable soil [2]. Further, the effects of soil compaction, reduced soil volume, and paved surface are investigated in several studies [18,19]. If the soil volume is becoming too shallow, with time the roots start uplifting and cracking the pavement [20]. This in turn causes high costs for road or pavement maintenance, which is reported to be one of the first reasons for removing trees in urban areas [21].

In summary, while there are several studies dealing with space requirements of trees [10,22,23], the present study differs from the existing studies as it (1) is specific to urban trees; and (2) investigates the space requirements for six different tree species worldwide; and (3) provides a data set for each tree species representing the temporal dynamic of the tree structure. It is important to state that we do not see this study as a species comparison in the usual sense, which would not be possible with our data. Rather, we intend to compare different urban tree species, each under conditions where it can be considered to be typical and highly adapted. Based on the analyses, conclusions for space requirements of existing and planned tress, as well as conclusions on the potential benefits of urban trees, can be drawn. This leads to the following research questions:

(1) Is there a relationship between space limitations of typical urban tree species (in the sense mentioned above) and allometric relationships?
(2) Does soil sealing limit the growth of urban trees?
(3) How do typical urban tree species (in the sense mentioned above) differ in terms of aboveground biomass and carbon storage?

2. Materials and Methods

2.1. Data Acquisition

For this study we used data from urban trees that were collected in six metropolises worldwide. The data are a subset from samples acquired in the overarching project Response of Urban Trees on Climate Change funded by the AUDI Environmental Foundation. The field campaigns took place between October 2010 and June 2014 in the cities of Berlin, Brisbane, Hanoi, Houston, Munich, and Paris. Altogether, our data comprise 1097 trees, with an average of 183 trees per city, with a minimum of 126 (Brisbane) and a maximum of 240 trees (Berlin). In each city the most common local urban tree species was chosen. While the overarching project included trees in the city centers, suburban zones, and in rural outskirts, only the former were selected for the study at hand.

Selecting criteria for sample trees were: (1) health; and (2) that the trees were not pruned. An overview of the selected cities and species is given in Table 1.

Table 1. Sample description of tree species, within the cities, geography (latitude, longitude), sampling size, and time. Only trees in an urban environment are considered.

Species	Common Name	City	Country	Location	Number of Trees	Sampling Time
Aesculus hippocastanum L.	Horse-chestnut	Munich	Germany	48°8′ N 11°35′ E	231	2013
Araucaria cunninghamii AITON ex. D.DON	Hoop pine	Brisbane	Australia	27°28′ S 153°1′ E	126	2013
Khaya senegalensis (DESR.) A.JUSS.	African mahogany	Hanoi	Vietnam	21°2′ N 105°51′ E	163	2012
Platanus x hispanica MÜNCHH.	London plane	Paris	France	48°51′ N 2°21′ E	171	2013
Quercus nigra L.	Water oak	Houston	USA	29°45′ N 95°23′ W	166	2014
Tilia cordata MILL.	Small-leaved lime	Berlin	Germany	52°31′ N 13°24′ E	240	2010, 2012, 2013

For each tree, diameter increment time series are available from two increment cores taken from orthogonal directions at breast height. As the tree diameter d was measured, the diameter time series could be reconstructed backwards. Additional information about the sampling is described in Pretzsch *et al.* [10]. In the study at hand we transformed the diameter time series into basal area (ba) and basal area increment (iba) time series, because in contrast to diameter increment, basal area increment is directly related to a tree's biological production [24] and thus more appropriate for the allometric analyses shown below. Total tree height (h) and height to crown base (hcb) are also available, together with crown radii (r) measured in the eight cardinal and sub-cardinal directions, as suggested by Preuhsler [25]. The mean crown radius (cr) was calculated as the quadratic mean of these eight crown radii in Equation (1).

$$cr = \sqrt{\left(r_N^2 + r_{NW}^2 + \ldots + r_{NE}^2\right)/8} \tag{1}$$

Based on the mean crown radius, the crown projection area is then given by the following Equation (2), ensuring a bias-free transition between crown radius to crown projection area.

$$cpa = cr^2 \times \pi \tag{2}$$

Moreover, tree height and height to crown base (*cb*) were recorded by using a Vertex IV ultrasonic hypsometer.

In order to quantify a tree's spatial confinement by soil sealing like asphalted pavement or concrete surfaces, the unsealed area around the stem base was measured for each tree in four cardinal directions with a measuring tape. We used this information for calculating the variable *SCON*, which expresses the degree of confinement due to soil sealing. It is calculated as follows in Equation (3):

$$SCON = 1 - \frac{npa}{cpa} \tag{3}$$

where *cpa* is the crown projection area (m^2) and *npa* is the measured non-paved area (m^2). Table 2 gives an overview of the tree characteristics covered by our data. *A. cunninghamii* covers the broadest diameter range (15.7–129.5 cm) and the largest diameter was measured for *P. x hispanica* with 144 cm. The largest maximum *cr* with 14.8 m was also measured for *P. x hispanica*. The tallest tree was of the species *K. senegalensis* with 36 m, and this species also showed the highest range for ring widths. *A. hippocastanum* (232 years) and *P. x hispanica* (234 years) covered the largest age range within our sampled trees. *Npa* was largest for *A. cunninghamii* with 410 m^2, and smallest for *T. cordata*, *A. hippocastanum*, and *K. senegalensis* with 0.5 to 100 m^2.

2.2. Allometric Analyses

Plant allometry is a concept that is used in this study to relate tree dimensions to each other as well as to relate plant size and increment. It has a strong theoretical foundation [26–28] which, together with its mathematical compactness, makes it a powerful tool for applications in science and practice [22]. It is very common to use the double-logarithmic form of the allometric equation, especially in empirical study, because it makes the relation between two plant variables x and y, say x = stem diameter, y = height, accessible to linear regression models (Equation (4)):

$$\ln y = k + c \cdot \ln x \tag{4}$$

Here, the constants c and e^k are the allometric scaling coefficient and the allometric factor, respectively. Embedded in this context, the backbone of our analyses is a linear mixed effects model (Equation (5)), which describes the allometric relationship between the annual basal area increment *iba* (cm^2/y) and the corresponding basal area *ba* (cm^2) at the beginning of the corresponding year.

$$\ln iba_{ij} = \beta_0 + \beta_1 \cdot \ln ba_{ij} + b_i + \varepsilon_{ij} \tag{5}$$

This model was fitted to the retrospective tree growth data of each city separately. The indexes i and j represent the j^{th} observation of the i^{th} tree, β_0 and β_1 are fixed effect parameters, b_i is a random effect on tree level with $b_i \sim N\left(0, \tau^2\right)$, and ε_{ij} are i.i.d. errors.

In order to estimate the influence of spatial restriction on basal area increment we extended this model to Equation (6) by including the variable *SCON* which describes the confinement of a tree's growing area by soil sealing as defined in Equation (3) above.

$$\ln iba_{ij} = \beta_0 + \beta_1 \cdot \ln ba_{ij} + \beta_2 \cdot SCON_i + b_i + \varepsilon_{ij} \tag{6}$$

Table 2. Tree characteristics for each species.

Species	***d* (cm)**			***cr* (m)**			***h* (m)**			***rw* (mm) [1]**			**age (year)**			***npa* (m^2) [2]**			***SCON***		
	Min	**Mean**	**Max**	**Min**	**Mean**	**Max**	**Min**	**Mean**	**Max**	**Min**	**Mean**	**Max**	**Min**	**Mean**	**Max**	**Min**	**Mean**	**Max**	**Min**	**Mean**	**Max**
Aesculus hippocastanum	27.2	63.6	116.9	2.9	5.5	9.0	7.4	16.1	27.2	0.32	1.61	7.91	17	118	249	1.00	15.08	100.00	0.00	0.83	0.99
Araucaria cunninghamii	15.7	40.7	129.5	1.6	3.5	11.6	6.1	17.3	33.5	0.75	3.63	6.50	19	52	182	3.90	79.85	410.00	0.00	0.36	0.96
Khaya senegalensis	44.1	73.4	123.1	3.1	6.5	11.7	14.1	22.6	36	0.63	5.30	18.55	13	53	142	1.00	11.18	100.00	0.07	0.91	1.00
Platanus x hispanica	40.3	64.8	144.0	2.7	6.6	14.8	6.84	18.8	34.5	0.41	2.54	10.93	20	104	254	2.00	33.59	140.00	0.20	0.78	0.99
Quercus nigra	34.2	61.5	98.0	3.4	7.1	11.9	10	15.9	22.8	0.82	3.96	12.55	16	52	101	1.50	33.82	150.00	0.00	0.66	0.98
Tilia cordata	25.2	45.5	81.1	2.5	5.1	9.5	8.1	16.3	29.1	0.22	1.63	5.38	34	85	194	0.50	25.31	100.00	0.00	0.81	1.00

[1] n *rw A. hippocastanum* = 193, *A. cunninghamii* = 62, *K. senegalensis* = 144, *P. x hispanica* = 133, *Q. nigra* = 183, *T. cordata* = 227; [2] n *npa A. hippocastanum* = 231, *A. cunninghamii* = 126, *K. senegalensis* = 163, *P. x hispanica* = 171, *Q. nigra* = 166, *T. cordata* = 144. *d*: diameter at breast height (1.3 m), *cr*: crown radius, *h*: tree height, *rw*: ring width, tree age, *npa*: non-paved area, and *SCON*: degree of a trees spatial confinement.2.2. Allometric Analyses

When fitting this model, we restricted the tree growth data to the years after 1980, because *npa* was only measured once at survey time, and we refrained from assuming it was in effect for four decades or more. With preliminary versions of Equation (6) we also tested for the presence of interactions between *SCON* and *ba*, which, however, were not significant. Due to the comparably short time series from the restricted data set, we did not obtain plausible estimates for the allometric slope β_1 when fitting Equation (6). We therefore decided to keep the allometric slopes β_1 from the fitted Equation (6), and to use the following model (Equation (7)) for assessing the influence of *SCON*:

$$\ln iba_{ij} - \beta_1 \cdot \ln ba_{ij} = \alpha_0 + \alpha_1 \cdot SCON_i + b_i + \varepsilon_{ij} \tag{7}$$

Here, α_0 and α_1 are the fixed effects parameters to be estimated with the model. Thus, for estimating a tree's basal area increment *iba* from its basal area *ba* and a given spatial confinement *SCON*, without considering tree-specific random effects, the Equation (8) can be used:

$$\widehat{\ln iba} = \alpha_0 + \beta_1 \cdot \ln ba + \alpha_1 \cdot SCON \tag{8}$$

Analogously, if the spatial confinement effect shall not be considered explicitly in the estimation of basal area increment, the fit results of Equation (6) can be applied with Equation (9):

$$\widehat{\ln iba} = \beta_0 + \beta_1 \cdot \ln ba \tag{9}$$

Both equations allow for estimating a tree's temporal basal area development by using them in the following alternative serial calculations (Equations (10) and (11)):

$$ba_{t+1} = ba_t + e^{\alpha_0 + \beta_1 \cdot \ln ba_t + \alpha_1 \cdot SCON} \tag{10}$$

$$ba_{t+1} = ba_t + e^{\beta_0 + \beta_1 \cdot \ln ba_t} \tag{11}$$

The index t represents one point of time, $t + 1$ is the point of time one year later. Starting with a given initial value for basal area ba_{t_0}, basal area development for any reasonable time span can be projected. As a common initial value we chose $ba_{t_0} = 78.54\ \text{cm}^2$, which corresponds to a diameter at breast height of 10 cm, a size at which urban trees are often planted. We projected basal area development for 200 years, in case of Equation (10) with three different values for *SCON*, representing total absence of non-paved area limitation, medium, and maximum limitation as found in the data for each tree species.

