Crown architecture and its role in species interactions in mixed boreal forests

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Academic dissertation

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ABSTRACT

The species specific growth patterns make plastic crown architecture respond in different manner to different environments modifying their influence to neighbours. The main aims of this thesis were to separate the effect of neighbour species identity from the abundance, size and proximity of the neighbours in between-tree competition and to link crown architecture with hydraulic architecture by identifying the associated within-tree variation of crown traits.

The empirical part of the work was based on digitising three-dimensional (3D) crown architecture and measuring xylem anatomy. Digitising allowed the development of crown architecture models for *Betula pendula* (Roth.) and *Pinus sylvestris* (L.). The models were further applied to simulate light transmission in mixed stands.

Crown architecture of the studied species responded to increased competition intensity primarily by reducing branch number and size. Proportional biomass distribution to foliage and main branches over the stem increased in young *B. pendula* with increasing competition intensity, whereas *Pinus sylvestris* used the opposite strategy. In addition to competition intensity, crown architecture of the studied species showed plastic responses to the species identity of neighbouring trees. Lower overall growth but added height growth indicating stronger competition was found in mixtures of *B. pendula* and *Pinus sylvestris* when a tree was surrounded by interspecific neighbours compared to trees surrounded by intraspecific neighbours. Both species-specific effects on resource gradients and non-resource signals remain plausible explanations for this result: *B. pendula* transmitted more light than *Pinus sylvestris* at simulated dense stands.

Hydraulic architecture was shown to be interlinked with crown architecture as the conduit diameter varied as a function of tree compartment, branching hierarchy, leaf area and distance from the apex.

The results suggest that the use of detailed tree structure models and species-specific competition analysis is useful in predicting and understanding growth in mixed boreal stands.

Keywords: *Betula pendula,* competition, crown plasticity, *Pinus sylvestris*, radiation transmission, xylem anatomy

ACKNOWLEDGEMENTS

LIST OF ORIGINAL ARTICLES

The thesis is based on the following research articles, which are referred to in the text by their Roman numerals. The articles are reprinted with the kind permission of the publishers.

I　　　Kaitaniemi, P. and Lintunen, A. 2010. Neighbour identity and competition influence tree growth in Scots pine, Siberian larch and silver birch. Annals of Forest Science 67: 604. http://dx.doi.org/10.1051/forest/2010017

II　　　Lintunen, A. and Kaitaniemi, P. 2010. Responses of crown architecture in *Betula pendula* to competition are dependent on the species of neighbouring trees. Trees 24: 411–424. http://dx.doi.org/10.1007/s00468-010-0409-x

III　　　Lintunen, A. and Kalliokoski, T. 2010. The effect of tree architecture on conduit diameter and frequency from small distal roots to branch tips in *Betula pendula*, *Picea abies* and *Pinus sylvestris*. Tree Physiology 30: 1433–1447. http://dx.doi.org/10.1093/treephys/tpq085

IV　　　Lintunen, A., Sievänen, R., Kaitaniemi, P. and Perttunen, J. 2011. Models of 3D crown structure for Scots pine (*Pinus sylvestris*) and silver birch (*Betula pendula*) grown in mixed forest. Canadian Journal of Forest Research 41: 1779–1794. http://dx.doi.org/10.1139/x11-092

　　　　　Lintunen, A., Sievänen, R., Kaitaniemi, P. and Perttunen, J. 2012. **Corrigendum:** Models of 3D crown structure for Scots pine (*Pinus sylvestris*) and silver birch (*Betula pendula*) grown in mixed forest. Canadian Journal of Forest Research 42: 2153. http://dx.doi.org/10.1139/cjfr-2012-0443

V　　　Lintunen, A. Sievänen, R., Kaitaniemi, P. and Perttunen, R. 2013. Analysing species-specific light transmission and related crown characteristics of *Pinus sylvestris* and *Betula pendula* using a shoot-level 3D model. Canadian Journal of Forest Research, Published on the web 11 July 2013, http://dx.doi.org/10.1139/cjfr-2013-0178

Anna Lintunen was responsible for the summary of this thesis. She is the main author in II, IV and V, had equal contribution with Tuomo Kalliokoski in III, and was the second author in I. Anna Lintunen, Pekka Kaitaniemi and Tuomo Kalliokoski all participated in the fieldwork. Laboratory work in III concerning above-ground parts was responsibility of Anna Lintunen and below-ground parts of Tuomo Kalliokoski. Statistical analyses were carried out by Anna Lintunen in II and V all inclusively, in III above ground (Tuomo Kalliokoski below ground), in IV for *Betula pendula* (Pekka Kaitaniemi *Pinus sylvestris*) and in I together with Pekka Kaitaniemi. In IV and V, Risto Sievänen was responsible for writing the model code and Jari Perttunen for the technical details concerning the use of LIGNUM-model. The experimental setups and ideas for the articles were gained together with all the authors.

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INTRODUCTION

Plastic crown architecture

Crown architecture refers to the shape, size and placement of tree structures in three-dimensional (3D) space and to the constructional organisation of the branching system (Godin et al. 1999). A variety of crown architectural designs exist among and within tree species to fulfil the number of functions a crown is responsible for. The way in which crown architecture is formed determines the location of leaves that are further responsible for light capturing and photosynthesis and the within-tree transport distances and costs. Crown architecture also influences the microclimate at various crown parts, affects the vulnerability to external mechanical stresses, e.g. wind and snow load, and affects reproduction efficiency by determining the position of flowers and fruits.

The key to understanding the formation of a tree's crown architecture is in understanding how tree architecture and physiology interact (Ford 1992). Crown architecture determines the local environmental conditions within tree crowns and influences the layout of contact surfaces between the environment and the physiological processes involved in resource acquisition, whereas physiology produces new materials for constructing the architecture (Ford 1992). Tree crown architecture is composed of subunits, individual branches and shoots that may have largely autonomous carbon economies, so the growth and survival of these crown units are sensitive to their local environments (Sprugel et al. 1991; Nikinmaa et al. 2003; Sachs 2004). This modular structure (Harper 1977) allows high structural plasticity at multiple hierarchical levels as a response to the changing growth environment (Sorrensen-Cothern et al. 1993).

Plastic response to the environment requires highly evolved sensing systems of external conditions, i.e. light quantity and quality, temperature, water status, carbohydrate status, mechanical loading and chemical compounds. Leaves, active buds, chlorophyll containing cells of twigs and stems etc. respond to their local environmental conditions by modifying their internal properties that further cause either growth responses in meristems or physiological responses. To architecturally adjust to the changing environment with optimal patterns, the integration of environmental and internal information is required (Vandenbussche and Van Der Straeten 2004). The internal information is gene-based and transmitted mainly via hormonal signals (Vandenbussche and Van Der Straeten 2004) regulating species-specific growth patterns (Hallé et al. 1978), the degrees of individual crown plasticity and growth pattern alterations due to ontogenetic development (Vandenbussche and Van Der Straeten 2004).

Between-tree interactions

Plants are highly sensitive organisms that interact with each other in limiting, enhancing and neutral ways. They alter resource availability as well as the physical and chemical environments in their surroundings. Competition is a limiting interaction and can be defined based on either competition mechanisms and resource acquisition (Grime 1974; Tilman 1982) or the outcome, reduction of fitness due to shared demand for a limited growth resource (Silvertown and Charlesworth 2001). The latter is more commonly used in forest

sciences and competition is defined as interaction between trees leading to the reduction of biomass production per individual (Silvertown and Charlesworth 2001).

The growth of the surrounding trees continuously modifies the above-ground environment mainly by decreasing the available amount of photosynthetically active radiation (PAR). The photosynthetic production of a tree is dependent on radiation availability and the light interception efficiency of its crown (Ballaré 1999). Light as a growth resource and shading as a competitive effect are asymmetric in nature, meaning that the growth resources are distributed unevenly (Weiner 1990) as higher trees shade shorter ones. Thus above-ground competition usually leads to variations in size between the competing individuals (Weiner 1990).

Neighbouring trees also communicate through non-resource signals including the perception of neighbour proximity via photoreceptors that monitor light quality, i.e. wavelengths (Aphalo and Ballaré 1995; Smith 2000), mechanical crown collision (Meng et al. 2006) and chemical signalling mainly with volatile organic compounds (Baldwin et al. 2006; Heil and Karban 2010). Even when all the above-mentioned sources of communication signals between plant individuals have been blocked, seedlings have sensed their neighbours suggesting that unknown communication channels still exist, sensing e.g. magnetic fields or sounds (Gagliano et al. 2012). Non-resource signals are used by plants to recognise neighbours, even separate relatives from other species, and prepare for competition before actual resource competition occurs (Aphalo and Ballaré 1995; Murphy and Dudley 2009; Gagliano et al. 2012).

Increasing interest in maintaining structural and compositional complexity in managed forests and in alternative forestry practices has increased the need to study tree interactions in mixed stands (Knoke et al. 2008; Kuuluvainen 2009). The potential importance of the competitive trees' species-identity is well recognized for tree growth, and has been demonstrated in several studies (e.g. Sumida et al. 2002; Canham et al. 2004; Uriarte et al. 2004; Boivin et al. 2010; Thorpe et al. 2010). A plastic response in tree growth and architecture may be dependent on the neighbouring species, because species-specific differences exist e.g. in growth allocation, light interception structures such as crown profile (Horn 1971; Yokozawa et al. 1996), individual leaf size, spectral leaf characteristics and leaf density (Jahnke and Lawrence 1965; Gates 1980), in resource uptake timing and the ratio of needed resources (Goldberg 1987) and in the crown characteristics causing mechanical disturbance due to wind sway (Meng et al. 2006).

Hydraulic tree architecture

Where light is used to photosynthesis, water is also needed, as water is lost in transpiration through the open stomata simultaneously with the CO_2 uptake for use in photosynthetic reactions. Water is transported from the ground to transpiring and photosynthesising leaves in the xylem vascular network consisting of conduits. The anatomy of the within-tree vascular network is here referred to as hydraulic tree architecture. The volume flow of water within this network is proportional among other factors to the fourth power of the radius of the xylem conduits, thus linking hydraulic architecture directly to its conductivity (Zimmermann 1978*b*).

New xylem tissue is formed continuously in the cambium and the anatomy of the tissue is determined by the external environment and internal physiology leading to hydraulic architecture that has the potential to function well at any given time or environment

(Lachenbruch et al. 2011). Hydraulic architecture at tree level reflects the environmental conditions e.g. water availability and air temperature (Villa-Salvador et al. 1997; Noshiro and Baas 1998; Schreiber et al. 2012). Crown architecture growth is also reflected in hydraulic architecture as the xylem anatomy varies according to e.g. stem diameter (Olson and Rosell 2012), transport distance (e.g. West et al. 1999*a*) and the need for mechanical support (e.g. Christensen-Dalsgaard et al. 2007).

From an evolutionary point of view, branching networks and vascular networks are coupled and jointly optimised (e.g. West et al. 1999*a*; Sperry et al. 2008) by evolutionary drivers such as space-filling geometry to maximise the carbon uptake by foliage and sap flow through conduits, the enforcement of biomechanical constraints uniformly across a plant, optimising hydraulic conductance to leaves and minimising embolism (Savage et al. 2010). Linking branching networks with vascular networks was among the first modelled by Leonardo da Vinci as area-preserving branching (Richter 1970). The idea of area-preserving branching was furthered in the pipe model theory, which states that the amount of foliage is proportional to the sum of cross-sectional sapwood areas of the woody parts that bare them (Shinozaki et al. 1964). Behind this theory is the simplistic idea of a tree as a bunch of pipes (i.e. conduits), each connecting one root unit to one unit of foliage. A linear relationship between foliage mass (or area) and sap wood area has been found to serve as a good approximation of reality across tree species (e.g. Grier and Waring 1974; Schneider et al. 2011), although there is evidence to show that better statistical fit is gained with a non-linear relationship (Kershaw and Maguire 2000; Kantola and Mäkelä 2004; Schneider et al. 2011) and that the pipe model ratio can vary within a tree (Berninger and Nikinmaa 1994; Mäkelä and Vanninen 2001) or depending on the tree species, tree size and environmental conditions (Coyea and Margolis 1992; Berninger and Nikinmaa 1994; Mencuccini and Grace 1995; Berninger et al. 2005; Schneider et al. 2008). However, if number of conduits and conduit size are allowed to vary and the effect of conduit size on likelihood of cavitation (Sperry and Tyree 1988) is considered together with pit structure increasing the resistance to water transport (Sperry et al. 2005) the pipe model relationship has shown to hold (Hölttä et al. 2011).

A model that has gained a lot of attention during this century is the universal scaling of vascular networks ('WBE model', West et al. 1999*b*), in which the conduits taper from the stem base to the leaves with a given scaling factor, to prevent the loss of water transport capacity caused by increasing transport length, i.e. the hydraulic architecture of plants conforms to the energy minimisation principle. The model incorporates an intentionally simple representation of plant vascular architecture, as the main focus is to show how all metabolism scales with plant size. Conduit tapering as a function of the number of tree segments is assumed to be continuous at the whole-tree level and the number of conduits is unchanged throughout the entire crown. The WBE model has gained contradictory results concerning stems (Anfodillo et al. 2006; Coomes et al. 2007; Mencuccini et al. 2007) and only few studies have considered branches in addition to the main stem (Atala and Lusk 2008; Sellin et al. 2008) when testing the WBE theory. When branches have been considered, the whole-tree conduit tapering pattern has not been continuous at the tree level (Mencuccini et al. 2007; Atala and Lusk 2008; Nygren and Pallardy 2008; Sellin et al. 2008).

Construction and maintenance of the vascular network requires carbon. The WBE model does not account for carbon costs, unlike Murray's law (McCulloh et al. 2003) that maximises hydraulic conductance per given carbon investment or a model by Mencuccini et al. (2007) that maximises the carbon assimilated in photosynthesis per given carbon

investment. Another aspect that has not been considered in previous models is that the conductance of water within a plant is not only restricted by the resistance caused by small conduit lumen size, but also by the resistance caused by the size of the porous pits connecting one conduit to another (Sperry et al. 2005; Choat et al. 2006) and by the spreading of embolism-causing gas within the xylem network (Tyree and Sperry 1989). A model by Hölttä et al. (2011) maximises carbon-use efficiency, but also takes pit structure into account in increasing the resistance to water transport and constricting the spreading of embolism.

Savage et al. (2010) developed the WBE model into a more flexible and realistic model by adding optimal space-filling of the vascular system along with trade-offs between hydraulic safety and efficiency. Their model allows species variation in the network design rules and describes vascular networks more realistically compared to the original WBE model. The latest model introduced by Sperry et al. (2012) is even more flexible and realistic as it incorporated into the previous work by Savage et al. (2010) a numerical model with species-specific packing functions and empirical inputs for predicting water flow. The model allows various traits to compensate other traits, thus enabling a comparison between evolutionary solutions for species growing in different habitats (Sperry et al. 2012; von Allmen 2012).

Architectural approach and modelling in forest sciences

Architectural study in forest sciences is based on reconstruction methods. Crown architecture reconstruction includes botanical aspects such as branching relationships and shoot type information, and geometrical aspects such as spatial location, orientation, size and shape of each element (Sinoquet and Rivet 1997). Architecture reconstruction is used when investigating e.g. tree organisation and form, past and present form diversity, architectural variability within an individual, links between structure and function, feedback between biomechanics and growth and architectural plasticity in forms of acclimation and adaptation (Fourcaud et al. 2008). The most detailed and precise tree crown reconstruction can be achieved using contact 3D digitising with special equipment recording the 3D position of sensors inside a magnetic field created around the target (Sinoquet and Rivet 1997; Rodriguez et al. 2012). This method is laborious, whereas the use of high-definition photographs or terrestrial laser scanning and ranging (Moorthy et al. 2011; Côté et al. 2011) are less time consuming but also include higher imprecision, especially when the crown skeleton is covered by foliage (Delagrange and Rochon 2011).

As reconstruction methods have their limitations, architectural models are of great benefit for forest research. Hallé and Oldeman (1970) drew morphological static descriptions of tropical tree crowns in early 1970s. Several methods have been introduced to model crown architecture since these pioneer studies. Possibly the most commonly used mathematical framework for modelling plant architecture and growth is the Lindenmayer-system (Prusinkiewicz and Lindenmayer 1990). Other formalisms are based on botanical concepts (de Reffye et al. 1988) and multi-scale tree graphs (Godin et al. 1999). Most resent modelling studies aim to combine process modelling with architectural development to predict long-term plant development (de Reffye 1997; Perttunen et al. 1998; Prusinkiewicz and Rolland-Lagan 2006). Functional-structural plant models (FSPM) are dynamic architectural models that describe the development of 3D plant architecture determined by physiological processes of the plant that are further dependent on the

environment (Sievänen et al. 2000; Hanan and Prusinkiewicz 2008; Fourcaud et al. 2008; Vos et al. 2010).

Architecturally realistic crown models can be used in forest management and horticulture (Cieslak et al. 2011) to predict and better understand plant growth, but also to predict log quality (e.g. Kellomäki et al. 1999; Mäkinen et al. 2003), biomechanical tree properties (Anten and Schieving 2010), herbivore diversity (Espírito-Santo et al. 2007), rainfall interception (Nadkarni and Sumera 2004) and understory plant community structures due to overstory light transmission (Deal 2007). The precision of modelling light transmission at forest stands can be enhanced with an adequate description of species-specific canopy architecture, especially at spatially diverse forest stands such as mixed stands (e.g. Sinoquet et al. 2005), as tree species coexisting in similar light environments can vary widely in foliage display and branching architecture (Hallé et al. 1978). It remains unclear how species-specific architectural diversity affects light transmission: crown density or leaf area index (LAI), foliage dispersion, leaf inclination angle and the vertical foliage distribution are all architectural characteristics that may influence light transmission (Sampson and Smith 1993; Duursma et al. 2011). Species-specific growth patterns also affect light transmission dynamics by changing architectural properties over time.

The simplest way to describe light transmission in a forest is to use the Beer-Lambert model (Monsi and Saeki 2005), in which light penetration is proportional to the cumulative LAI, but underestimations of light transmission are produced in stands with between- and within-tree foliage grouping (e.g. Oker-Blom 1986, Bartelink 1998, Chen et al. 2008). Methods of detailed light transmission modelling that are able to consider differences in between- and within-tree light transmission include ray tracing (Cieslak et al. 2008), radiosity (Chelle and Andrieu 1998), a grid-based method where the target crown is divided into a number of cubic volume elements (also called voxels) and the radiation penetrating to each volume element is calculated (Wang and Jarvis 1990) and methods based on the statistical presentation of the heterogeneity (Bernier et al. 2001).

Motivation for the thesis and study aims

This thesis studies crown architecture and its role in competitive species interactions in boreal, mixed forests. The work was motivated by the high structural plasticity of architecture and by the increasing interest towards diverse forest management favouring stands that consist of tree individuals of varying species and/or age. This makes the information on mutual interactions of the main tree species of specific practical importance for designing forest management systems in the future. The main focus here is on two ecologically and economically important species in Finland, *Betula pendula* (Roth.) and *Pinus sylvestris* (L.). The study covers young and mature developmental stages, with main emphasis on early mature stage as the competitive status of trees is mostly established during the first 30 years. The scientific challenge of the work lies in the modular structure of plants and how such entities produce structures over time and how to measure and describe such a system.

In general, a variety of experimental field designs have been used in interspecific competition study (Park et al. 2003). Two species are grown in varying proportions at stand level in replacement and additive designs, resulting in stand-level yield responses (Park et al. 2003). These designs have shown that the volume yield over rotation is slightly higher or lower compared to the yield of a pure stand in mixtures of *B. pendula* and *Pinus sylvestris*

(e.g. Lappi-Seppälä 1930; Mielikäinen 1980). However, the spatial arrangement of trees is usually uneven within mixed forest stands, which suggests that adding detail to measurements of competitive effects might be of particular value (Park et al. 2003). Neighbourhood design is based on the idea that the performance of a target tree is affected by the number, biomass, cover or distance and size of the neighbouring individuals (Park et al. 2003). Various competition indices have been developed for the use of neighbourhood design to describe the stand (e.g. Rouvinen and Kuuluvainen 1997). Mixtures of *B. pendula* and *Pinus sylvestris* have been studied surprisingly little at tree level with an intention to separate the species-specific competitive effect of the neighbouring trees. Smaller spatial-level research is needed, because the architectural plasticity creating variation between individuals has mainly been connected to above-ground competition (Weiner 1990) taking place in a rather restricted area where the crowns interact (Cole and Lorimer 1994). Valkonen and Ruuska (2003) used neighbourhood design in mixtures of *B. pendula* and *Pinus sylvestris*, and found an effect of neighbour species on various crown characteristics of *Pinus sylvestris*. I wished to continue this work by studying the competitive tree-level effect of different neighbour species on the crown architecture of *B. pendula* and *Pinus sylvestris* in mixed forests (I, II).

Detailed measurements of competitive responses are also crucial in understanding tree growth in mixed forests. It is clear that the complex and dynamic crown architecture responds to the presence of neighbours in various manners and at several organisational levels (e.g. Aphalo and Ballaré 1995; Osada et al. 2002; 2004). The absolute height increment, relative growth rate of branches, leaf thickness and specific leaf area have been found to decrease and the ratio between stem height and diameter to increase with increasing competition intensity in young *B. pendula* grown in mixed stands under *Pinus sylvestris* (Messier and Puttonen 1995). Growth allocation prioritising the stem over needles and branches, has also been found to increase (Vanninen and Mäkelä 2000), foliage mass has been found to be allocated higher up in the crown (Mäkelä and Vanninen 1998) and maximum branch diameter to decrease (Valkonen and Ruuska 2003) with competition in *Pinus sylvestris*. These results also imply that the wood quality and mechanical properties can be increasingly accurately predicted with detailed information of competitive responses in mixed forests. This work analysed the competitive responses of crown architecture at the branch- and shoot-level (I, II, and indirectly also in IV).

Crown architecture is connected to hydraulic architecture (Olson and Rosell 2012). The connection is described with metabolic scaling theory that predicts that the tree water flow rate and biomass growth rate both scale with tree mass (Brown et al. 2004). Based on this rather simple relationship, analytical models have derived general scaling expectations for hydraulic architecture in plants regarding conduit tapering and conduit packing, i.e. the allocation of wood cross-sections to water conduction (West et al. 1999*a,b*; Savage et al. 2010). It is seldom that the whole-tree hydraulic architecture is analysed at various hierarchical levels with the approach above, although even small differences in between branch conductivities may have a strong implication on crown dynamics (Nikinmaa et al. 2003). I wanted to do this for *B. pendula*, *Picea abies* (L.) H. Karst. and *Pinus sylvestris*, to see whether the scaling of hydraulic architecture predicted by the WBE theory holds in the studied species across different hierarchical scales (III).