In order to link basal area with vertical and horizontal space requirements, we fitted two additional allometric models (Equations (12) and (13)):

$$\ln h_i = \beta_0 + \beta_1 \cdot \ln d_i + \varepsilon_i \tag{12}$$

$$\ln cr_i = \beta_0 + \beta_1 \cdot \ln d_i + \varepsilon_i \tag{13}$$

where h is tree height, *cr* crown radius, and d is a tree's diameter at breast height. The latter can be easily obtained if basal area is known by $d = \sqrt{ba \cdot 4/\pi}$. Both models were fitted city-wise by ordinary least squares (OLS) regression. As only one height and crown radius per tree were available from the field survey, including tree-level random effects was not necessary.

2.3. Tree Biomass Estimates

Based on the statistical models shown above, temporal tree development in terms of basal area (diameter), height, and crown radius can be estimated. In order to link those projected tree dynamics to biomass and carbon storage, the tree biomass has to be estimated. We focus on total aboveground woody biomass (w), which can usually be estimated as a function of stem diameter at breast height (d) and tree height (h).

For all species covered by this study, such equations for estimating w were available as by Jenkins *et al.* [29] for *A. hippocastanum*, Eamus *et al.* [30] for *A. cunninghamii*, Clément [31] for *K. senegalensis*, Yoon *et al.* [9] for *P. x hispanica*, Clark *et al.* [32] for *Q. nigra*, and Čihák *et al.* [33] for *T. cordata*.

The biomass equations are based on forest tree data, and thus on trees under competition by other trees, excepting the equation for *P. x hispanica,* which is based on urban tree data. Trees in urban areas are mostly open-grown without competing trees, which calls the applicability of the above-mentioned equations into question. To account for this we apply a factor of 0.8 to the traditional biomass equations.

Based on the aboveground biomass we determine the related carbon storage by multiplying the biomass with 0.5 [34].

3. Results

3.1. Growth and Space Requirements of Urban Trees Based on Allometric Relationships

In Table 3 the results of the linear regression models, one per species, for the 'basal area-basal area increment' allometric relationship Equation (5) are shown for all tree species. The allometric exponent β_1 was in all cases different from zero on a significance level $p < 0.0001$ and varied from $\beta_1 = 0.4747$ for *A. cunninghamii* in Brisbane to $\beta_1 = -0.0057$ for *A. hippocastanum* in Munich. The scaling parameter β_0 was in a range between $\beta_0 = -4.5288$ for *A. cunninghamii* and $\beta_0 = -5.8743$ for *T. cordata*. τ^2 describes the variance of the random effects on tree level.

Table 3. Linear regression models for the basal area to basal area increment allometry (Equation (5)) for all six species (ordered according to latitude).

Species	β_0	SE (β_0)	p (β_0)	β_1	SE (β_1)	p (β_1)	τ^2
Araucaria cunninghamii	−4.5288	0.0533	<0.0001	0.4747	0.0127	<0.0001	0.0637
Khaya senegalensis	−4.9173	0.0523	<0.0001	0.0028	0.0260	0.9145	0.1711
Quercus nigra	−4.8455	0.0416	<0.0001	0.1077	0.0097	<0.0001	0.2201
Platanus x hispanica	−5.5322	0.0570	<0.0001	0.0325	0.0138	0.0185	0.3447
Aesculus hippocastanum	−5.8001	0.0322	<0.0001	−0.0057	0.0084	0.4924	0.1535
Tilia cordata	−5.8743	0.0302	<0.0001	0.1425	0.0061	<0.0001	0.1453

Parameter estimates (β_0, β_1) with standard errors (SE), significances (p), and the variance of the random effect (τ^2).

Further model results of the allometric relationships between "tree height-stem diameter" and "crown radius-stem diameter" are shown in Tables 4 and 5.

Table 4. Linear regression models for stem diameter (d) to tree height (h) Equation (12) for all six species (ordered according to latitude).

Species	β_0	SE	β_1	SE	r^2	RSE	F	p
Araucaria cunninghamii	0.6599	0.1417	0.5945	0.0391	0.6510	0.1955	231.72	<0.0001
Khaya senegalensis	−0.1319	0.2416	0.7560	0.0566	0.5550	0.1510	178.51	<0.0001
Quercus nigra	1.8093	0.2149	0.2312	0.0524	0.1060	0.1521	19.47	<0.0001
Platanus x hispanica	0.9630	0.2343	0.4708	0.0566	0.2900	0.2135	69.07	<0.0001
Aesculus hippocastanum	0.1092	0.1986	0.6410	0.0480	0.4370	0.1651	178.03	<0.0001
Tilia cordata	1.6825	0.2246	0.2868	0.0591	0.0900	0.1976	23.56	<0.0001

Parameter estimates (β_0, β_1) with standard errors (SE), coefficients of determination (r^2), residual standard errors (RSE), F-values, and significances (p).

Table 5. Linear regression models for stem diameter (d) to crown radius (cr) Equation (13) for all six species (ordered according to latitude).

Species	β_0	SE	β_1	SE	r^2	RSE	F	p
Araucaria cunninghamii	−1.3881	0.1209	0.7147	0.0333	0.7880	0.1668	460.15	<0.0001
Khaya senegalensis	−0.7786	0.3394	0.6134	0.0793	0.2710	0.2157	59.79	<0.0001
Quercus nigra	−0.7962	0.2130	0.6691	0.0519	0.5030	0.1508	165.96	<0.0001
Platanus x hispanica	−0.5391	0.2298	0.5775	0.0556	0.3900	0.2094	108.06	<0.0001
Aesculus hippocastanum	−0.9663	0.1695	0.6431	0.0410	0.5180	0.1409	245.77	<0.0001
Tilia cordata	−0.0336	0.1929	0.4342	0.0507	0.2360	0.1675	73.27	<0.0001

Parameter estimates (β_0, β_1) with standard errors (SE), coefficients of determination (r^2), residual standard errors (RSE), F-values, and significances (p).

The relationship of stem diameter to tree height shows the highest scaling parameter for *K. senegalensis* (β_1 = 0.76) in Hanoi and lowest for *Q. nigra* (β_1 = 0.23) in Houston. For β_0 only *K. senegalensis* (β_0 = −0.13) shows a negative value, all other species have positive values with the highest for *Q. nigra* (β_0 = 1.81). In comparison to this, allometric exponents for the relationship of stem diameter to crown radius are in a smaller range. The scaling factors are positive for all species and in a very narrow range (β_1 = 0.43 for *T. cordata*, β_0 = 0.71 for *A. cunninghamii*). The lowest allometric exponent is β_0 = −1.39 for *A. cunninghamii* and the highest is for *T. cordata* with β_0 = −0.03.

Based on the allometric relationship of 'basal area-basal area increment' and the estimated coefficients (Table 3) the diameter growth of a distinct tree species at a specific age can be projected. It has to be mentioned that the term age concisely means the age at breast height of the tree. Further, by taking the results of the other allometric relationships 'tree height-stem diameter' and 'crown radius-stem diameter' (Tables 4 and 5) into account this kind of time-specific extrapolation can be extended to the tree height and the crown diameter growth.

A time-series for 200 years was calculated on the base of a stem diameter of 10 cm starting in year 0. The results for the three estimated parameters d, cr, h, and for all six tree species are shown in Figure 1. For all three allometric relationships a visualization of the standard errors of β_1 is added in the appendix (Figure A1).

For the stem diameter growth (Figure 1a) *K. senegalensis* in Hanoi shows the highest growth over time, while the lowest was calculated for *T. cordata* in Munich. At an age of 100 years, for example, *T. cordata* has a diameter at breast height of 42 cm, whereas *K. senegalensis* is about 92 cm. Similar findings can be seen for the temporal dynamics of the tree height-diameter relationship (Figure 1b). *K. senegalensis* marks the upper level, in contrast the lowest level, which is obvious for *A. hippocastanum* until an age of 130 years. Between this range the species *Q. nigra*, *T. cordata*, and *P. x hispanica* remain at the lower border, unlike *A. cunninghamii*, which is close to the level of *K. senegalensis*. A different temporal distribution was found for the crown radius (Figure 1c). The upper limit is represented by *Q. nigra* in Houston, having a cr of about 9 m at an age of 100 years. In contrast, at the same time the species *A. cunninghamii* in Brisbane, *T. cordata* in Berlin, and *A. hippocastanum* in Munich have crown radii of about 5 m. The study is a comparison of well-adapted trees for specific regions, but not a mere species comparison.

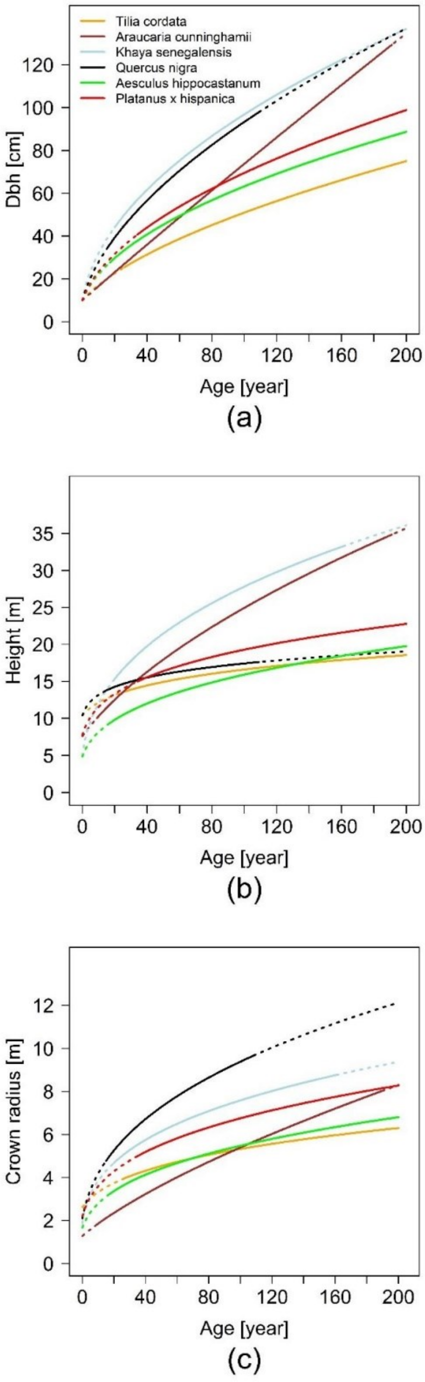

Figure 1. Allometric relationships for (**a**) diameter at breast height; (**b**) tree height; and (**c**) crown radius based on allometric model parametrizations for all six tree species (based on values of Tables 3–5). Dotted lines show projections which are not covered by measured data.

3.2. Impact of Paved Surface Area on Urban Tree Growth

As mentioned above, urban trees are often limited by non-paved area, especially in city centers. During our measurements the "non-paved surface area" (*npa*) was also recorded for tree species, if possible. This parameter, in the form of SCON Equation (3), is included in linear mixed effect models, one per species, for the ba-iba allometry Equation (7). The output of the models can be seen in Table 6, and the significances of α_1 indicate that the additional factor SCON is only significant for two species, *K. senegalensis* and *A. hippocastanum*. *Q. nigra* was also significant, but the results are not further shown, due to a not-plausible positive coefficient α_1, which can be explained by a very narrow range of the recorded values for *npa*.

Table 6. Linear regression results for the basal area—basal area increment allometry and the influence of SCON Equation (7) for all six species (ordered according to latitude).