While static crown architecture can be measured, description of its dynamic development over time is easiest achieved with the help of models. Several possibilities to model stand-level development of *B. pendula* and *Pinus sylvestris* exist: an empirical approach is offered by structural simulation models (e.g. Mäkinen et al. 2005), whereas a

functional approach is offered by physiological process-based models (e.g. Mäkelä and Mäkinen 2003; Härkönen et al. 2010). Empirical models are based on massive field measurements and empirical equations producing the tree structure as a function of developmental stage and selected environmental variables. Process-based models typically use empirically measured yield measurements and allocation parameters and produce the tree structure based on physiological processes in a given environment. Empirical models might be more accurate, but process-based models offer flexible tools to model stand structure and growth in changing environmental conditions, and thus combining these two approaches seems logical. LIGNUM (Perttunen et al. 1998) is a functional-structural shoot-level growth model parameterised for *Pinus sylvestris*. Another 3D shoot-level growth model has also been developed for *Pinus sylvestris* (Kellomäki and Strandman 1995; Kellomäki et al. 1999), where shoot growth responds to the local light climate. However, as the growth simulation of crown architecture starting from the seedling stage needs huge amounts of computational time at stand-level simulations (Sievänen et al. 2008; Wang et al. 2011), the use of these models would benefit from a detailed empirical crown architecture model. No empirical models are available for *B. pendula* or *P. sylvestris* that would enable the construction of shoot-level 3D crown architecture without a growth simulation. Creditable work has been performed in modelling the characteristics of the main branches of *B. pendula* and *Pinus sylvestris* (Mäkinen and Colin 1998; 1999; Mäkinen 1999; 2002; Mäkinen et al. 2003), but the main purpose of these models has been to validate timber quality, thus neglecting side branches and foliage. An empirical shoot-level crown architecture model is created with LIGNUM modelling framework for *B. pendula* and *Pinus sylvestris* in this thesis (IV).

Further, I used the created empirical crown architecture models of *B. pendula* and *Pinus sylvestris* to analyse light transmission in simulated forests with different species mixtures (V). The potential importance of interspecific differences in light transmission has been recognised (Canham et al. 1994; Constabel and Lieffers 1996; Bartelink 1998; Messier et al. 1998). Several light transmission models for forest stands have been developed, and some allow the inclusion of species-specific tree-level variables e.g. foliage densities (e.g. Bartelink 1998; Da Silva et al. 2007) and foliage inclination angles (Stadt and Lieffers 2000), but only a few models (Mõttus et al. 2006; Duursma et al. 2011) actually linking the detailed species-specific crown architecture and light transmission have been introduced (Messier et al. 1999). The few results have shown that species-specific variation in light transmission is closely correlated with the shade-tolerance and successional status of the species (Canham et al. 1994; Messier et al. 1998) and with the degree of foliage grouping between conifers and broadleaved species (Bartelink 1998; Messier et al. 1998).

The overall objective of this work was to analyse and develop methods to describe between species interaction in forest stand development. To achieve this objective the aims of this work were to:

1) use the response of multiple shoot- and branch-level crown traits of *B. pendula* (I, II) and *Pinus sylvestris* (I) to separate the effect of neighbour species identity from the abundance, size and proximity of the neighbours in between-tree competition,

2) link crown architecture with hydraulic architecture in *B. pendula*, *Picea abies* and *Pinus sylvestris* (III) by identifying the associated within-tree variation of crown traits (I, II, IV), and

3) model 3D crown architecture of *B. pendula* and *Pinus sylvestris* (IV) to simulate the light climate in different mixtures of these two species (V), with the purpose of analysing the potential role of light behind the species-specific competitive effects found in (I) and (II).

MATERIAL AND METHODS

Study design and material

I studied three conifers and two deciduous species growing in Finland and used in forestry: *Alnus glutinosa* (L. Gaertner)*, B. pendula*, *Larix sibirica* (Ledeb.)*, Picea abies* and *Pinus sylvestris*. The distribution areas of all the studied species partially overlap in Eurasia (Hämet-Ahti et. al. 1992). The main focus is on two pioneer species, *B. pendula* and *Pinus sylvestris,* which compete actively for light and growing space (de la Rosa et al. 1998).

This work is based on two study designs and two sets of even-aged mixed stands henceforth referred as A and B (Tables 1 and 2). Articles II and IV were based on both study designs, article III on a subsample of study design A and article I was based on study design B. A design attempted to study tree architecture and hydraulic architecture, and the stands were selected to form age and site fertility gradients. Three sites of medium-high fertility (the *Myrtillus* type, MT) represented different age classes. The site of high fertility (the *Oxalis-Myrtillus* type, OMT) and medium-low fertility (the *Vaccinium* type, VT) of the medium age class formed a fertility gradient together with the medium-aged MT site (Cajander 1949). All of the mixed stands in this data set consisted of *B. pendula, Picea abies* and *Pinus sylvestris*. The stands were located in southern Finland around the Hyytiälä Forestry Field Station (61º 50'N, 24º 18'E, Fig. 1). Details of the study stands are presented in Table 1. From each site, four healthy looking individuals per species were selected as study trees (a total of 60 trees).
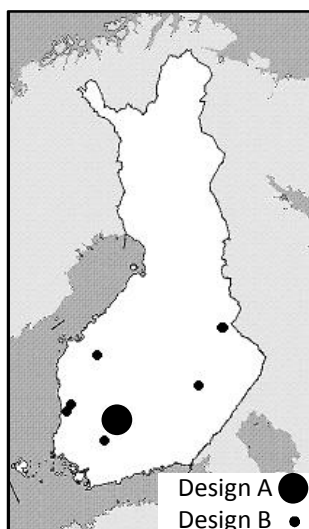
Figure 1. Map of Finland showing the locations of the stands in study designs A and B.

Table 1. Selected characteristics of the mixed boreal stands of study design A. The stands formed age and site fertility gradients.

		Study tree characteristics				Stand characteristics			
Site	Species	Nr. of study trees	Mean age, years	Mean height, m		Fertility	Stage	Mean height [d], m	Basal area, m² ha⁻¹
1	B[a]	4	13	5		MT[e]	Sapling	5	4
	S[b]	4	15	4					
	P[c]	4	13	4					
2	B	4	29	13		MT	Pole	10	22
	S	4	28	10					
	P	4	30	12					
3	B	4	48	21		MT	Mature	16	30
	S	4	55	21					
	P	4	51	21					
4	B	4	36	19		OMT[f]	Pole	12	24
	S	4	34	14					
	P	4	36	15					
5	B	4	32	12		VT[g]	Pole	9	13
	S	4	41	10					
	P	4	31	11					

[a]*Betula pendula*; [b]*Picea abies;* [c]*Pinus sylvestris*; [d]trees with $D_{1.3}$ < 50% of study tree $D_{1.3}$ were not included; [e]OMT *Oxalis-Myrtillus* type; [f]MT *Myrtillus* type; [g]VT *Vaccinium* type

Design B investigated crown interactions, i.e. how crown architecture is affected by competition and neighbouring species. The stands consisted of two or more tree species in the dominant crown layer, including *A. glutinosa, B. pendula, L. sibirica* and *Pinus sylvestris*. The 12 mixed stands were located in Finland, between latitudes 60° N and 63° N and longitudes 21° E and 29° E (Fig. 1). The crown architecture of a total of 73 *B. pendula* and 73 *Pinus sylvestris* individuals were measured. To ensure that the crown characteristics of the study trees properly reflected the potential effects of neighbour species, the selected study trees were surrounded with a five-m radius by individuals of mainly one neighbour species in the same crown layer. Details of the study stands are presented in Table 2. The sampling scheme conformed to a fractional factorial design as all species combinations were not present at all sites, but those available partially overlapped to facilitate the analysis of the most ecologically interesting effects (e.g. Zaluski and Golaszewski 2006). All the sites were experimentally established or otherwise planted mixed stands representing the medium fertility forest site type, MT (Cajander 1949).

Table 2. Selected characteristics of the mixed boreal stands of study design B. Each study tree was surrounded by individuals of one main neighbour species (all stands represented the same fertility type, MT).

	Study tree characteristics					Stand characteristics		
Site	Species	Neighbour species	Nr. of study trees	Mean age, years	Mean height, m	Stage	Mean height [e], m	Basal area, $m^2 ha^{-1}$
1	B[a]	B, P	6	21	9	Pole	8	11
	P[b]	B, P	6	19	8			
2	B	B, P, L[c]	7	13	7	Sapling	8	14
	P	B, P, L	6	16	7			
3	B	B, P, L	4	11	5	Sapling	6	11
	P	P, L	7	14	5			
4	B	B, P	6	17	13	Sapling	10	20
	P	B, P	6	21	9			
5	B	B, P, A[d]	7	29	17	Pole	11	28
	P	B, P	4	33	18			
6	B	B, P	6	21	10	Pole	8	15
	P	B, P	6	22	8			
7	B	B, L	4	23	15	Pole	12	25
	P	B, P	5	21	11			
8	B	B, P, L	3	32	14	Pole	16	24
	P	B, P, L	7	31	15			
9	B	B, P	6	22	10	Pole	8	13
	P	B, P	6	21	10			
10	B	B, P, L, A	14	4	2	Sapling	2	1
	P	B, P, L	13	5	1			
11	B	B, L, A	8	4	2	Sapling	2	<1
	P	B, P, L	11	4	1			
12	B	P	2	21	11	Pole	10	22
	P	B, L	4	23	10			

[a]*Betula pendula*; [b]*Pinus sylvestris*; [c]*Larix sibirica*; [d]*Alnus glutinosa*; [e] trees with $D_{1.3} < 50\%$ of study tree $D_{1.3}$ were not included

Measurements

Architecture

To study crown architecture and its role in species interactions, the 3D architecture of all the study tree crowns in both data sets was measured after felling. Each crown was cut into approximately 1.5 m long sections and the architecture measured in a wind shelter with a digitising device (Polhemus Inc., Colchester, VT, USA) that records each plant point where a pointer is set in the form of 3D coordinates. Branch-level crown architecture was described using branch frequency (i.e. the number of side branches per axis length), branch length, branching angle (i.e. the forking angle from the previous axis) and topology.

Branching topology was determined using the Gravelius order (GO, MacDonald 1984) that assigns the order number 0 for the stem, 1 for the main branches forking from the stem and higher order numbers for the lateral branches (Fig. 2). Shoot-level architecture was described using shoot frequency (i.e. the number of shoots per axis length), shoot length, shoot angle (i.e. the forking angle from the previous axis), topology (GO) and identification of the shoot type separating the current year's shoot from older ones and long shoots from short ones in *B. pendula*. Shoot topology followed a similar logic as the branches (Fig. 2), assigning the order number 1 for shoots forking from the stem. Branch characteristics were measured from all the main branches, and characteristics describing lateral branches and shoots were measured from the crown top and from two to five sample branches along the crown (Fig. 2).

To simulate crown biomass, we measured the stem diameter and collected density samples from the stem base and below each sample branch (Fig. 2). The base diameter of each first-order branch was measured along with branch diameters of higher branching orders from the sample branches. We also collected two wood density samples from each sample branch (Fig. 2). Mass, area and inclination of a total of 150 individual leaves were sampled along with needle samples from different crown locations in design A, to analyse foliage characteristics in different crown parts during tree ontogeny (Fig. 2). Diameter growth from the past 10 years was measured in study design B, to analyse neighbour effect on diameter growth.

Measurements of neighbouring trees were carried out and the main neighbour species was defined in study design B, to examine the importance of competition intensity and species identity on crown architecture (I, II). The neighbouring trees were defined as trees within a five-m radius that belonged to the same crown layer as the study tree. Each neighbouring tree was characterised by their distance to a study tree, tree height and diameter at breast height, and twelve competition indices (CI1 to CI12) were formed based on these characteristics (Table 2 in I, Rouvinen and Kuuluvainen 1997) and used as measures of competition.

Architectural measurements were conducted at different stages of growing season. To avoid error to the results concerning unfinished growth for the measurement year, current year's elongation growth was ignored.
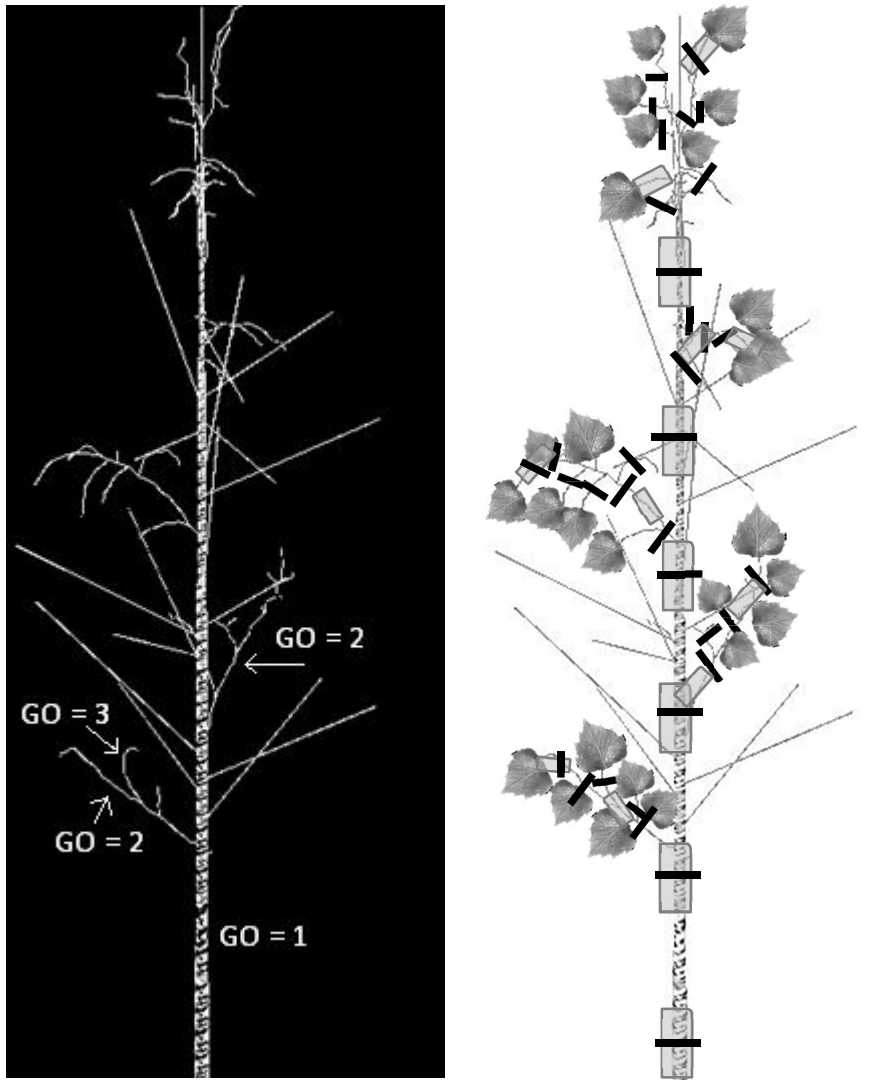
Figure 2. The digitised woody skeleton of a 5.3 m *Betula pendula* tree is presented on the left, with a visualisation of the used branching hierarchy system, Gravelius orders (GO). A straight line depicts where only a branch chord was measured. The right hand side presents sampling of woody discs for hydraulic architecture measurements (black lines), stem and branch sections for wood density measurements (grey boxes) and leaves for measuring leaf area, dry weight and petiole hydraulic architecture. Stem samples were collected from the stem base and below each sample branch. Three branch discs and three leaves per branching hierarchy were collected from each sample branch along with two branch sections for the density measurements.

Hydraulic architecture

Vascular samples were collected to analyse the xylem anatomy variation along the water transport pathway (III). Details of the below-ground study can be seen in article III. To analyse the effect of the transporting distance on above-ground xylem anatomy, six stem discs were collected from the stems of three *B. pendula*, *Picea abies* and *Pinus sylvestris* individuals from study design A. The first disc was collected from just above the root collar, and the other five from below each sample branch (Fig. 2). The organ and branching pattern effects on xylem anatomy were studied by collecting three branch discs from the sample branches on each existing GO (Fig. 2). To analyse the vascular anatomy in the most distal, transpiring organs in *B. pendula*, the vascular anatomy of three leaf petioles together with leaf area were measured from each GO in each sample branch.

The imaging procedures were designed to cover the conduit anatomy variation in cross-sections of different tree compartments, and are presented in Table 3 in article III. We measured all the directions of variation in conduit anatomy, especially from the six stem discs by analysing radial change in a cross-cut, by vertically following a single growth ring of a defined year and by analysing the growth ring of a defined number from the pith representing a vertical series of annual height growth stages (Burdon et al. 2004). First, the transverse sections of the stem, branch and petiole samples were cut using a microtome, the fragile petioles embedded in paraffin. Then all the sections were stained and preserved as permanent samples. We took images of the vascular samples with digital camera attached to a microscope. We next determined the conduit diameter and frequency from the images, and further estimated the total conductive area. The total number of conduits measured in the study was over 100 000.

Analyses

Analyses of the neighbour tree effect on crown architecture

We analysed the effect of neighbour trees on the performance of *B. pendula* and *Pinus sylvestris* (I). Long-term effects of neighbours on tree growth were assessed using the average annual height increment and width of annual growth rings in the stem from the previous ten years. The number of living branches per unit crown length was additionally counted to obtain an estimate of branch production with potential implications on timber quality. Short-term growth responses were assessed from the sample branches by measuring the average length of all the one- and two-year-old shoots and average growth vigour, i.e. total shoot length proportional to total branch length.

The neighbour effect on *B. pendula* crown architecture was analysed in more detail in II. Long-term neighbour effects were assessed using the number, length and angle of all first-order branches, whereas short-term effects were analysed from the sample branches using growth vigour, the number of short and long shoots and length of long shoots. Neighbour effect variation at different crown locations was analysed using variables describing the interaction between a neighbour effect and the relative height within a crown or branching hierarchy. Relative height within a crown was assumed to represent the relative light level and branch age within the crown, and branching hierarchy to represent apical control.

Neighbour effect was divided into species identity and competition intensity within a five-m radius. Competition intensity was represented in the analyses of both articles with

competition indices that operated using various combinations of basal area, diameter and the distance and height of competitors and the subject tree to indicate competition intensity. The present values of competition indices could be assumed to correlate with their past values and thus be proper tools for analysing long-term impacts as well, because the stands had not undergone any recent thinning operations. The developmental stage of the tree was also accounted for in the analyses, to be able to separate the effect of tree ontogeny from neighbour effects and to analyse the changes in neighbour effect with tree ontogeny (II).

The explanatory powers of neighbour effects, developmental stage of the tree and location of the target shoot/branch within the crown (II) were examined in an explorative manner, starting from a full list of explanatory factors and proceeding through a stepwise removal of non-informative factors until a final model was reached. Each model was fitted to the data using linear mixed models with site as a random factor in (I) and generalised linear models with a linear link function in (II). Shoots and branches within a tree were considered repeated observations in (II).

Hydraulic architecture analyses

To study the link between crown architecture and xylem anatomy (III) in detail, we compared the conduit diameter and frequency in different tree compartments (roots, stem, branches of different hierarchy levels, leaf petioles) and in different growth rings from pith to bark in the stem. We also studied how xylem anatomy varies with radial distance from pith to bark in the branches and how xylem anatomy in the leaf petioles is connected to leaf area in *B. pendula*. As the data were hierarchical, the conduits were studied using linear mixed models having a nested structure for each species. The studied explanatory variables describing the location of the sample inside the tree were considered fixed effects and the correlation structure inside the trees was accounted for through random effects. The Tukey-Kramer paired multiple comparisons method was used to compare class variables.

We analysed the scaling of conduit diameter as a function of distance from the stem/branch apex (III) as presented by the WBE model (West et al. 1999*b*), to see if the conduit structure minimises hydraulic resistance and conforms to the energy minimisation principle. Instead of using a number of segments as in the original WBE model, we used the distance from the apex as a scaling factor, as presented by Anfodillo et al. (2006), because it is impossible to distinguish all the segments in an adult tree:

$$a_k \propto l^{\frac{1}{4}} \qquad\qquad\qquad (1)$$

where a_k is the conduit radius and l is distance from the apex. The theoretical value of the exponent, 1/4, is derived from the original scaling parameter, 1/6, divided with the relationship between the distance and tree diameter that should have a value of 2/3 based on the elastic similarity model (West et al. 1999*a*). To compare our results with the original WBE exponent, the derived exponent in Equation 1 must be multiplied with a correction factor of 0.84, because tree height is approximated in the WBE model (Anfodillo et al. 2006).

Crown architecture reconstruction

A set of empirical equations were constructed for *B. pendula* and *Pinus sylvestris* to predict local crown characteristics on the basis of various local- and tree-level variables (IV). The equations were built recursively: the constructed crown properties at lower branching orders were used as input for the calculations of crown properties at higher branching orders. The choice of final explanatory variables from a large set of potential variables with assumed ecological importance was based on the model fit. Each model was fitted to the data using generalised linear models with a linear link function. Linear relationships and a normal probability distribution were found to adequately accurately describe the effects of explanatory variables in most cases. The final models consisted of 20 and 17 predicted crown characteristics in the case of *B. pendula* and *Pinus sylvestris*, respectively (Tables A1 and A2 in IV). Some random variation was included in the models (see details in IV). The models were tested against available reported branch- and tree-level crown measurements.

The 3D crown models were realised within the LIGNUM model (Perttunen et al. 1996). The construction of trees proceeded piecewise: first the stem, next the main branches and so on until GO five was reached in *B. pendula* and GO four in *Pinus sylvestris*. Modular tree architecture in LIGNUM consists of four structural units that allow the realistic examination of details: tree segment, bud, branching point and axis (Perttunen et al. 2001). Needles are considered cylinders surrounding needle-bearing tree segments in conifers, whereas regularly formed leaf blades are connected with petioles to the segments in broadleaved species (Perttunen et al. 2001). The model's input information can be a partially digitised tree or consist of only a few simple variables: tree height, crown height, diameter at breast height and four competition indices (Rouvinen and Kuuluvainen 1997).

Modelling light environment

We modelled forest stands with different mixtures of *B. pendula* and *Pinus sylvestris* and simulated the light environment in the middle of each stand to analyse the differences in shading due to species-specific crown architectural designs (V). The stands consisted of a circular plot with a twenty-m radius in which the 3D tree crown structure was simulated in detail and of a homogeneous edge forest extending to infinity, with properties derived from the trees on the circular plot. We had two sets of forest stands: 10 pole stage stands (stand height 8 m, hereafter called young stand) and 10 early thinning stage stands (stand height 16 m, hereafter called mature stand). Furthermore, two densities were considered within these two groups: dense and sparse. The densities were based on the recommended basal area for managing *B. pendula* or *Pinus sylvestris* forests of given height (Hyvän metsänhoidon… 2006). All four stand groups had five different mixtures of *Pinus sylvestris* and *B. pendula*: 100%, 80%, 50% and 20% of *Pinus sylvestris*, and finally 100% *B. pendula*. We simulated ten replicates of all the 20 stands with a randomly deviating number of trees from the given average and a random positioning of trees within the circular plot.

The 3D trees within the circular plots were constructed based on the crown architecture models presented in article IV. We simplified the structure of the circular plots (Table 1 in V) so that the tree individuals were identical within a species, thus including competition effects on crown features as stand averages, but ignoring local crown interactions, such as individual crown asymmetry. To reduce the effect of this limitation, a stand-specific crown radius was used as the minimum distance between tree individuals in the simulations. The crown architecture models predict some foliage details e.g. total area and length of needles

in *Pinus sylvestris* and the number, area, inclination and azimuth angle of leaves in *B. pendula*, but some had to be added for the light simulations: the needle angle in *Pinus sylvestris* was set to 40° (Smolander and Stenberg 2003) in current year shoots and to 60° in older shoots (based on observational values), and the shape of *B. pendula* leaves was set to a constant triangle.