Species	α_0	SE (α_0)	p (α_0)	α_1	SE (α_1)	p (α_1)	τ^2
A. cunninghamii	−4.6109	0.0769	0.0000	−0.0005	0.1116	0.9964	0.0765
K. senegalensis	−3.4053	0.3660	0.0000	−1.4998	0.3928	0.0002	0.2249
Q. nigra	−5.5567	0.1794	0.0000	0.7648	0.2221	0.0007	0.2222
P. x hispanica	−4.9857	0.2699	0.0000	−0.5632	0.3251	0.0856	0.3752
A. hippocastanum	−5.3079	0.0997	0.0000	−0.4056	0.1306	0.0022	0.2028
T. cordata	−5.7364	0.1721	0.0000	−0.1285	0.1954	0.5119	0.1868

Parameter estimates (α_0, α_1) with standard errors (SE), significances (p), and the variance of the random effect (τ^2).

The effect of the degree of spatial confinement by soil sealing on the parameters diameter, height, and crown radius for the species *K. senegalensis* in Hanoi and *A. hippocastanum* in Munich is depicted in Figure 2. Thereby three classes of the variable *SCON*: no limitation (*SCON* = 0), 50% limitation (*SCON* = 0.5), and high limitation (*SCON* = 0.9) were considered.

For *A. hippocastanum* only a slight influence of the limitation factor can be seen. Still, the trees with the lowest degree of limitation show the highest growth levels. In contrast, for *K. senegalensis* a strong relationship between the non-paved area and the tree growth can be found. Thereby, all *K. senegalensis* trees were mid- to high-restricted. Due to this, only these two classes could be shown in Figure 2. To give an example of the influence of the restricted non-paved area, the tree height of a 100 year old high-limited tree is 60% of the tree height of a similar-aged medium-limited tree. For the stem diameter growth a value of 50% can be accounted. With increasing age, the growth of the trees is increasingly inhibited. These findings show that restricted *npa* influences tree growth, but that the effect is species-specific and can be weak, as in the case of *A. hippocastanum* in Munich, or strong, as in the case of *K. senegalensis* in Hanoi. These findings can be reported for five of the six investigated species (Table 6).

3.3. Biomass and Carbon Storage Estimation for Urban Trees

Finally, the aboveground woody biomass of the species was estimated by species-specific equations from literature. The amounts of produced above ground biomass clearly vary from species to species (Figure 3). A 100 year old *T. cordata* tree in Berlin has a biomass of 0.7 t compared to a similar-aged *Q. nigra* tree in Houston with 3.3 t. The differences in the total aboveground biomass of the tree species increase with the age of the trees. Lowest biomass productivity by the age of 160 years is shown by *T. cordata* in Berlin and *P. x hispanica* in Paris with 1.3 t and 2.5 t per tree, respectively. For the same age, *A. hippocastanum* and *K. senegalensis* have a biomass of 3.5 and 4.2 t, respectively. With values of 5.2 and 5.9 t per tree the highest biomass values are achieved by *A. cunninghamii* and *Q. nigra*.

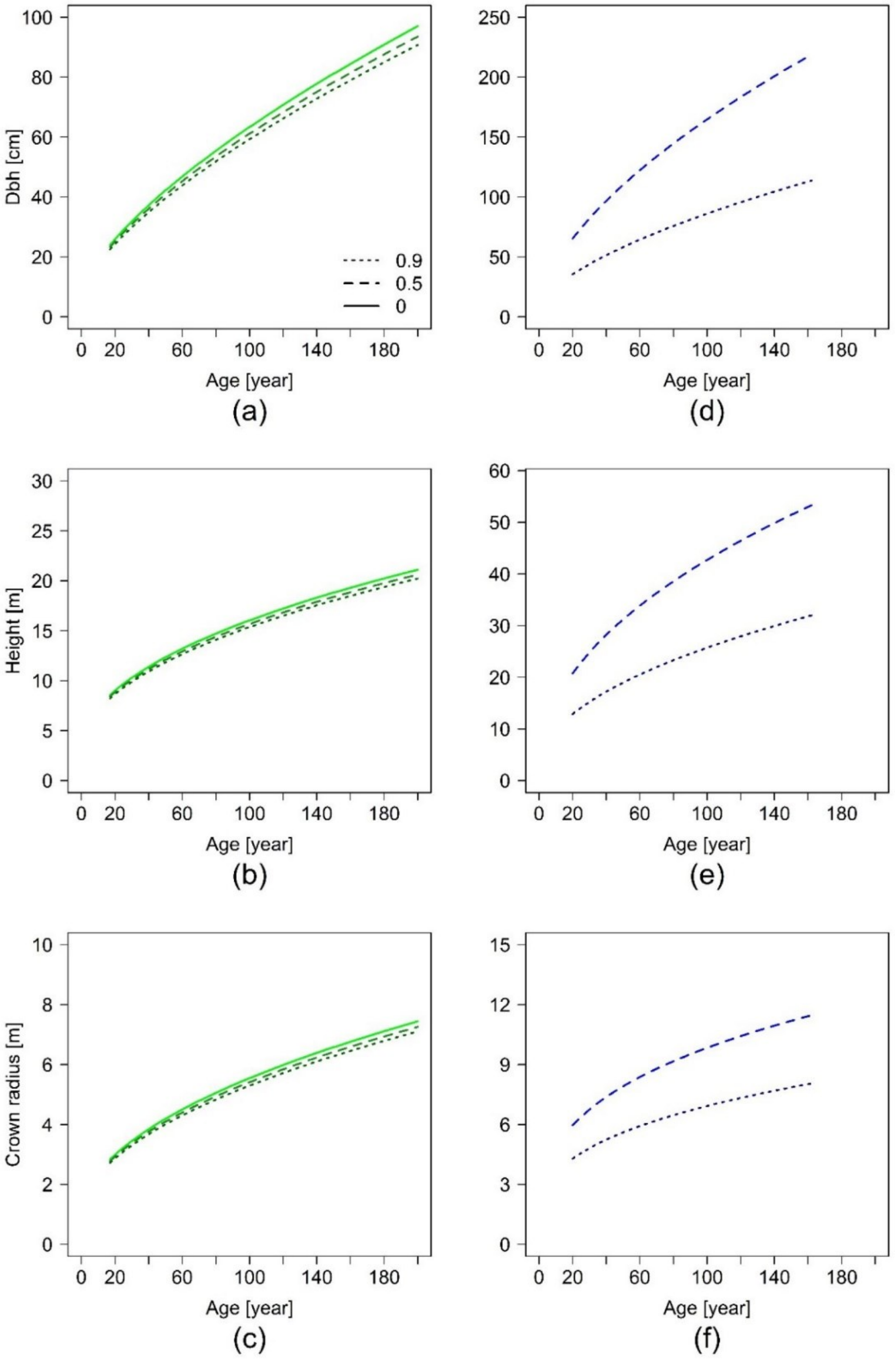

Figure 2. Effect of *SCON* on allometric growth relationships for diameter at breast height , tree height, and crown radius depending on age for the species *Aesculus hippocastanum* (panels **a**–**c**) and for *Khaya senegalensis* (panels **d**–**f**); solid line: no limitation, dashed line: 50% limited, and dotted line: highly limited (90%).

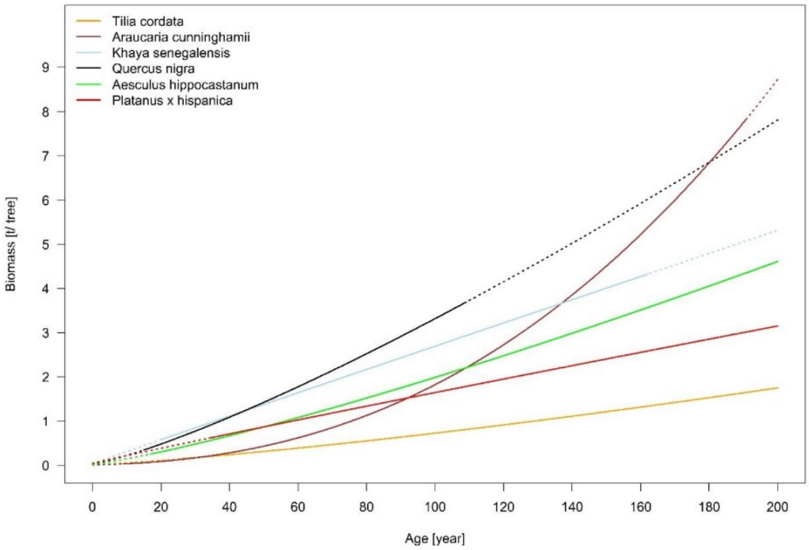

Figure 3. Estimated aboveground woody biomass for six tree species in urban environments, based on allometric equations. The data include the correction factor of 0.8 for transferring a stand biomass equation to urban trees. Dotted lines show projections which are not covered by measured data.

A comparison of the calculated carbon storage based on the measured tree parameters are shown in Figure 4, taking all available trees and the resulting average age into account (Tables 1 and 2). *A. hippocastanum* has the highest range from 122 to 4575 kg per tree and on average has 1106 kg per tree stored carbon; trees with lesser capacity include *P. x hispanica* (188–3038 kg per tree), *Q. nigra* (133–2145 kg per tree), and *K. senegalensis* (290–2161 kg per tree), the lowest values, as well as the smallest range, are attributed to *T. cordata* (71–1087 kg per tree) and *A. cunninghamii* (12–3531 kg per tree). The difference between the carbon storage (Figure 4) and the estimated biomass (Figure 3) is due to a variation in diameter at breast height (*dbh*)-range between the species, which can be seen in Table 2.

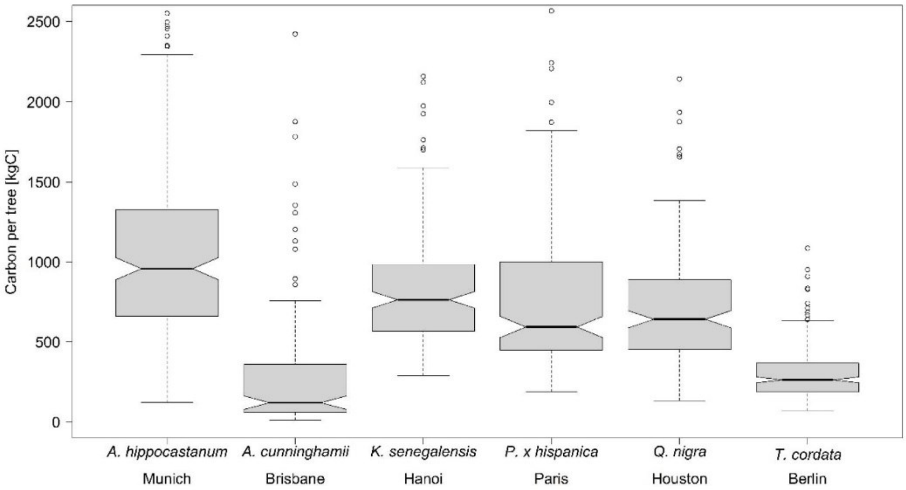

Figure 4. Carbon storage capacity of the investigated tree species in urban areas (cities), based on the measured data for diameter and tree height.

4. Discussion

4.1. Generalizabilty of the Identified Relationships

As mentioned in the introduction, this study cannot be interpreted as a usual species comparison, which would require a research design where the same set of species is observed under the same range of conditions. Our point is to compare urban tree growth and space requirements across a broad geographic climatic gradient based on a set of species that can be considered to be typical and highly adapted to the respective conditions. Some of the data we use are a subset of a data set that was used by Pretzsch *et al.* [10], where many urban tree species, including those dealt within the study at hand, are assigned to a small set of allometric types. This suggests that our findings can at least be roughly generalized for other species from the same allometric type and the same climate zone, and that they are representative for typical urban trees under the respective conditions.

In this context, the advantage of using allometric relations in contrast to other equation types is their strong foundation in biological theory. Thus, they are more than a mere description of a data set within the bounds of the sampled tree dimensions, as the parameter estimates transport direct biological information. An important consequence of this fact, allometric relationships can be extrapolated much more reliably than usual best-data-fit models. Species that show similar allometry can actually be considered to be comparable in terms of the variables involved. Furthermore, the allometry between tree size and size growth allows us to include temporal dynamics in our study, which are meaningful, albeit less precise, even when extrapolated due to their foundation in biological theory.

4.2. Growth and Space Requirements of Urban Trees Based on Allometric Relationships

Tree size and structure as described by tree allometry determine most functions and services of urban trees, such as shading, carbon fixation, or aesthetic embellishment. This underlines the relevance of a correct and species-specific quantification of tree allometry, which is in the focus of the study. Our continent-overarching study revealed the considerable extent to which allometry, and thus functions and services, can vary between species and change with proceeding tree ontogenesis. The study arrives at quantifying the allometry of six tree species common in urban environments. The quantification is relevant for practical planting guidelines for urban trees, for improving urban tree growth models, and parameterizing integrated tools for urban landscape planning.

The fundamental relationship of our analysis between basal area and basal area increment, which gives us the possibility of tracing back stem diameter growth and delivering us a sound scaling relationship, is based on increment cores. The results of our projected allometric relationships show that there are interspecific differences in urban tree allometry. The relationship of stem diameter to tree height shows the highest scaling parameter for *K. senegalensis* ($\beta_1 = 0.76$) in Hanoi and lowest for *Q. nigra* ($\beta_1 = 0.23$) in Houston. For β_0 only *K. senegalensis* ($\beta_0 = -0.13$) shows an unexpected negative value, all other species have positive values with the highest for *Q. nigra* ($\beta_0 = 1.81$). In comparison to this, allometric exponents for the relationship of stem diameter to crown radius are in a smaller range. The scaling factors are positive for all species and in a very narrow range ($\beta_1 = 0.43$ for *T. cordata* in Berlin, $\beta_0 = 0.71$ for *A. cunninghamii* in Brisbane). The lowest allometric exponent is $\beta_0 = -1.39$ for *A. cunninghamii* and is the highest for *T. cordata* with $\beta_0 = -0.03$. The results indicate that the growth of each species is individually based. Height growth, for example, increases from *A. hippocastanum* over *P. x hispanica* and *A. cunninghamii* to *K. senegalensis*, while crown radius expands from *A. cunninghamii* over *A. hippocastanum* and *P. x hispanica* to *Q. nigra*. These differences in growth dynamics for the specific species are highly relevant for urban forestry managers and planers. They need to know the space requirements of different species and how they will expand in the future in order to avoid potential conflicts with urban infrastructure.

Pretzsch *et al.* [22] state that interspecies differences in tree allometry exist in forest stands. They applied a similar method as in the present study and highlighted that competition can change plant morphology, and that allometric relationships represent structural configurations of forest stands on a species-specific or a general scaling level. Their analysis was based on stem slices of different tree species from forest stands in southern Germany.

The results of the present study show that differences in tree allometry are not only present in forest stands due to competition, but are similarly found in urban areas. Pretzsch *et al.* [10] also investigated crown allometry of different urban tree species, but without taking the temporal dynamic of the species into account. Their findings resulted in five allometric crown extension types, which also covered a distinct range of expansion and showed species-specific differences. These allometry types can also serve as a means of generalizing the results shown in this study.

4.3. Impact of Paved Surface Area on Urban Tree Growth

Our results show evidence that the restricted non-paved area limits tree growth in urban areas. Thereby, we could demonstrate that the level of growth limitation due to spatial confinement by sealed surfaces is species-specific.

This finding might be explained by water supply and the tree species' water storage capacity. Quigley [18] assumes that urban tree growth is slower than in forest stands due to the fact that a distinct proportion of the roots is below the pavement, and in this way is cut off from precipitation water. The reduction of water supply might be the main disadvantage of the restricted non-paved area affecting tree growth. The water storage capacity, which is very limited in the case of paved surfaces, is investigated for different tree species by Xiao and McPherson [13]. They state that this capacity is very species-specific and age-dependent.

Another study showed that the pavement type and profile design have an influence on tree growth, as well as the compaction, but that the pavements themselves do not cause a reduced growth rate [23]. We used the area of non-paved surface as a parameter for the influence of restricted area and found a trend for species-specific growth reduction with increasing restricted area.

The conflicts of roots with urban infrastructure are reviewed by Randrup *et al.* [35] in the way of analyzing the most relevant factors causing problems with tree roots in urban areas. As main factors they list among other things: species with a large maturity size, fast growing species, trees planted in restricted soil volumes, shallow irrigation, restricted distance between tree and sidewalk, and, in general, trees older than 15 to 20 years. Of these factors the restricted soil volume and shallow irrigation are likely to be given if the non-paved surface area is limited. Due to this limitation in non-paved area our analysis showed a significantly reduced growth, especially for *K. senegalensis*.

4.4. Comparison of Biomass and Carbon Storage Capacities of Different Urban Tree Species

McPherson *et al.* [7] investigated the differences in biomass between forest and urban trees and concluded that forest trees on average contain 20% more biomass than urban trees at a given height and stem diameter. Following their suggestion, we multiplied the outcomes obtained with the traditional biomass equations with a factor of 0.8 in order to achieve more realistic estimates for our urban trees. This factor is also considered in the i-Tree Eco/Urban Forest Effects (UFORE) model developed in the USA [36]. In contrast, Russo *et al.* [37] did not use such a factor for their study in Bolzano, Italy, due to their assumption that not all urban trees are open-grown. McHale *et al.* [6] also compared forest and urban biomass values and equations and stated that the value of 20% difference in biomass should be re-evaluated.

In Table 7 the results of two other urban tree studies on C storage [8,9] are compared with the values of the present study. For *T. cordata* the C storage values found by Moser *et al.* [8] are in a similar range to our findings. Both studies investigated *T. cordata* trees in German cities, which means that both studies took place within the same climate region. The minimum and mean C storage values of the present study are higher, due to the fact that less small trees were sampled and the mean diameter is higher. Again, Moser *et al.* [8] did not apply the correction factor of 0.8 and Yoon *et al.* [9] used it for avoiding an overestimation of the urban tree biomass for their estimations. Despite the fact that the two studies were done in different climate regions, and assuming that the two studied *Platanus* species (*P. x hispanica* and *P. orientalis*) show the same growth patterns, the C storage of the tree individuals fit together when based on their diameter.

Table 7. Comparison of carbon storage capacity based on the estimation of above ground woody biomass for trees in the present study with other studies in urban areas and the related diameter range.

Species	C Storage (kg/tree)			d (cm)
	Min	Mean	Max	Min–Max
Platanus x hispanica	259	702	2956	40–144
Platanus orientalis [1]	83	-	406	23–48
Tilia cordata	71	303	1087	25–81
Tilia cordata [2]	8	196	1341	6–107

[1] Data from Yoon *et al.* [9]; [2] Data from Moser *et al.* [8].

These results show that although a comparison of different studies is difficult due to different diameter ranges and different equations that might be used for the estimation, still the findings indicate that a tree species performs in a similar range on different sampling locations.

4.5. Carbon Storage Capacity of T. Cordata on City Scale

The present study estimates the temporal dynamic of urban tree growth and expansion. On this basis an estimation of the annual net carbon fixation of urban trees' woody biomass for a whole city is possible. Different studies [37–39], which quantified above-ground carbon storage on a city-wide scale, show that more research in this field is needed. For deriving a plausible estimation on the city scale the diameter distribution of the tree collective has to be known. For *T. cordata* a sample of 61,000 trees in Berlin [40] delivered us this distribution. In total, *T. cordata* trees amounted to 155,000 in 2014, by having a share of 35% of all street trees in Berlin [40]. By using the above mentioned biomass equation for *T. cordata* [33], which takes the diameter and the tree height into account, the carbon storage of this species sums up to 31.17 million tons C. On the base of the mean tree age of the respective diameter class the annual net average C-fixation of one single lime tree was calculated with 2.8 kg C year^{-1}, which results in an annual C-fixation for all lime trees in Berlin of 430 t C year^{-1}. Assuming a per capita C consumption of 1.5 t C year^{-1} for the year 2012 for Berlin [41], the annual carbon-fixation of lime trees corresponds to a carbon consumption of 284 inhabitants of Berlin.

Comparing the average value of 2.8· kg C year^{-1} of the present study to a similar study from Italy by Russo *et al.* [37] shows that with 2.8 kg C year^{-1} our estimation is out of his range, which lies between 9.79 to 43.06 kg C year^{-1}. It has to be mentioned though that *T. cordata* represents the lowest level of biomass production and carbon sequestration from our investigated species. This means that the other investigated species are within the range of Russo's values, which represent diverse tree species. Further, the differences between the studies might be due to the fact that the study by Russo *et al.* [37] included trees from urban areas as well as forest stands.

Schreyer *et al.* [42] derived the carbon storage per tree of different structure types in the City of Berlin. They list a value of 1,028,427 t carbon for the entire city of Berlin. In comparison, we quantified the value of 31,170 t C for 155,000 *Tilia* trees. If we take into account that *T. cordata* has a low C fixation rate compared to other species, and that just one third of Berlin's vegetation is represented with our selection, the total values of the two studies might fit together.

5. Conclusions

In summary, the results show the species-specific allometries of a set of typical urban trees worldwide, under the conditions they are typically found and best adapted to, by taking the temporal dynamic into account. The enlargement of diameter, tree height, and crown radius size are very species-specific and vary between the six investigated urban tree species. It can also be shown that the impact of paved surface inhibits tree growth. A significant impact of the non-paved area was found for the species *A. hippocastanum* in Munich and *K. senegalensis* in Hanoi. The estimations for above ground biomass are also species-specific and show the highest values for the deciduous species *Q. nigra* in Houston and the lowest for *T. cordata* in Berlin.

Our study gives statistically solid quantitative information about how typical urban tree species develop worldwide with specific regard given towards space requirements, which we deem useful for urban managers. Linking this information with the allometric species types as identified in Pretzsch *et al.* [10], the applicability of our study is beyond the species investigated here. With this knowledge better adaption of treatments for urban trees, which are in potential conflict with urban infrastructure, is possible; this information might be useful in supporting the benefits of urban trees. As a result, the additional costs for tree maintenance and care, which are well reported [2], can be reduced and a more effective way of managing might be possible.

Future research in this field is needed for an extended understanding of the growth behavior of urban trees and its temporal dynamic, specifically in relation to anthropogenic decisions, like paving surfaces. Last but not least, further investigations on urban tree biomass and carbon storage worldwide are important against the background of rising interest in urban air quality.

We based our study on both countries with long experience in urban tree research and countries that presently have begun caring for and investigating urban trees. As such, we tried to contribute to a continuous improvement of the appreciation, research, and knowledge base of urban trees worldwide.

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Author Contributions: Hans Pretzsch, Thomas Rötzer, and Enno Uhl conceived and designed the experiment; Jens Dahlhausen performed the experiments and analyzed the data; Peter Biber contributed statistical analysis tools; Jens Dahlhausen and Peter Biber wrote the paper. Thomas Rötzer and Enno Uhl revised the manuscript.