The radiation transmission inside each circular plot was evaluated using the LIGNUM model (Perttunen et al. 2001; Sievänen et al. 2008). LIGNUM only considers PAR. The incoming PAR was assumed to have been emitted from 10×16 sky sectors, whose brightness were derived from the radiation distribution of standard overcast sky (Ross 1981; Perttunen et al. 2001). Tree transmission was calculated by ray casting: we tested for the existence of any shading elements in the ray's path from four positions along each main branch in the target crown towards each sky sector (Perttunen et al. 1998; Perttunen et al. 2001). Transmittance through a needle cylinder was calculated as (Oker-Blom and Smolander 1988; Perttunen et al. 1998):

$$\mu = \exp[-K(\varphi)(A_f / V_f)l] \qquad (2)$$

where φ is the angle between the direction of light ray and shoot axis, K is a function given in Oker-Blom and Smolander (1988), A_f is the needle area of the shoot, V_f is the needle cylinder volume and l is the distance the ray has travelled inside the needle cylinder. Transmittance in the leaves of *B. pendula* was constant with a value of 0.06 (Ross 1981). Shading caused by the woody parts of trees was considered complete, with no transmittance. The shading effect of trees surrounding the circular plot was calculated simply by using the Beer-Lambert law based on foliage area densities and extinction coefficients (Saeki 1960; Monsi and Saeki 2005). The incoming radiation on to a specific position in the target tree crown was calculated as a sum of the light intensity coming from all sky sectors.

Differences between species mixtures in light transmission simulated for the whole growth period were statistically analysed using linear mixed modelling. With a mixed model we were able to treat the nested structure of data using ten repeated simulations with random tree placement within each stand type. The Tukey–Kramer paired multiple comparisons method was used to compare the species mixtures.

RESULTS

Neighbour species and competition effects on crown architecture (I, II, IV)

The crown architecture of the studied species, *B. pendula* and *Pinus sylvestris*, was affected by the species identity of the close neighbour trees based on the field measurements (Table 3). Height growth of *B. pendula* was accelerated by competition in the presence of *Pinus sylvestris* or *L. sibirica* and that of *Pinus sylvestris* in the presence of *B. pendula*. Diameter growth in either species was not affected by the neighbour species. Growth vigour was highest when *B. pendula* grew with intraspecific neighbours and lowest with *L. sibirica*. On the contrary, the growth vigour of *Pinus sylvestris* was highest with *L. sibirica* and lowest with *B. pendula* neighbours. *B. pendula* growing with intraspecific neighbours or with *Pinus sylvestris* grew shoots rather densely in limited number and size of branches, whereas

the number and length of branches was highest when neighboured by *L. sibirica*. Similarly in *Pinus sylvestris*, branch number was highest with *L. sibirica* and lowest with *B. pendula*.

The effects of the number, size and distance of neighbours on crown architecture were analysed simultaneously with neighbour species identity. Competition intensity decreased growth vigour, defined as the ratio between annual shoot length and total branch length in both studied species, except for younger *B. pendula* trees where the effect was the opposite. *Betula pendula* responded to competition by growing a longer and thinner stem with a shorter crown, fewer, shorter and thinner main branches, longer shootless branch sections, less short shoots in most cases, but more current long shoots. Competition intensity had a negative effect on the height growth, individual shoot length, branch number per crown length and probability of needles occurring in a shoot in *Pinus sylvestris*.

Table 3. Effects of neighbour species identity on crown characteristics of *B. pendula* and *Pinus sylvestris* ($P \leq 0.05$). Mean values (± 95% confidence interval) of crown characteristics with different neighbours are presented.

| | Neighbouring species: | | | |
	Alnus glutinosa[c]	*Betula pendula*	*Pinus sylvestris*	*Larix sibirica*
Betula pendula				
Height growth (cm year [-1])	-	49.1 (7.9)	54.3 (8.0)	54.4 (10.0)
Growth vigour[a]	0.14 (0.06)	0.19 (0.09)	0.11 (0.03)	0.10 (0.07)
Branch (GO1) number[b]	3.8 (0.5)	5.2 (0.3)	5.8 (0.4)	6.5 (0.3)
Branch (GO1) length (cm)	75.3 (7.6)	102.0 (7.0)	101.2 (5.6)	112.2 (10.1)
Short shoot number (No Branch[-1])	-	53.0 (5.5)	46.5 (5.5)	54.3 (9.5)
Pinus sylvestris				
Whorl distance (cm)	-	51.9 (6.5)	47.6 (6.5)	47.9 (6.7)
Growth vigour[a]	-	3.1 (0.5)	3.6 (0.4)	4.1 (0.7)
Branch (GO1) number (No m[-1])	-	10 (2)	11 (2)	13 (2)

[a]Total length of (long) shoots divided by the total branch length [b]Mean number of main branches per 10% of crown length [c]A hyphen represents a situation where *A. glutinosa* was not analysed or a statistically significant estimate was not gained

Link between crown architecture and hydraulic architecture (III)

Tree compartment alone explained most of the longitudinal variation in conduit anatomy. The water-conducting conduits tapered and their frequency increased from stem to branches, and further to the leaf petioles in *B. pendula* (Fig. 3). Conduit diameter was larger in the main branches of *B. pendula* and *Picea abies* than in the lateral branches, but no statistically significant difference was observed in *Pinus sylvestris* (Fig. 3). Conduit frequency was also lower in the lateral branches of conifers compared to the main branches, which led to a decreasing total conductivity from the main to the lateral branches per given branch cross-sectional area. Conduit diameter increased and conduit frequency decreased in the leaf petioles of *B. pendula* with increasing individual leaf area. The conduits in a leaf petiole connected to the largest observed leaf were on average 50% wider compared to a petiole connected to the smallest leaf. The total water conducting area decreased from stem to branches in all studied species, but increased slightly from branches to leaf petioles in *B. pendula*.

  Conduit diameter increased inside the crown with distance from the apex and scaling corresponded with predictions made by the WBE model at the whole-tree level (Fig. 4). Regarding the differences between the three species, *B. pendula* had the highest scaling coefficient, 0.39 on average. However, a more detailed analysis revealed that the scaling parameter values changed from one tree compartment to another rather than remained uniform inside a tree, as assumed by the WBE model (Fig. 4). Conduit diameter increased downwards in the stem within a growth ring of a defined year (second growth ring from the bark), especially in *B. pendula*. Conduit diameter within a growth ring with fixed cambium age (second growth ring from the pith) did not change in *B. pendula* and decreased downwards in most studied conifer individuals (Fig. 4). The assumptions of a constant conductivity ratio, constant tapering and no conduit furcation made by the WBE model were not fulfilled. The average conduit furcation number, i.e. the ratio between the total number of conduits in distal and proximal segments found in this study varied between 1.0 and 1.3 from tree to tree and from tree compartment to another.
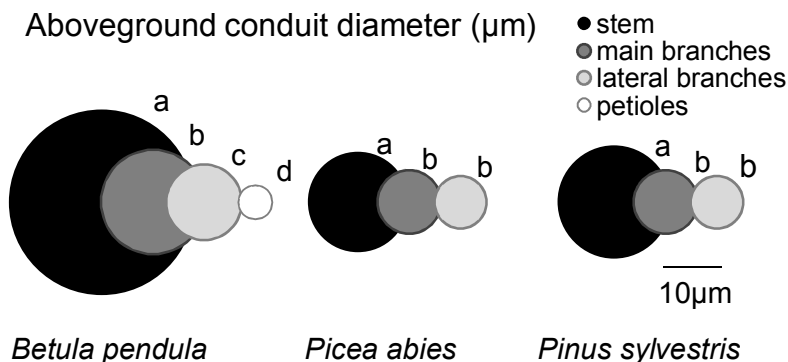

Figure 3. Mean conduit diameter in sapwood of different crown compartments of *Pinus sylvestris, Picea abies* and *Betula pendula*. Early wood only was measured in the conifers. Different letters indicate significant differences between tree compartments within each species (Tukey-Kramer test at $p < 0.05$).
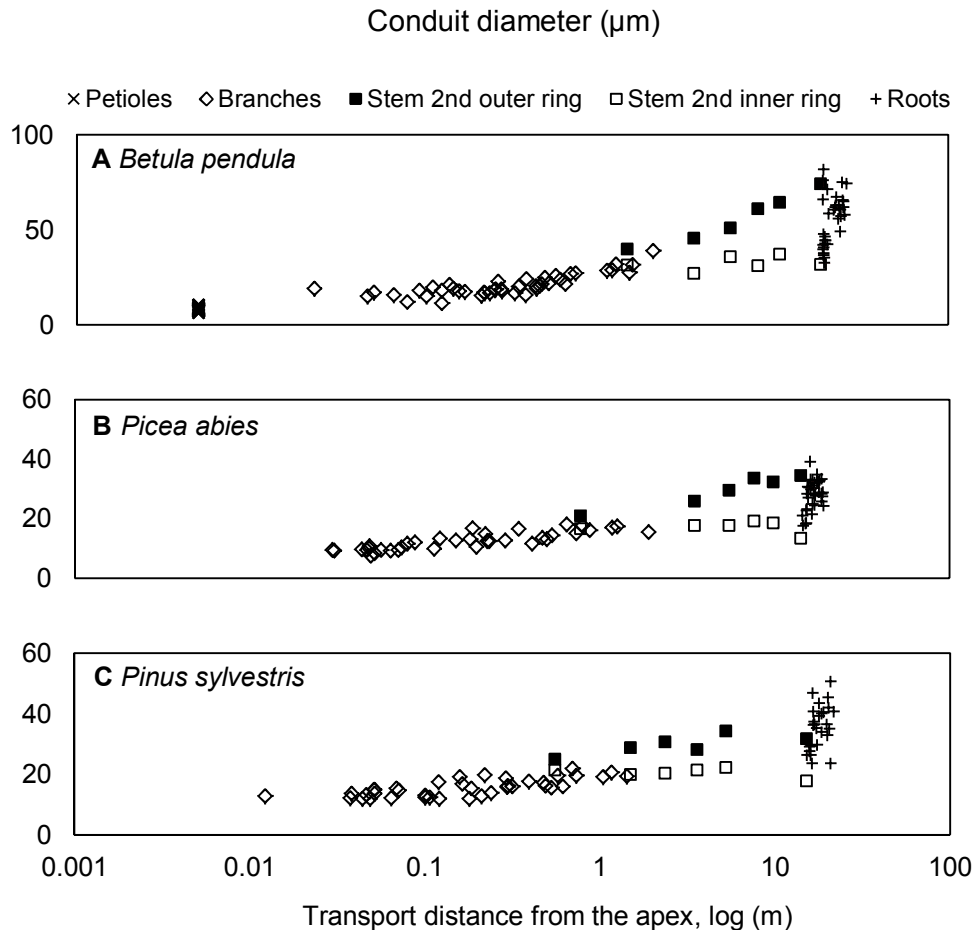
Conduit diameter (µm)

Figure 4. Mean conduit diameter in three tree individuals presented against a logarithmic distance from the apex. Different tree compartments are denoted with different symbols. In the stem, the second growth ring from the bark and the second growth ring from the pith are shown separately. Observations resemble predictions made by the WBE model at tree level ($R^2 = 0.81–0.82$), but the scaling factors vary between tree compartments (Table 4 in III).

Modelling crown architecture (II, IV)

The simulation models for crown architecture of *B. pendula* and *Pinus sylvestris* were based on branch-, shoot- and leaf-level empirical equations. Branch characteristics varied vertically from the crown base to the top. The frequency of the main branches (GO = 1) increased from the base to the upper parts of the crown in both species (Fig. 5). The increasing distance between branch whorls in the upper crown parts was compensated by the increasing number of branches per branch whorl in *Pinus sylvestris*. Branch frequency was higher and changed less from the crown base to the top in *Pinus sylvestris* compared to *B. pendula* (Fig. 5). Length and diameter of the main branches decreased in both species

towards the crown top, where the branches were younger (Fig. 5), but a branch with a fixed length had a higher diameter in the upper crown parts than in the lower parts in *Pinus sylvestris*. Branch angle decreased with increasing height within the crown in *B. pendula* and increased slightly in *Pinus sylvestris*. At a fixed relative height, a decreasing branch angle was related to increasing branch length in *B. pendula*, meaning that longer branches do not necessarily lead to a horizontal expansion of the crown due to smaller branch angles. The frequency, length and diameter of lateral branches in *B. pendula* were higher the longer the mother branch, and the lower the GO.

The number of short and long shoots (Fig. 6A) in a branch axis of *B. pendula* was dependent on branch size, while the number of lateral shoots (Fig. 6B) in *Pinus sylvestris* was not. The number of long shoots in *B. pendula* and the number of shoots in a branch whorl of *Pinus sylvestris* became more numerous towards the crown top and with decreasing GO (Fig. 6C, D). Shoots of both species also became longer towards the crown top (see Fig. 7A). Despite the observed trend, a wide variation occurred in long shoot growth throughout the crown in *B. pendula* (Fig. 7B). Not only vertical location affected the growth of long shoots, but branching hierarchy as well, because the longest shoots were found in the main branches of both species (see Fig. 7A).
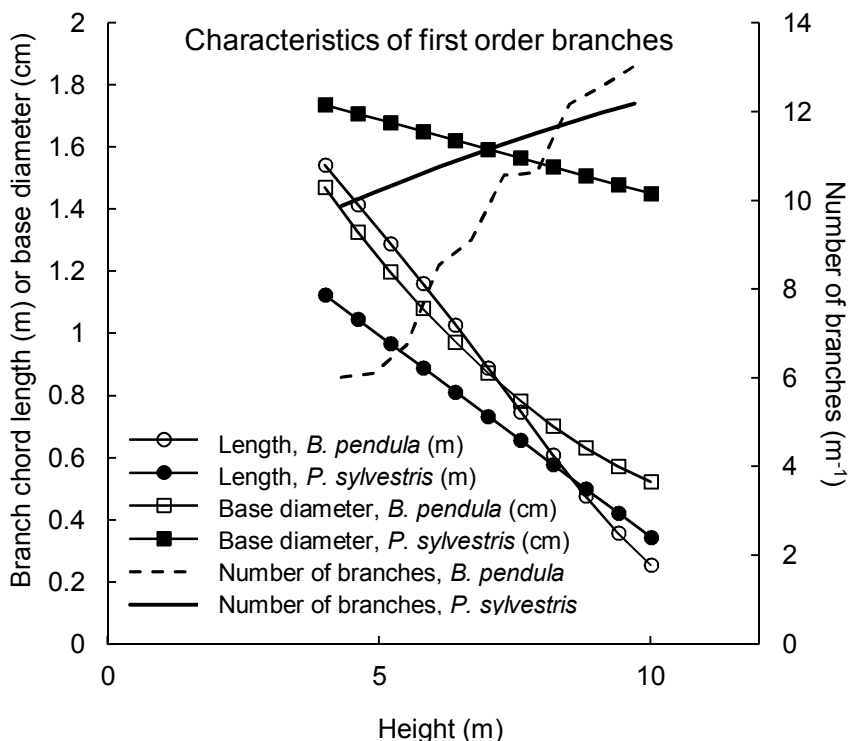

Figure 5. Characteristics of main branches (GO = 1) within the crown of a ten-m high *Betula pendula* and *Pinus sylvestris*. The figure is based on empirically produced model equations in Tables A1 and A2 in IV, where input information was Height (H) = 1000 cm, diameter at breast height (DBH) = 10 cm, crown height (CH) = 400 cm, age = 20, CI6 = 3, CI7 = 10, CI9 = 0.2.
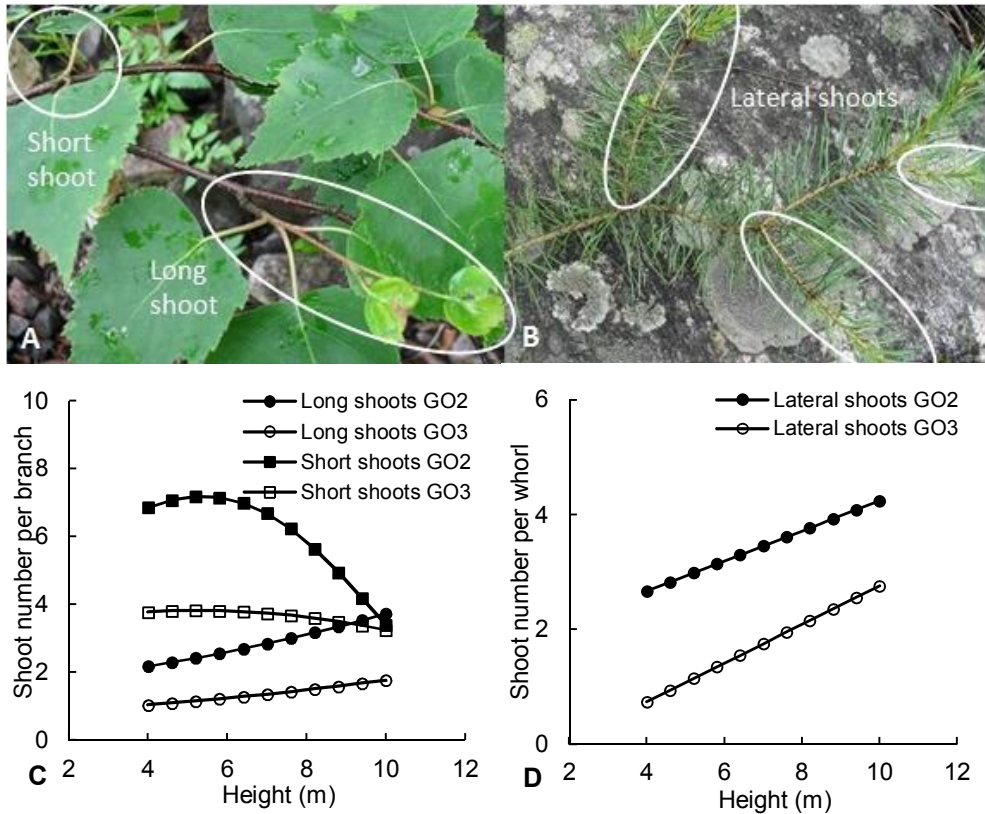
Figure 6. Shoot characteristics of the studied species. **A** Picture of a *Betula pendula* with two types of shoots; long shoots that elongate and produce new leaves throughout a growing season, and short shoots that only grow a couple of millimetres per year and typically bear two leaves. Short shoots are responsible for most of the foliage display and retain the capacity to convert into long shoots. **B** Lateral shoots in current year's branch whorls are responsible for elongation in *Pinus sylvestris* (growth of the previous four years is visible in the picture). **C** A modelled number of long and short shoots in a branch axis of *Betula pendula* and **D** a modelled number of lateral shoots in a branch whorl of *Pinus sylvestris* are presented at varying heights and at two different branching hierarchies. The model equations used are empirically produced and visible in Tables A2 and A1 in IV, see input information from the legend of Fig. 5.

Figure 7. Within-crown variation of the length of long shoots in *B. pendula* presented with raw data in **A** and with least square means and 95% confidence intervals (Vehanen and Kaitaniemi 2007, data from II) in **B**.
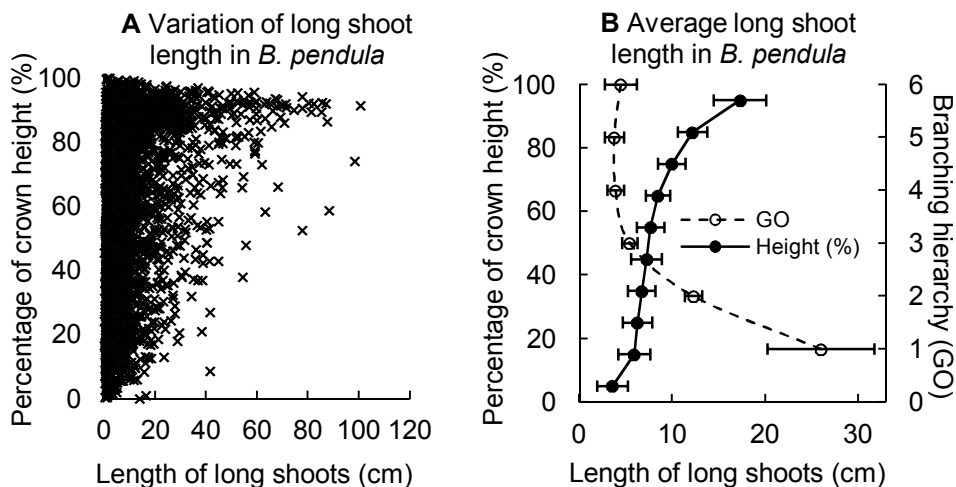
Leaf area in the short shoots of *B. pendula* increased towards the crown top in younger trees, but more mature trees exhibited an opposite trend. In *Pinus sylvestris,* needle area per shoot increased vertically towards the crown top and with shoot diameter, whereas it decreased with shoot age. The leaf angle in *B. pendula* became more vertical, changing 53° from the crown base to the top and leading to a higher light-capturing surface deeper in the crown compared to the upper crown parts. The mean specific leaf area for *B. pendula* was 13.6 $m^2 kg^{-1}$. The specific leaf area in *Pinus sylvestris* decreased and current-year needle length increased with the size of the shoot; needle length also increased vertically inside a crown.

Biomass distribution into various crown components with increasing competition intensity and stem slenderness (height/diameter) was estimated with the crown architecture simulations presented in IV (Fig. 8). Increased competition intensity and stem slenderness substantially decreased the absolute biomass of all crown components, but increased the share of foliage (GO3–4) and main branches, while decreasing that of the stem in *B. pendula* (Fig. 8A). Competition and stem slenderness in *Pinus sylvestris* increased the proportional biomass distribution to the stem at the expense of the main branches and foliage (GO3–4, Fig. 8B).
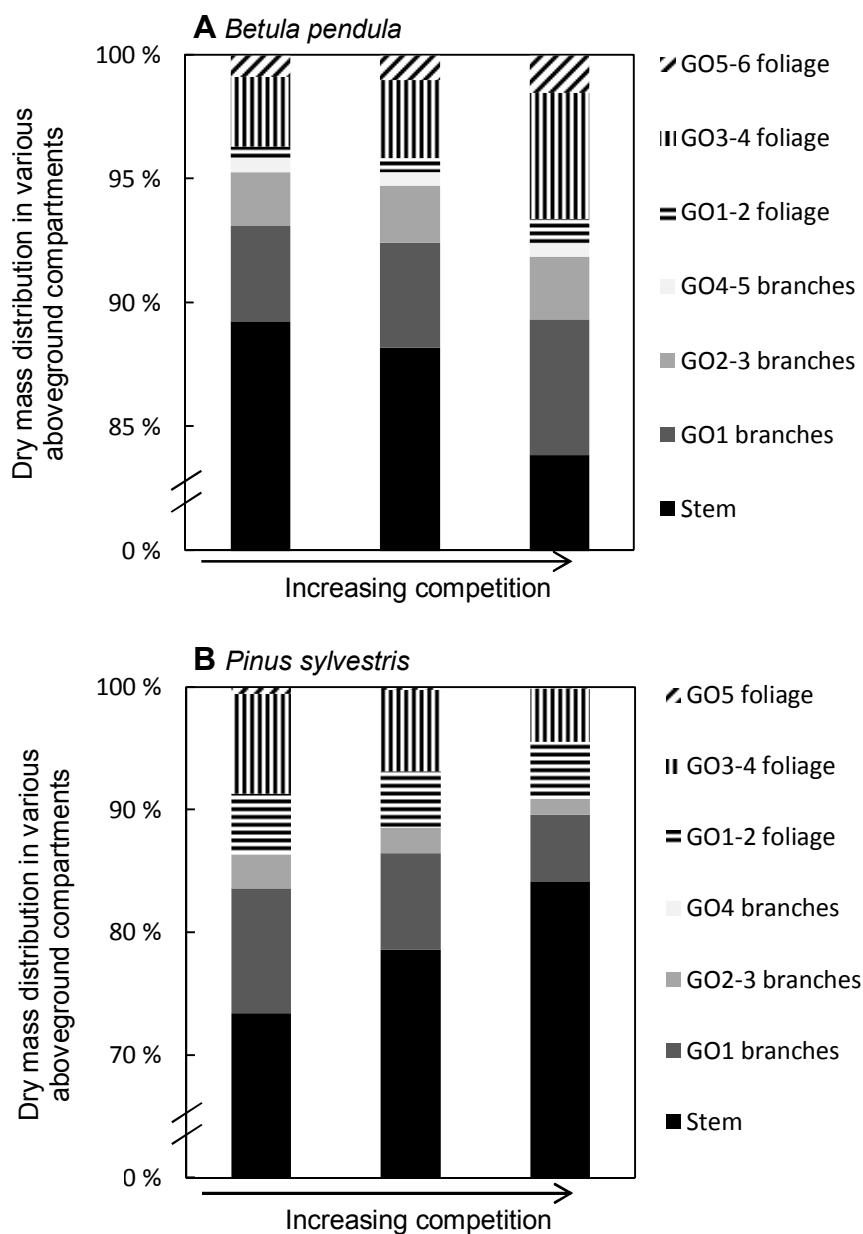
Figure 8. Biomass distribution into various crown compartments in simulated **A** *Betula pendula* and **B** *Pinus sylvestris* crowns (IV) is presented against increasing competition intensity and stem slenderness. Competition intensity is increased by increasing competition indices from the minimum to the maximum measured from the field data. Tree height was set to 10 m and diameter at breast height to 11.6, 10.5 and 7.7 cm (from left to right) to correspond with diameters measured in the field for *B. pendula* at given competition intensities. The modelled total crown dry biomass decreased with increasing competition intensity from 31 kg to 15 kg in **A** and from 38 kg to 17 kg in **B**.