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Abbreviations

The following abbreviations are used in this manuscript:

awb	aboveground woody biomass
ba	basal area
cb	crown base
cr	mean crown radius
cpa	crown projection area
hcb	height to crown base
iba	basal area increment
npa	non-paved area
OLS	Ordinary least squares
SCON	Spatial confinement of a tree

Appendix A

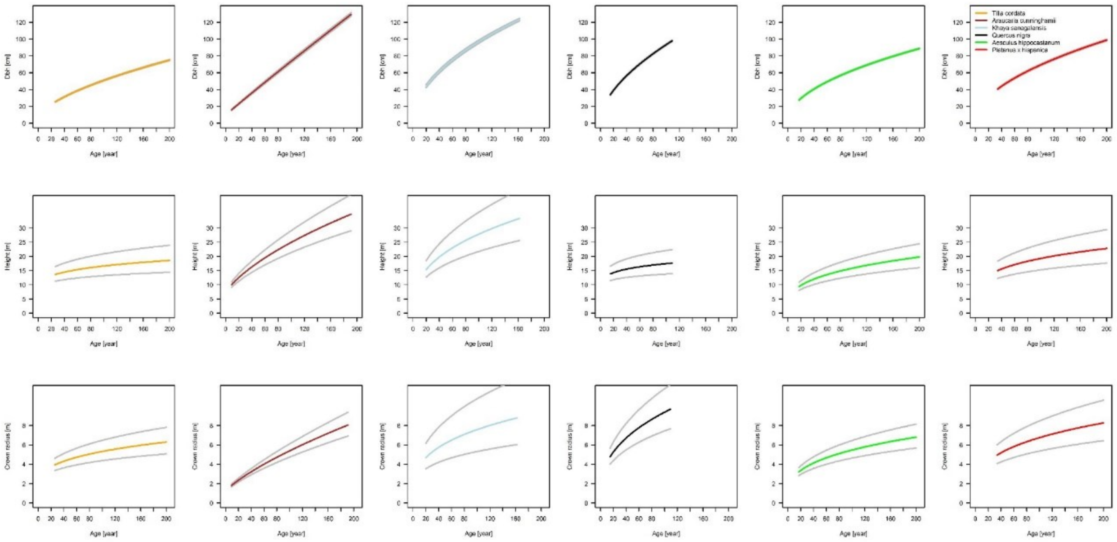

Figure A1. Allometric relationships for diameter at breast breast height (upper line), tree height (middle line) and crown radius (lower line) based on allometric model parametrizations for all six tree species (based on values of Tables 3–5). The coloured lines show the best-fit lines, and the grey lines indicate the visualized standard error of β_1.

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ORIGINAL PAPER

Urban climate modifies tree growth in Berlin

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Abstract
Climate, e.g., air temperature and precipitation, differs strongly between urban and peripheral areas, which causes diverse life conditions for trees. In order to compare tree growth, we sampled in total 252 small-leaved lime trees (*Tilia cordata* Mill) in the city of Berlin along a gradient from the city center to the surroundings. By means of increment cores, we are able to trace back their growth for the last 50 to 100 years. A general growth trend can be shown by comparing recent basal area growth with estimates from extrapolating a growth function that had been fitted with growth data from earlier years. Estimating a linear model, we show that air temperature and precipitation significantly influence tree growth within the last 20 years. Under consideration of housing density, the results reveal that higher air temperature and less precipitation led to higher growth rates in high-dense areas, but not in low-dense areas. In addition, our data reveal a significantly higher variance of the ring width index in areas with medium housing density compared to low housing density, but no temporal trend. Transferring the results to forest stands, climate change is expected to lead to higher tree growth rates.

Keywords Urban heat island effect · Growth trend · Urban trees · Lime trees

Introduction

At present, about three quarters of Europe's inhabitants live in urban or peri-urban areas and their share continues to increase (United Nations 2012). Ongoing urbanization entails changes in the local climate and other environmental conditions: (i) a stronger absorption of short-wave radiation due to a lower albedo and multiple reflection due to buildings, (ii) lower evapotranspiration values due to higher degrees of sealed surface, (iii) a higher atmospheric counter-radiation due to horizontal super elevation and a higher degree of air pollution, and (iv) a lower wind speed.

As a consequence, the average annual air temperature in major cities can be 1 to 3 °C warmer than in the neighboring rural areas (e.g., Rötzer 2007; United States Environmental Protection Agency 2014). Maximum differences occur at night with up to 12 °C found for US cities (United States Environmental Protection Agency 2014). Thereby, air temperature difference between the city center and its rural areas rises with the size of the urban population. For the city of London, Graves et al. (2001) found that air temperature decreased by 0.09 °C per mile with increasing distance from the city center. This gradient, however, differs strongly between cities. On average of 419 big cities, Peng et al. (2012) found a mean annual daytime surface urban heat island effect of 1.5 ± 1.2 °C, while the air temperature difference between urban and rural areas may be 2°–10 °C (Shepherd 2005). Besides resulting from different geographical locations, these differences can be attributed to country-specific styles of construction and architecture as well as to country-specific economic systems (Kuttler 2004).

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Along with air temperature, precipitation is higher in cities by 5 to 10% compared to their rural surroundings (Rötzer 2007). These long-term averages, as well as extreme events like heat waves, have negative consequences for the urban environment and human health. For Berlin, the largest German city, Scherer et al. (2014) observed that between 2001 and 2010, 5% of all deaths were directly related to increased air temperature. Dugord et al. (2014) state that the potential heat-stress-related risk is highest in the center of cities.

In many ways, urban trees play an important role for urban ecology and life quality in a city. Green areas, e.g., parks, gardens, or street trees, within cities improve the thermal conditions for human well-being by reducing the air temperature, especially in summer (e.g., Gill et al. 2007). Thereby, trees improve the microclimate through air cooling better than grass, which dries out quicker. Meier and Scherer (2012) studied the role of leaves and investigated the urban tree canopy temperature for different species in Berlin. They found that the small-leaved lime tree (*Tilia cordata* Mill.) is a suitable tree species for reducing air temperature due to lower crown temperature. Related studies by Leuzinger et al. (2010) show that the main factors for urban tree temperature are leaf size, location, stomatal conductance, and canopy architecture. They conclude that the cooling effect of urban trees is species-specific, and small-leaved trees, such as lime trees, show a lower leaf-to-air temperature difference at very high ambient air temperature (> 35 °C) and thus have a higher potential to cool down the immediate environment. Along with esthetic and cultural values, trees provide further environmental services such as filtering particulate matter (PM_{10}, $PM_{2.5}$) from the air, increasing biodiversity, or fixing carbon (McPherson et al. 1997; Nowak et al. 2013).

However, there are also several stress influences on urban trees, particularly in the view of climate change. Pauleit et al. (2002) summarize the main challenges for tree life in urban areas of European countries. For Germany soil, de-icing salt, elevated summer temperature, and frost damage are the main influencing factors for stress on trees. Further, water supply plays a fundamental role for tree growth. In cities, it is often impaired by sealed surfaces hampering water infiltration into the rooting zone (Gillner et al. 2013, Randrup et al. 2001). In addition, urban soil compaction might lead to a reduction of soil oxygen and water exchange, resulting in immediate as well as long-term effects on tree health and growth (Randrup et al. 2001). Furthermore, stress can emerge from subsurface pollution and mechanical disturbances (Quigley 2004). Despite the fact that a lot of factors influencing urban tree growth are well known, knowledge on their specific contribution to trees' growth and vitality is still limited. While structural changes of trees caused by changing climate conditions are already reported (Pretzsch et al. 2015; Moser et al. 2015), these studies do not consider differences in the housing density within a city.

Projections for the future development of the abovementioned changing conditions are predicted as becoming more extreme, especially in urban areas (McCarthy et al. 2010). Thus, when compared to forest-stands, urban trees are already more affected by changing climate conditions, which may result in both positive or negative effects on tree growth. Due to this, the urban areas give us the opportunity to investigate the response of urban species to climate change (Farrell et al. 2015). These unique possibilities have been little noticed until now but enable us to already study today the changes of our ecosystems due to climate change (Youngsteadt et al. 2015). Thereby, the differences in environmental conditions between high- and low-dense areas in cities can be large, while the spatial distances are small.

Time series of tree stem growth provides valuable information about growth trends and environmental changes (Schweingruber 1996). Forest science has been using the indicative potential of time series of tree size growth for a long time to quantify the site quality by site-indexing (Skovsgaard and Vanclay 2008), to measure various effects of silvicultural treatment such as pruning, thinning, or fertilization (Assmann 1970), to provide pieces of evidence and claim for compensation in cases of damage of forest by e.g., building operations, and increasingly to eco-monitor human impact on forest ecosystems (Cherubini et al. 2004; Pretzsch 1989) or climate change (Briffa et al. 2004; Pretzsch et al. 2014; Uhl et al. 2013). With just a few exceptions mainly dealing with tree damage or dieback (Eckstein et al. 1981; Gillner et al. 2014, Helama et al. 2012), urban trees so far were hardly used for revealing growth trends and environmental changes (Cook and Kairiukstis 1992). The main reason may be a higher reluctance against sampling urban trees, as any damage or even drop out caused by increment coring is easily compensated by neighboring trees in forests but not in the case of solitarily growing trees in streets or parks. In this study, tree-ring patterns from the center and peripheries of a metropolis were analyzed with regard to the long-term trends in growth.

For a better understanding of urban tree growth influenced by the small-scale environmental conditions, we investigate the long-term growth of *T. cordata* and the growth response on the changing climate conditions in an urban environment. To do so, we use time series analyses of tree stem growth. Measuring and analyzing more than 200 small-leaved lime trees (*Tilia cordata* MILL.) starting from a gradient in the center of the city of Berlin to the surrounding forest, we look at tree-ring patterns and their dependencies on the environmental conditions. Analyzing these data, we focus on the following research questions:

1. How do lime trees generally grow in the city of Berlin and its surroundings?

2. Is there a relation between the growth behavior of lime trees and environmental conditions, e.g., climate variables or housing density?
3. Does the sensitivity differ depending on housing density?

Materials and methods

Site description

Berlin is situated within the North-German young moraine landscape. The Warsaw-Berlin glacial valley crosses the city from South-East to North-West. South and North-East of Berlin is bordered by the Teltow-Barnim highlands. Topography varies moderately between 34 m to 115 m asl. Berlin covers an area of 892 km^2, with a maximum expansion of 45 km in East-West direction and 38 km in North-South direction. With 3.5 Mio inhabitants, Berlin is the most populated city of Germany. Berlin is subdivided in 12 districts (Fig. 1), from which 9 were selected for sampling. The share of green areas in the city amounts to more than 30% which is exceptionally high in comparison with other European metropolises (Kabisch and Haase 2014).

The region of Berlin belongs to the temperate climate zone with continental influence. Annual mean air temperature is 9.5 °C; the mean precipitation amounts to 578 mm with a typical peak between April and September (1961–1990).

From the climate station in Berlin-Dahlem (52.41° N; 13.31° E), which is situated in the surrounding area of Berlin referring to a low housing density and from a second station at Berlin-Alexanderplatz (52.52° N; 13.41° E), which is located in the highly dense city center of Berlin, monthly climate data since 1961 are available. Climate data from the station Alexanderplatz were not available between 1961 and 1980 and between 1992 and 1999. Missing values were calculated by fitting a linear least squares regression for each of the two periods on the base of the two measured periods 1981–1991 and 2000–2011 (see appendix Table 5). Temperature respectively precipitation data of the site Berlin-Dahlem form the independent parameter data while the data of Berlin-Alexanderplatz are the dependent values. The regression equations of the first period (1981–1991) were used to estimate the data of the period 1961–1980; the regression equations of the period 2000–2010 were used for the calculation of the period 1992–1999 (see appendix Table 5).

Data acquisition

In total, 252 lime trees were measured in the city of Berlin and its periphery. Sampling campaign was conducted in three periods, in October 2010, in April 2012, and in October 2013. *Tilia cordata* was chosen as it is the most frequent street and park tree in Berlin. *Tilia cordata* is known as a shade tolerant and more or less drought-sensitive tree species (Köcher et al. 2009, Gillner 2012, De Jaegere et al. 2016). This species is able to absorb heavy metals (Gworek et al. 2011) but is more sensitive to emissions and road salt compared to other species like *Platanus* (Schütt et al. 2013).

For the sampling, only healthy trees were considered in order to exclude confounding effects caused by tree diseases. Trees were required to have a diameter at breast height (dbh) above

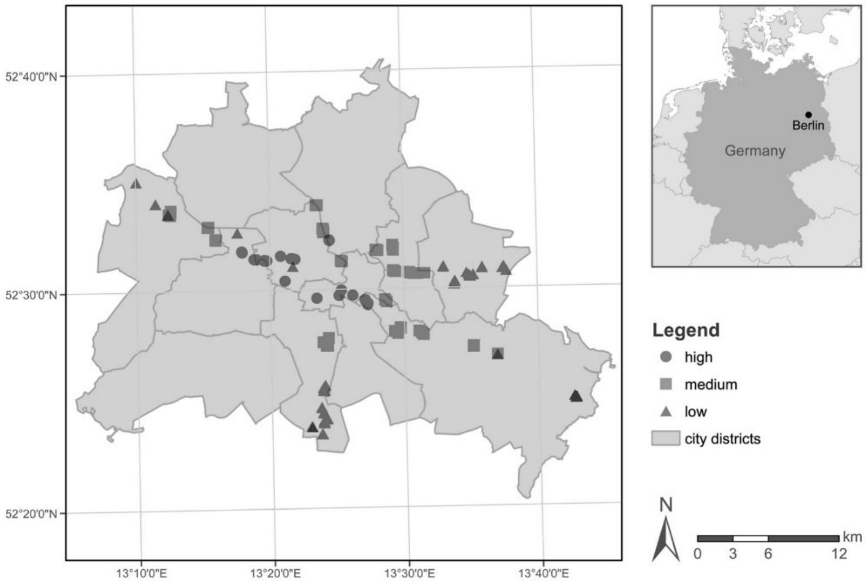


Fig. 1 Map of the sampling locations of this study, by housing density types: high (circle), medium (rectangle), and low (triangle) within the city of Berlin; the gray borderlines visualize the administrative city districts

40 cm, because otherwise the resulting tree-ring time series would not date back far enough for the purpose of this study. A full list of the selected trees and their parameters is shown in the supplement table. For each tree, the surrounding housing density was classified as “high” (hd), “medium” (md), or “low” (ld), based on the housing density map of Berlin (Urban Observatory, ESRI, 2014). This map displays land use data, with the three categories being classified based on square meters of land area per dwelling.

For all investigated trees, dbh was measured with a diameter tape, the crown radii in eight cardinal and sub-cardinal directions, and crown projection via the vertical sighting method (Preuhsler 1979). Tree height and height to crown base were recorded by using the Vertex IV ultrasonic hypsometer.

For the time series analysis, two increment cores were taken from each tree using a 5 mm increment borer. Where possible, the coring was done from north and east direction. At least two cores at an angle of 90° were taken for minimizing the error rate due to a non-concentric growth. The 504 cores were polished on a sanding machine with 320 grade sandpaper. After preparation, the tree-ring widths were measured with a Digital Positiometer after Johann (Johann 1977) using the software Lignometer. Radius was derived by backwards calculation using the year ring width values. Out of this, the basal area was calculated by means of quadratic mean radius of the two cores per tree. Current annual increment was examined by the difference between the basal areas of two consecutive years of basal area. Cross-dating was conducted firstly visually and then by using the dplR library in R (Bunn 2008). Dimensionless ring-width indices (RWI) were calculated by fitting a smoothing spline of 0.67 of series length with a 50% frequency cutoff. Strength of the common signal is expressed by the EPS (Expressed Population Signal) value using a 50-year moving window. A resulting EPS value above 0.84 (Wigley et al. 1984) indicates an adequate strength of the common signal for the time series and confirms further use of the data.

Quantifying general growth trends

For analyzing the general growth trend of *T. cordata*, the data set was split into the two periods, 1961–1990 and the period after 1990. The general growth trend is analyzed in a first step for trees in low-dense areas, to exclude the urban impacts, and thereafter for trees in high-dense areas. Doing so, the influence of the urban environment on the general growth trend is considered. A detailed description can be found in the digital appendix.

Sensitivity of the annual tree increment

For analyzing the sensitivity, which means in our case the oscillation of RWI along the mean value, we used the variance of the RWI (see digital appendix).

Analysis of the relationship between growth and climate parameters

By using a fitted mixed linear model the relationship between the growth of high- and low-dense urban trees and climate conditions was tested (see digital appendix).

Results

Air temperature in the city of Berlin was continuously higher over the last 50 years in comparison to the rural site (see Fig. 2 and Table 2). Differences of the 10-year means range from 1.1 °C in the first decade (1961–1970) to 1.4 °C in the last decade (2001–2010). Based on the decadal means (Table 1), the annual air temperature of both sites increased during the 50-year period, in the city center from 9.7 to 11.1 °C and in the periphery from 8.6 to 9.7 °C. The differences of the precipitation amounts of the two sites are largest in the last 20 years, showing higher precipitation sums in the periphery (Table 1).

Most of the sampled trees (107) are situated in a low housing density environment (Table 2), scarcely less (102) in the medium dense area, and the fewest (43) in the city center. Based on the mean values of the measured tree parameters, slight differences among the different housing density classes can be reported. Average tree height and mean growth are largest in the low-density zone, the trees in the medium-density zone show the highest age range, and the trees in the high-density zone have the greatest crown projection area. For the low-dense and high-dense sites, the average growth rate is on a very similar level, but on the medium dense site, it is remarkably lower. Same findings can be stated for the related standard deviation.

The mean courses of the annual radial increment (Fig. 3) show a typical age-related growth trend. This is the case for

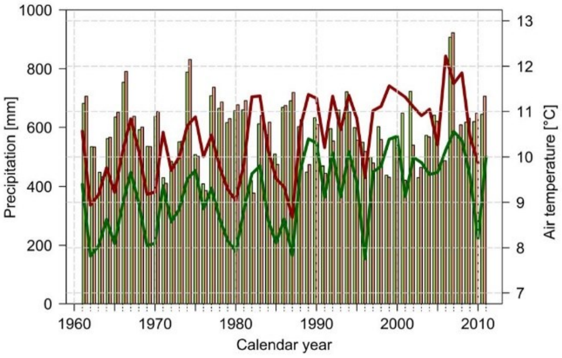


Fig. 2 Air temperature (annual mean; solid line) and precipitation (annual sum; bars) from the climate station “Alexanderplatz” in the city center (red) and from the peripheral station “Dahlem” (green) in Berlin for the period 1961–2011

Table 1 Climatic parameters (air temperature and precipitation) for the "Alexanderplatz" climate station in the city center (CC) and for the station "Dahlem" in the periphery (PP) of Berlin are shown as decadal means. Δ indicates the difference between CC and PP.

	City center	Periphery	Δ
Air temperature [°C]			
1961–1970	9.7	8.6	1.1***
1971–1980	10.0	8.9	1.1***
1981–1990	10.4	9.2	1.2***
1991–2000	10.9	9.6	1.3***
2001–2010	11.1	9.7	1.4***
Precipitation [mm]			
1961–1970	611	601	10
1971–1980	589	582	7
1981–1990	591	582	9
1991–2000	533	570	− 37***
2001–2010	591	622	− 31

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

the complete data set, as well as for the single housing density classes. Standard deviation is lowest for the younger years of the course.

General growth trends

The overall growth trends of lime trees in the low-dense areas of Berlin are illustrated in Fig. 4 in form of the Delta values of the mean basal area increment (Δig). Data are calculated for three age classes (below 40 years, 41 to 80 years, and above 81 years) and depicted over the time period from 1991 to 2011. The reference line symbolizes the growth of all low-dense lime trees estimated from the applied Bertalanffy model (Eq. 1–3 in digital appendix). The fact that the growth course of the younger trees steadily remains above the reference line shows that the growth rate is at a higher level than the average growth. The mean Δig of young trees, aged < 40 years, shows that during the last 20 years, these young trees have grown on average 10 cm^2 yr^{-1} more (linear regression slope = 0.893 cm^2 yr.$^{-1}$; $r^2 = 0.62$). Trees of higher age indicate a slow increasing trend which exceeds the reference line by the mid or end of the 90's. For trees, aged between 41 and 80 years, the Δig increases by 0.234 cm^2 yr.$^{-1}$ ($r^2 = 0.19$), when considering the complete period. Thereby, the course is not consistently increasing and shows two lows for the drought years 1997 and 2004. The oldest trees have the slightest increase (slope = 0.210 cm^2 yr^{-1}; $r^2 = 0.21$) over the considered period, but still show a higher growth than the reference after the year 2004.

For investigating the influence of housing density on tree growth, Fig. 5 displays the difference in growth between high- and low-dense areas. For doing so, two age groups (trees aged younger 60 years or older 60 years) are defined. This division was based on previous analysis of the growth data in 10-year intervals (see appendix Figs. 7, 8, 9, and 10). The data is presented as Delta values and thus directly relates the growth values from high- to low-dense areas. In difference to the before shown results (Fig. 4), the following analysis takes only the measured data into account.

For the younger trees, it can be said that on average positive values, representing a better growth in the high-dense areas, are found between 1981 and 2000, with a first short decline around 1990, 1995, and 1997. Before the year 1981, as well as after 2000, the younger trees grew better in low-dense environments. In difference, before 2002, the older trees grew on average better in the low-dense areas. Before 1976, as well as after 2002, the growth of trees older than 61 years was higher in the high-dense areas, except the year 2007. Interestingly, the comparison of the two age classes shows that the growth reactions to housing density, between younger and older trees, are always opposing. These differences illustrated in Fig. 5 might be related to the ambient climate conditions which vary due to housing density.