Neighbour species effects on simulated light transmission (V)

The average intensity of transmitted light was higher in dense *B. pendula* stands compared to dense *Pinus sylvestris* stands (Fig. 9). The difference in light transmission was significant between young dense *B. pendula* stands and pure *Pinus sylvestris* stands or 80% *Pinus sylvestris* mixtures and between 50% and 80% *Pinus sylvestris* mixtures (Fig. 9). Mature dense pure *B. pendula* stands and 80% *B. pendula* mixtures also transmitted more light compared to pure *Pinus sylvestris* stands (Fig. 9). No statistically significant differences were observed among sparse mature stands, but of the sparse young stands, the 20% and 80% *B. pendula* mixtures transmitted significantly more light compared to pure *Pinus sylvestris* stands (Fig. 9).

Analysed crown characteristics showed that *Pinus sylvestris* had a larger total needle area that was situated higher in the crown compared to *B. pendula,* especially in dense mature stands, thus creating a layer in the upper canopy that attenuated light efficiently (Fig. 9). However, more foliage grouping occurred at tree level in *Pinus sylvestris* compared to *B. pendula*. Accordingly, light transmission per downwards cumulative LAI was higher in pure *Pinus sylvestris* stands compared to *B. pendula* stands when LAI was defined as half of the total needle area per unit ground surface area (Monteith 1973; Chen and Black 1992).
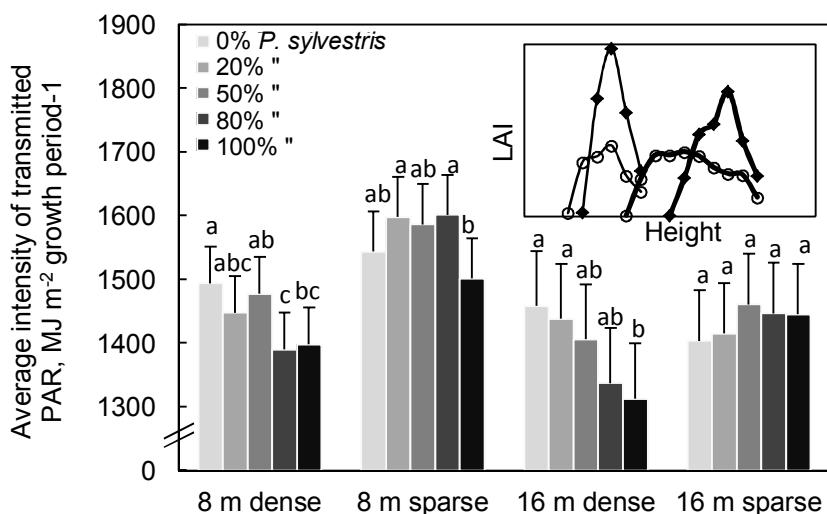
Figure 9. The average incoming light intensity is presented against the *Pinus sylvestris* percentage at different virtual stand types. Self-shading of the target tree was ignored. The maximum, unshaded radiation from all sky sectors in a growth period is 2055 MJ m^{-2}. Error bars present 95% confidence intervals and different letters indicate significant differences between species mixtures within each stand type (Tukey–Kramer test at $P < 0.05$). The insert shows the vertical foliage distribution in dense young (thin line) and mature (thick line) *Betula pendula* (circles) and *Pinus sylvestris* (squares) stands (see Fig. 6 in V).

DISCUSSION

Crown architecture responses to neighbour species identity

The studied tree species responded with plastic changes in their architecture to the species identity of their neighbours. Lower overall growth but added height growth indicating stronger competition was found in mixtures of *B. pendula* and *Pinus sylvestris* when a tree was surrounded by interspecific neighbours compared to trees surrounded by intraspecific neighbours. In the case of light demanding pioneers like the studied species, competition over growth resources typically decreases the overall biomass increment of an individual, but increases allocation to height growth (Anten and Hirose 1998). Both Lappi-Seppälä (1930) and Mielikäinen (1980) report *B. pendula* to gain height faster in mixtures with *Pinus sylvestris* compared to monocultures. Lappi-Seppälä (1930) also reported higher growth of *Pinus sylvestris* in *B. pendula* mixtures, whereas Valkonen and Ruuska (2003) and Frivold and Frank (2002) found that the height growth of *Pinus sylvestris* was unaffected when the proportion of *B. pendula* within the stand increased. Mielikäinen (1980), in turn, found the volume growth of *Pinus sylvestris* to be poorer in mixed stands than in pure stands, when the proportion of *B. pendula* exceeded 20%, while a slight positive effect was suggested at lower *B. pendula* proportions. All these previous results refer to stand level averages.

The more detailed analysis of *B. pendula* responses to neighbour species identity revealed that, with the exception of growth vigour, branch- and shoot-level crown architecture seemed unaffected by the species identity of the close neighbours in mixtures of *B. pendula* and *Pinus sylvestris*. *Betula pendula* had high shoot frequency in its rather few and short branches when growing with intraspecific neighbours or *Pinus sylvestris*, whereas the number and length of branches was highest when neighboured by *L. sibirica*. *Pinus sylvestris* also had more branches in the presence of *L. sibirica* compared to other neighbouring species. To my knowledge, corresponding prior studies have not been published. The results add a new dimension to competition analysis making mixed species stands quite complex systems in comparison to monocultures.

Generally, a growing pattern producing dense and spatially limited crowns seems an efficient use of growing space (Day and Greenwood 2011), which limits physical contact between individuals, thus preventing damage caused by crown collision (Meng et al. 2006). The suggested growing pattern also allows high biomass allocation to photosynthesising foliage at the expense of branches (Borchert and Tomlinson 1984). Contrastingly, looser architecture with longer branches when neighboured by *L. sibirica* is possibly linked to the typically sparse crown of *L. sibirica* (Hämet-Ahti et al. 1992). A sparse crown penetrates light well and causes less physical contact with neighbouring trees. A sparser crown with neighboured by *L. sibirica* gives *B. pendula* the advantage of minimising self-shading (Takenaka 1994).

The light simulations found that *B. pendula* canopies transmit more light than *Pinus sylvestris* canopies. The species-specific crown architecture differences affecting light transmission were mainly observed in dense stands. Higher light penetration is typically measured under a canopy consisting of shade-intolerant tree species compared to a canopy consisting of shade-tolerant species (Messier et al. 1998). Differences between shade-intolerant *Betula* and *Pinus* families have usually been reported as small (Messier et al. 1998; Stadt and Lieffers 2000). In this study the higher light attenuation of dense *Pinus*

sylvestris canopies seemed to be related to high foliage area and the dense foliage layer blocking light efficiently in the upper *Pinus sylvestris* canopy.

Both species-specific resource and non-resource signals remain plausible explanations for the observed effect of neighbour species identity on the crown architecture of the studied species. The use of competition indices did not adequately account for all the differences in tree characteristics that may affect resource uptake by trees as suggested by our light simulation results. It seems that in the case of *B. pendula*, better growth vigour and less pressure for height growth among intraspecific neighbours compared to *Pinus sylvestris* neighbours could be explained with a higher simulated light transmission of *B. pendula* crowns compared to *Pinus sylvestris*.

Light transmission differences could not explain the field study results concerning the response of *Pinus sylvestris* to neighbour species identity suggesting milder competitive effect of *Pinus sylvestris* neighbours compared to *B. pendula* neighbours. Possible species-specific differences affecting other competitive effects than light include the amount and quality of litter production (e.g. Priha and Smolander 1997; 1999) and root competition (Coates et al. 2009; Kalliokoski et al. 2010) involving mycorrhizae (Dehlin et al. 2004). Species-specific non-resource signals can also be detected by trees before resource competition occurs (Aphalo and Ballaré 1995; Aphalo and Rikala 2006; Gagliano et al. 2012). These effects are currently not fully understood (Gagliano et al. 2012), but recognised signals include differences in the spectral composition of light reflected from the foliage of various neighbouring species (Smith 2000), chemical signals (Heil and Karban 2010) and differences in species-specific crown architecture affecting wind velocities that trees van sense as proximity signals (Aphalo and Ballaré 1995). Crown collision through swaying is a more direct wind effect, which has been reported to decrease the crown cover, branch length and shoot density of individuals (Meng et al. 2006).

Studies on the competitive effect of similar-sized neighbouring trees representing different species have generally shown evidence supporting stronger interspecies competition (e.g. Sumida et al. 2002; Gagliano et al. 2012), but also supporting stronger competition within a species and between closely related species (e.g. Canham et al. 2004; Uriarte et al. 2004; Boivin et al. 2010). Results supporting an equal competitive effect per plant biomass among neighbouring species can also be found in the literature (e.g. Goldberg 1987). Mechanisms behind the differences in the strength of intraspecies and interspecies competition include evolutionary theories e.g. kin selection that is based on the idea of cooperation between individuals sharing partly the same genes (Novak 2006; Murphy and Dudley 2009). Another aspect is resource partitioning that may promote species diversity by reducing the competition for limiting resources between co-occurring species (McKane et al. 2002).

Crown architecture and competition intensity

Competition indices representing the abundance, size and proximity of the neighbouring trees affected tree growth and structure in *B. pendula* and *Pinus sylvestris*. The uniqueness of this study was in the comprehensive examination of the above-ground responses of *B. pendula* and *Pinus sylvestris* to neighbour competition, including the analysis of various hierarchical structure levels. Competition intensity decreased the growth vigour of mature individuals of both species at the whole-tree level, which is an expected result based on earlier results (e.g. Anten and Hirose 1998). High competition indices contrastingly

increased the growth vigour of younger *B. pendula* trees. Competition indices most probably indicated the growth conditions of small-scale growth habitats around young trees that did not suffer from actual resource competition.