Table 2 Mean values of the measured tree parameters for the complete dataset (all) and the different housing density classes referring to the time period 1900–2011 (growth parameters) and 2011 (tree parameters)

	All	Low	Medium	High
Number of trees	252	107	102	43
dbh (cm)	44 (16.5–80.4)	44 (16.5–80.4)	45 (25.2–76.8)	42 (32.8–54.7)
Tree height (m)	17 (8–29)	18 (10–29)	16 (8–26)	16 (12–22)
Age range (year)	32–192	33–192	32–182	48–118
Crown projection area (m^2)	82 (20–286)	83 (21–286)	78 (20–199)	92 (33–148)
Avg. radial growth rate (mm yr^{-1})	2.26	2.44	2.06	2.38
Standard deviation of growth rate	1.00	1.16	0.82	0.89
Expressed Population Signal (EPS)	0.93	0.82	0.86	0.82

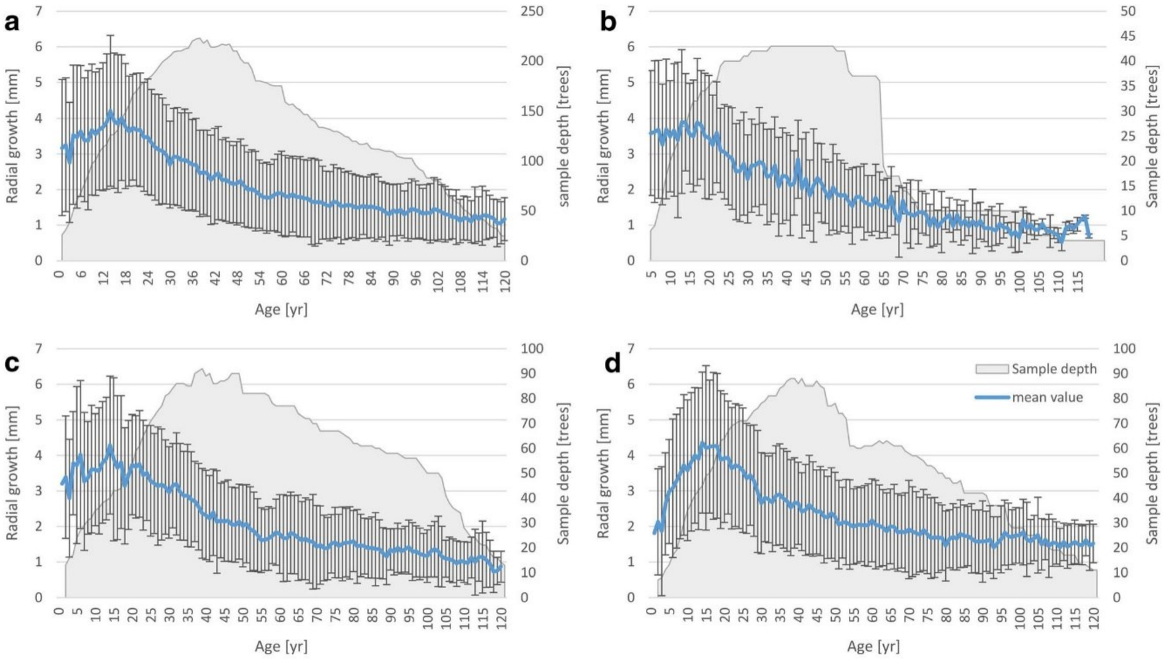


Fig. 3 Mean value (blue line) of radial growth average, sample depth (gray line), and standard deviation (bars) over age for all (**a**), "high-dense" (**b**), "medium-dense" (**c**), "low-dense" trees (**d**) referring to the period 1900–2011

Sensitivity of growth course

For investigating the growth sensitivity, the variances of RWI per housing density for the two observation periods were calculated and are depicted in Fig. 6. The variances are lowest in the ld (low-dense) areas and highest in the md (medium-dense) areas. Comparing the two periods, the variances for these two housing density classes decrease from the first to the second period, while the variances of the hd (high-dense) trees increase.

In a next step, the variances of the different trees were analyzed by using a Linear Mixed Effect model (Eq. 5 in digital appendix). Results summarized in Table 3 reveal significant differences between the classes ld and md, having higher variances in md areas. Variances of the hd areas were not significantly different from the ld areas. Further, the model reveals that the differences between the two observation periods reported above (Fig. 6) are not significant, neither in general nor for one of the housing density classes. In difference, the tree age at the time of coring (variable *end.age*) is

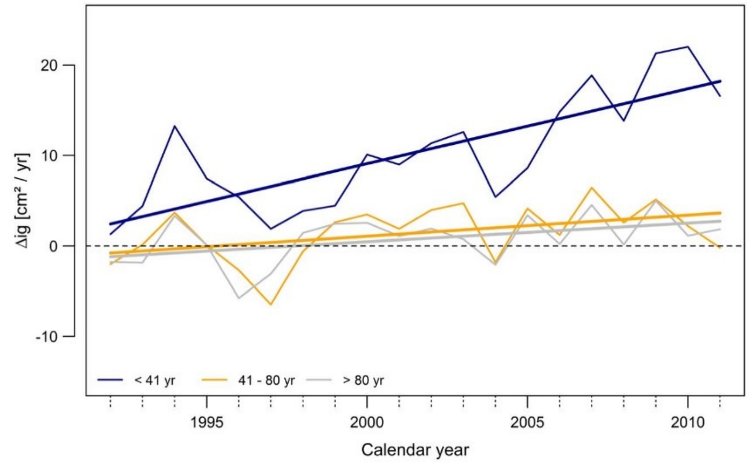
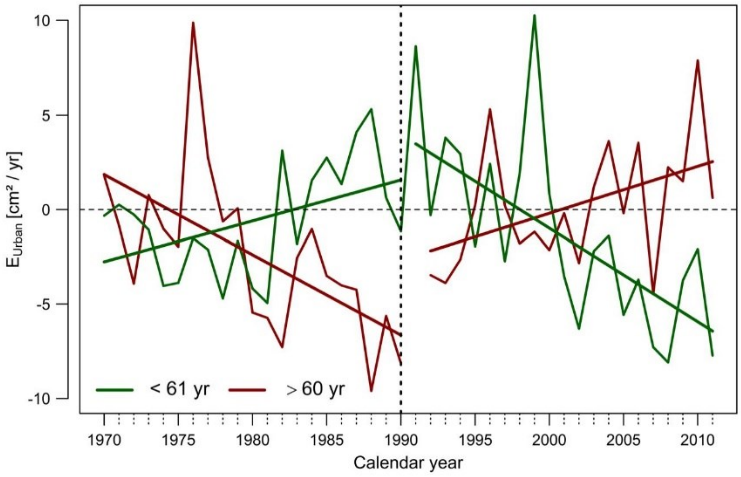


Fig. 4 Delta values of mean basal area increment (Δig) of the "low-dense" trees for the age classes < 41 years (blue), 41–80 years (yellow), and > 80 years (gray); bold graph indicates the linear trend

Fig. 5 Effect of urban climate on tree growth ($E_{Urban} = \overline{ig}_{hd} - \overline{ig}_{ld}$) shown for two age classes < 61 years (green) and ≥ 61 years (red), with the bold lines indicating the linear trend for the respective age classes and observation periods



highly significant which means that older trees have a higher variance than younger ones.

Relationship between growth and climate

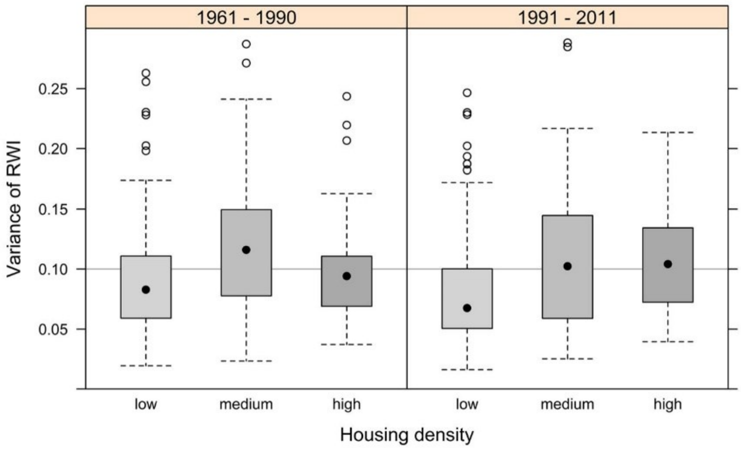
For analyzing the relationship of growth patterns and climate parameters, a linear mixed effect model (Eq. 6 in digital appendix) was applied. Influence of the parameters air temperature, precipitation, and DMI on RWI were tested in combination with varying coefficients like time period (*period1* (before 1990) and *period2* (after 1990)) as well as housing density. The results (Table 4) show significant effects of air temperature, precipitation, and DMI on RWI for the second period and high housing density. Precipitation and DMI further show a significant effect on RWI for the first period and high housing density. In difference, no significant effects of air temperature, precipitation, and DMI on RWI can be found in low-dense areas.

Thereby, air temperature has a positive effect on RWI, while the effect of precipitation is negative. Thus, the growth of trees in high dense areas seems to be benefitted by rising air temperature, while higher precipitation rates seem to stress the trees.

Discussion

Our findings regarding general growth trends show opposite growth trends before and after 1990. An explanation for these differences might be the increased urban development measures in Berlin starting after 1990 (Schmelcher 2011).

Fig. 6 Variances of RWI separated by housing density classes and growth periods illustrated as boxplots. The point within the box indicates the median



Correspondingly, we find a zonal effect, showing that during the last ten observed years, the trees in high-dense areas, younger than 60 years, are stressed by increased building density resulting in more extreme climate conditions. While air temperature varies only marginal between the two climate stations, precipitation shows a remarkable decrease during the last two decades for the city center, but not for the periphery. This reduction in water availability might be one reason for the growth decline of the young trees in highly dense areas during this period, whereas the older trees respond with higher growth to this change. Older trees might cope better with the reduced water supply, as they might generally be better adapted to limited resource supply than the younger trees. This finding contradicts with findings from Quigley (2004), who investigated forest and urban trees distributed in three different successional categories. For early successional trees, he finds that young trees are more tolerant to urban conditions, as they have faster growth rates in urban areas. However, this finding is not directly related to precipitation, but to urban conditions in general.

Looking deeper into the relationship between air temperature and housing density, Fenner et al. (2014) investigated different classes of both highly and less densely built-up areas within the city of Berlin. Looking at the period 2001 to 2010, they observed higher air temperature within the urban areas compared to the rural areas. These data confirm the data underlying the analyis of the current article, which also show higher air temperature for the climate station in the city center. These higher air temperatures in urban areas, in turn, were shown to prolong the vegetation period. In this context, Rötzer et al. (2000) reported an early flowering in urban areas.

Sensitivity can be understood as a kind of indicator for the vulnerability of tree growth to climate conditions (Gillner et al. 2013, Gillner et al. 2014, Schweingruber, 1996). As reported by Schweingruber (1996) for natural habitats, the trees with extreme environmental conditions show highest sensitivity. In the present study, the highest sensitivity was found in the medium-dense areas, before as well as after 1990. When transferring the finding from Schweingruber (1996) to the present finding, this would mean that the medium-dense sites are expected to have the most extreme environmental conditions. This cannot be proven with the climate data available for this study. However, the finding appears reasonable, considering that medium-dense areas have undergone the biggest change in recent years, as urban development mostly takes place in these areas.

While we already nowadays observe differences in climate conditions between urban and rural sites, future projections predict especially for the urban areas intensified climate conditions causing thermal stress and vulnerability to heat waves (McCarthy et al. 2010). In line with this, Bowler et al. (2010) point out that confounding variables such as ground cover, distance to sea, and height-to-widths-ratio of street canyons vary between different investigation sites and affect the local air temperature conditions. However, according to Jones (2004) and Parker (2004), no influence of urbanization on the large-scale warming is found.

Still, as aforementioned, the differences in tree growth found between different housing density sites are expected to be moderated by climate parameters. For example, Gregg et al. (2003) report for New York that ozone has a strong influence on tree growth. In this article, however, we focused on the climate parameters precipitation and air temperature. Like the results from our last model (see Table 4) show, air temperature and precipitation have strong influences on tree growth. Thereby, in high dense areas higher air temperature led to higher growth rates, whereas the opposite was the case in low-dense areas. These diverse findings can be confirmed by previous studies, which show that growth reactions on increased air temperature depend on several factors, e.g., tree species, latitude, or altitude (Carrer and Urbinati 2006, Way and Oren 2010). Regarding precipitation, our findings show that after 1990, higher precipitation led to lower growth in high dense areas, but higher growth in low-dense areas. In line with this, previous findings regarding the effect of precipitation on tree growth are confounding. David et al. (2015) confirm the availability of water as being one of the main limiting factors for urban tree growth in Paris. On contrary, De Jaegere et al. (2016) report in their review on *T. cordata* in European forest stands that above the precipitation threshold of 550–600 mm per year, water supply becomes secondary. The annual precipitation sum of Berlin is similar to the abovementioned value, but it has to be considered that in an urban environment due to the impervious runoff, a considerable amount of precipitation does not reach the tree roots. In line with this assumption, Dahlhausen et al. (2016) find a limitation in tree growth for different tree species in urban environments due to a restriction in non-paved area. Still, with the presented results, the statement of De Jaegere et al. (2016) can be confirmed for older trees, but not for trees younger 60 years.

Specific for *T. cordata*, De Jaegere et al. (2016) further state that this species is highly tolerant against heat waves and drought events, wherefor it has an important advantage to other species when adapting to the warming climate conditions. Correspondigly, the effects of climate parameters on tree growth are even higher for other tree species as reported by Friedrichs et al. (2009). In their study, they investigated the growth response of *Fagus*, *Pinus*, and *Quercus* in two German low mountain forest sites and found water availability as the main impact factor of tree growth. Further, they stated an increasing impact during

Table 3 *$VRWI_{ij}$* estimates from LME model (Eq. 5 in digital appendix)

	Estimate	std. error
Intercept	0.0412 ***	0.009928
Medium-dense	0.0303 **	0.009209
High-dense	0.0285	0.011929
Medium dense: High dense	− 0.0018	0.012148
Period1	0.0075	0.008599
End age	0.0005 ***	0.000097
Medium-dense × period1	0.0052	0.012310
High-dense × period1	− 0.0122	0.016061
Medium-dense × period1: High dense × period1	− 0.0174	0.016174

Period1 denotes the timespan 1961 to 1990. The reference level was set to period2 (1991 to 2011) and to low housing density

** $p < 0.01$, *** $p < 0.001$

the last decades. These findings are similar to those presented in the study at hand. Moser et al. (2016) investigated the annual growth and drought tolerance of *T. cordata* in two German cities and classified the species as moderate drought tolerant and found out that the growth reductions of *T. cordata* after a drought event were delayed compared to other species as *Robinia pseudoacacia* which was also investigated in their study. These findings confirm the species-specific reaction patterns as well as the drought tolerance.

Table 4 Results of selected linear combinations and coefficients based on model (6). *HD* high dense, *LD* low-dense

Independent variables	Estimate	std. error
Temp HD period1	− 0.166 **	0.056
Temp HD period2	0.487 ***	0.097
Temp HD period2: period1	0.653 ***	0.112
Prec HD period1	0.005 **	0.002
Prec HD period2	− 0.019 **	0.003
Prec HD period2: period1	− 0.024 ***	0.004
DMI HD period1	− 0.099 **	0.037
DMI HD period2	0.409 ***	0.074
DMI HD period2: period1	0.508 ***	0.083
Temp LD period1	− 0.007	0.047
Temp LD period2	− 0.028	0.079
Temp LD period2: period1	− 0.022	0.092
Prec LD period1	0.0009	0.002
Prec LD period2	0.002	0.002
Prec LD period2: period1	0.001	0.003
DMI LD period1	− 0.014	0.029
DMI LD period2	− 0.039	0.049
DMI LD period2: period1	− 0.025	0.057

Period1 denotes the timespan 1961 to 1990 and period2 denotes 1991 to 2011

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

Conclusion

Summing up, the study at hand represents a comprehensive data set on *T. cordata* growth patterns within the city of Berlin. The results reveal that through local climate, especially in terms of precipitation, housing density impacts urban tree growth.

The urban environment setting gives the opportunity to already today investigate possible effects of climate change on tree growth. While the growth patterns of forest stands cannot be transferred to urban trees, the analysis of urban trees might serve as a possibility to predict future growth behavior of forest stands. Thus, especially the results of the high-dense area are of high interest. These show stronger growth rates with rising air temperature and with decreasing precipitation, indicating that climate change could lead to higher growth rates.

However, when drawing such a conclusion, the following methodological considerations should be regarded. First, the sample size in the high dense area was relatively low. Differences between the urbanization zones might be explained by differences in the tree parameters (dbh, tree height, age range, crown projection area). Further, for the interpretation of the comparison of the different urbanization zones, other factors besides housing density, e.g., building development, might be important. Second, different soil water conditions in urban areas might have an influence on tree growth (Günther 2014). In the present article, it was considered whether the individual tree is situated within the glacial-valley (*gv*). However, as the parameter did not show a significant effect, it was not reported within the results. Third, climate change has further influences in specific in urban areas, e.g., higher atmospheric CO_2-concentrations, lower O_3-concentration, or fertilization through N-deposition. These changes in air quality parameters are expected to have a positive influence on tree growth (Churkina et al. 2010, George et al. 2007, George et al. 2009, Gregg et al. 2003, IPCC 2014, Kaye et al. 2006, Searle et al. 2012). On the downside, climate change also goes along with negative effects, e.g., drought events, which lead to reduced tree growth (Rötzer et al. 2013, Hartmann 2011, Pretzsch and Dieler 2011) or even tree death (Griess and Knoke 2011, McDowell et al. 2008, Allen et al. 2010). For the present article, it was not possible to relate air quality data to the tree growth data, because air quality data were not available in higher spatial resolution and over a longer period.

Last but not least, the review of De Jaegere et al. (2016) reveals that, due to the lack of observations, the expected impacts of climate change on the vitality of *T. cordata* is generally based on its biology and model calculations. Thus, further investigation on the impact of climate change on *T. cordata*, as well as on other tree species in urban environments, is needed.

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Appendix

Table 5 Statistical variables for the gap filling regressions for air temperature and precipitation

Parameter	Gap filling period	a	b	R^2
Air temperature	1961–1980	1.0263	0.9168	0.879
	1992–1999	0.7665	3.602	0.543
Precipitation	1961–1980	1.1735	93.664	0.947
	1992–1999	0.8541	26.039	0.4382

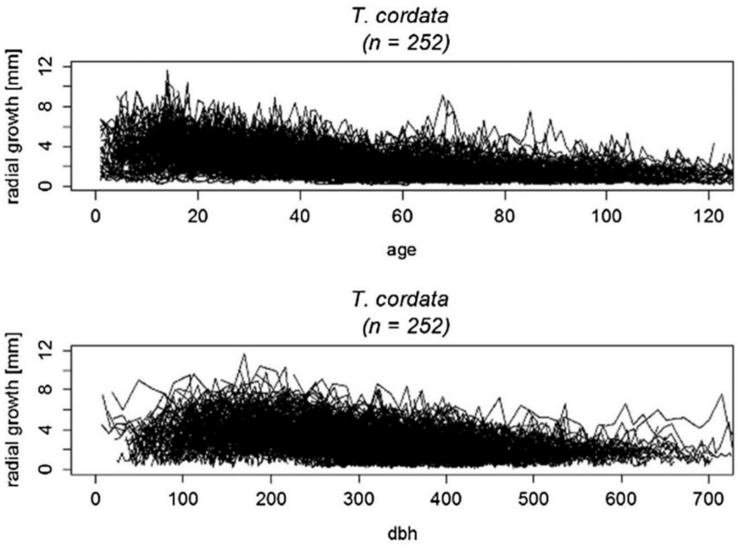

Fig. 7 Radial growth of all sampled lime trees in Berlin over age (upper) and over diameter at breast height (lower)

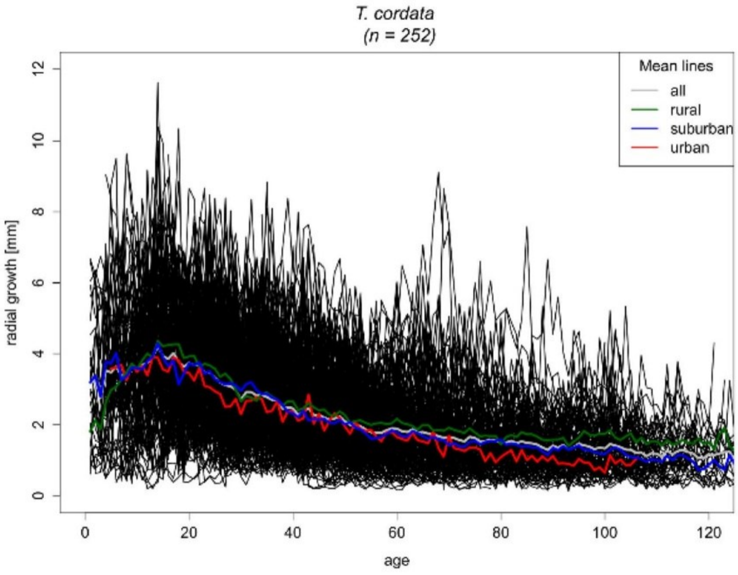

Fig. 8 Radial growth of all sample lime trees in Berlin and the mean lines for the different data subsets; low-dense (green), medium-dense (blue), high-dense (red), and for the total data set (gray)

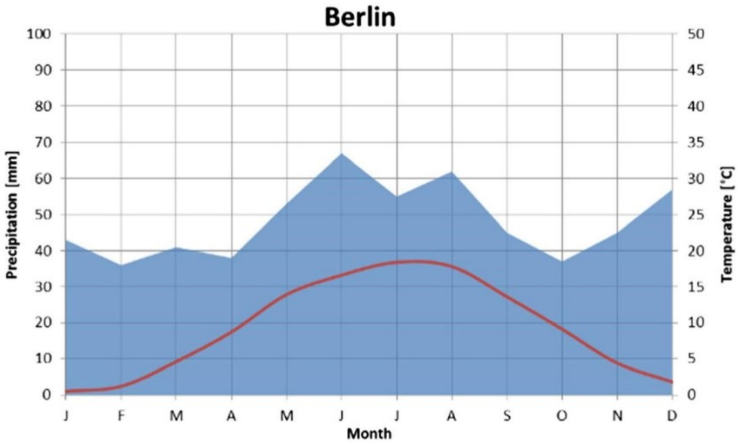

Fig. 9 Climate diagram for the city of Berlin (climate station Berlin-Dahlem) referring to the period 1961–1990

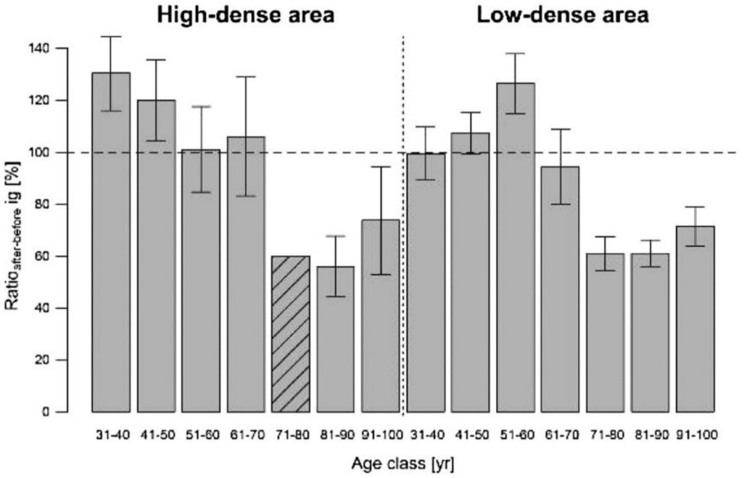

Fig. 10 Ratio$_{\text{after-before}}$ ig (ig$_{1991–2011}$/ig$_{1961–1990}$) for 10-year age classes (including the confidence intervals) comparing “high-dense” versus “low-dense” area. The crosshatched bar indicates that the sample size for this age class and area is below 50 trees

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