I found evidence for species differences in the more detailed response to competition as suggested by Thorpe et al. (2010). The ratio of tree height to breast height diameter, i.e. stem slenderness increased, crown length decreased, and the number and length of the main branches decreased with increasing competition intensity in *B. pendula*, as was expected based on previous studies (Jones and Harper 1987; Messier and Puttonen 1995; Umeki and Kikuzawa 2000; Mäkinen et al. 2003). However, the architecture simulation results suggested that proportional biomass distribution increased to foliage and the main branches and decreased to the stem in response to increasing competition intensity and stem slenderness in *B. pendula*. Similar results have been found previously for the living crown by Ilomäki et al. (2003). Decreased proportional biomass distribution to the stem with increasing competition intensity and stem slenderness may relate to a more efficient use of sapwood in crowns experiencing severe competition, as increased self-pruning reduces the amount of disused pipes within the crown (Ilomäki et al. 2003). However, Ilomäki et al. (2003) found an opposite trend at tree level i.e. the proportional biomass distribution to the stem increased. The reason why our tree-level (above-ground) simulation in Fig. 8 resembles the crown-level results of Ilomäki et al. (2003) is likely that the living crown represents almost the entire tree height in the simulated trees. The reason for this is that in Fig. 8 the trees are younger and the scale of competition is milder compared to the study by Ilomäki et al. (2003). Stem volume is in our crown architecture model simulated as one entity and thus the stem form function is similar below and within the living crown.

Competition intensity in *Pinus sylvestris* reduced height growth, crown expansion (length of shoots), the number of first-order branches and the amount of foliage from the inner crown. Stem diameter did not change. Mátyás and Varga (2000) also found that *Pinus sylvestris* responded to competition by increasing the height growth of young trees only moderately and decreasing height growth slightly after canopy closure. Overall production decreased in *Pinus sylvestris* with increasing competition intensity and stem slenderness, but proportional biomass distribution decreased to the foliage and large branches and increased to the stem in line with previous findings (Mäkelä and Vanninen 1998; Mátyás and Varga 2000; de Chantal et al. 2003). This allocation strategy of responding to competition intensity and stem slenderness with a decreased ratio of photosynthesising foliage to non-productive woody parts differs from that found in *B. pendula*. Species-specific growth patterns may possibly offer an explanation, as *Pinus sylvestris* has stronger apical control compared to *B. pendula* and thus allocates proportionally more resources to the main stem at the expense of main branches and foliage, to gain height during competitive stress.

Light distribution inside a canopy due to between-tree shading, and architectural solutions enhancing light harvesting are reflected in the variation of foliage, shoot and branch characteristics within the crown (Ballaré 1999). Our results showed that a higher location in the crown increased the number of shoots responsible for elongation growth as well as their length in *B. pendula* and *Pinus sylvestris*, and needle length in *Pinus sylvestris*. High shoot formation and growth at the top of the crown has previously been shown and associated with good light conditions (e.g. Mäkinen 1999; Goulet et al. 2000; Takenaka 2000; Kaitaniemi and Ruohomäki 2003; Niinemets and Lukjanova 2003) and hydraulic preference (Goulet et al. 2000; Nikinmaa et al. 2003). The strongest growing shoot individuals are situated under better light conditions, i.e. long leader shoots at the top of the

crown (Maillette 1982; Goulet et al. 2000). These shoots will likely remain unshaded for several years, which increases their production effectiveness and lifespan (Nikinmaa et al. 2003). If light was considered the only driving factor for shoot development, crowns would be bushy in shape (Nikinmaa et al. 2003), lacking apical control (Cline 1997). A more realistic crown architecture can be achieved by considering that the branch with the largest cross-sectional area in each branching point can supply the most water and nutrients for its shoots, thus having the highest sink strength (Nikinmaa et al. 2003). Accordingly, the branching hierarchy of the mother branch explained the shoot number and length in both studied species in this thesis. The decrease in shoot growth in relation to increased GO was also reported in *B. pendula* and in *Pinus sylvestris* by Maillette (1982) and Nikinmaa et al. (2003), respectively. The effect of branching hierarchy on shoot number and length results in efficient resource allocation to a few branch axis and shoots, leading them to gain length, direct growth and reach for light (Trewavas 2005). Shoot length variation was high throughout the crown in *B. pendula,* demonstrating potential heterogeneity in the local light climate of the shoots and within-tree competition between individual shoots as shown before in *Betula pubescens* (Kaitaniemi and Ruohomäki 2003).

The number of first-order branches increased and their size decreased towards the crown top in both studied species as shown before (Mäkinen and Colin 1998; Mäkinen et al. 2003; Gort et al. 2010). With a given branch length, the diameter of the first-order branches was higher in the upper crown parts compared to the lower parts, indicating that branch volume per length is higher in younger branches situated in better light conditions. Branch death is the explanation for this low number of living branches at the crown base, as the probability of death is high if a branch cannot gather enough light for its own maintenance (Sprugel et al. 1991). Larger branches at lower crown parts are generally a result of cumulative size with branch age. Branch diameter is known to be at its maximum at the widest crown point, after which once again it decreases towards the crown base (e.g. Mäkinen and Colin 1998) due to the reduced growth and longevity of the branches at the lowest crown parts (Kershaw et al. 1990).

The forking angle of first-order branches was higher in *B. pendula* compared to *Pinus sylvestris*. Branch angle decreased in *B. pendula* and increased slightly in *Pinus sylvestris* with increasing height within crown. A similar pattern has been shown for *B. pendula* by Mäkinen et al. (2003). If a short and a long branch were at the same height within the crown of *B. pendula*, the longer branch would have a smaller branch angle leading to less overtopping by neighbouring branches (Sumida et al. 2002). Similar results were found by Mäkinen et al. (2003). The number, length and diameter of lateral branches in *B. pendula* were in accordance with the requirements of mechanical loading (Farnsworth and Van Gardingen 1995) and the idea of apical control (Goulet et al. 2000): the longer the mother branch and the lower the GO, the higher the number and size of the lateral branches.

Leaf angle was found to become more vertical towards the crown top in *B. pendula*. This phenomenon is well-known in the literature as vertical leaves in the sun position enhance photosynthetic efficiency and leaf cooling, whereas horizontal leaves in the shade position maximises photosynthetic gain (e.g. Mc Millen and Mc Clendon 1979). This leaf angle distribution also helps to prevent severe self-shading within the crown (Posada et al. 2012).

Trees of differing height and age pose various physiological traits during ontogeny, to maximise their photosynthetic efficiency (e.g. Osada et al. 2002; 2004). The results indicated more vigorous growth and higher investment placed into long shoots compared to short ones in young trees compared to mature ones. The number of leading long shoots

situated in the stem was also lower and their length longer in young trees in the absence of between-tree competition. These results are in accordance with earlier studies (Bonser and Aarssen 1994), showing that crown shape is often less pointed in mature trees compared to young trees due to increased branching and decreased apical control (Day and Greenwood 2011). The foliage area per shoot increased from the crown base to the top in *Pinus sylvestris* and in young *B. pendula*, but decreased in the same direction in mature *B. pendula*. The same phenomenon has been observed before in *Betula papyrifera* (Ashton et al. 1998). Young *B. papyrifera* individuals had the largest and thickest leaves in the upper and outer parts of the crown and the smallest and thinnest leaves in the lower, inner parts. Old individuals, in turn, followed the typical sun-shade dichotomy with larger and thinner shade leaves in the lower parts of the crown and smaller and thicker sun leaves at the crown top. The high resource availability in small trees enables faster water movement to the leaves, which are exposed to high levels of irradiance, and results in maximising photosynthetic gain by collecting more light with low water-use efficiency (Ashton et al. 1998). The leaf area in the crown top of larger trees is probably limited by water availability (Ashton et al. 1998).

Linking hydraulic architecture with crown architecture

Plastic crown architecture was linked to hydraulic architecture in the studied species. Scaling of conduit diameter with distance from the apex was observed inside the branches and stem when a defined growth ring was followed. Similar results regarding various species have been shown before (Sanio according to Bailey and Shepard 1915; Zimmermann 1978*a*; Tyree and Zimmermann 2002; Anfodillo et al. 2006; Coomes et al. 2007; Sellin et al. 2008). However, scaling was negligible in the stem compared to more distal crown parts and steeper in *B. pendula* compared to the conifers (see also Mencuccini et al. 2007).

Transporting distance was not the only crown variable explaining hydraulic architecture. I found a linear relationship between leaf area and leaf petiole conduit size, a relationship that has rarely been published. Connecting leaf area to water transportation was possibly the most direct link between crown and xylem architectures, because carbon dioxide and water vapor exchange takes place through the same stomata openings on leaf surfaces. The result indicate that the larger the leaf area with high photosynthetic potential the higher the transpiration, which further leads to high transport demand achieved with large conduits (see also Lusk et al. 2012).

Xylem anatomy additionally varied between successive tree compartments, the smallest conduits and highest conduit frequencies being found from leaf petioles. These results correspond with earlier findings (Fegel 1941; Bailey 1958; Bhat 1981; Baas 1982; Tyree and Zimmermann 2002; Oliveras et al. 2003; Nygren and Pallardy 2008). I also found differences in conduit anatomy between branching hierarchies, as conduit diameter was larger in the main branches than in the lateral branches of *B. pendula* and *Picea abies*, but no statistically significant difference was observed in *Pinus sylvestris*. Conduit frequency was also lower in the lateral branches of the conifers compared to the main branches, but no difference was found in *B. pendula*. Earlier studies on deciduous species have shown a decrease in conduit diameter and an increase in conduit frequency from the main to the lateral branches (Atala and Lusk 2008; Nygren and Pallardy 2008; Sellin et al. 2008). Suggested biological mechanisms behind the acropetal decrease in cell

size are distance from the auxin source (Aloni 1987; 2001) and the turgor pressure gradient as turgor pressure decreases with increasing tree height leading to reduced cell expansion (Koch et al. 2004; Woodruff and Meinzer 2011). Acropetally increasing auxin levels lead to higher conduit density and smaller size of distal crown parts due to faster cell differentiation, and are thus available for cell expansion for only a brief period. The observed differences in conduit anatomy between different branching hierarchies could also accordingly be explained by apical control affecting the emitted auxin levels (Spicer and Gartner 1998; Wilson 2000). As a concrete implement between hydraulic and crown architectures, both turgor pressure and auxin levels are also known to be involved in branch elongation and leaf size (Woodruff and Meinzer 2011).

Conduits increased and decreased in diameter and frequency, respectively, from the core to the outer wood, a result agreeing with the study by e.g. Saranpää et al. (2000). This phenomenon is usually related to the effect of cambium ageing (Gartner 1995).

From our results we can conclude that hydraulic architecture showed plasticity in response to neighbour interactions indirectly through crown architecture, an approach seldom seen in the literature. Shorter branches in the presence of competition indicated a smaller branch sapwood area and smaller branch conduits; whereas a longer and thinner stem due to competition in *B. pendula* indicated a smaller stem sapwood area but larger conduits near the bark. Similarly, the crown architecture of *B. pendula* growing with intraspecific neighbours or *Pinus sylvestris* referred to smaller branch conduits compared to those in a crown growing with *L. sibirica*. Further, within-crown variation of leaf area suggested that petiole conduits increased in diameter towards the crown top in young *B. pendula*, whereas they increased downwards in mature *B. pendula*, suggesting an active role of leaf structure in crown level distribution of water use.

Optimal xylem anatomy maximises the water transport efficiency by simultaneously securing transport from disturbances caused by drought-cavitation (Sperry and Tyree 1988) and freezing (Sperry and Sullivan 1992) using a structure that also meets mechanical demands. This kind of hydraulic architecture design is dependent on crown architecture in several ways. The amount of water needed by different crown parts depends on the distribution of photosynthesising foliage, the distance water needs to be transported depends on the size of the tree, the efficient use of carbon to maximise water flow requires space-filling packing of conduits meaning that the total volume of conduits is dependent on branch volume, and the mechanical demands met by the xylem depend on the overall distribution of crown architecture. Thus as a plant grows, any part of it will experience changes in its external environment and internal physiology, leading to changes in hydraulic and mechanical demands (Day and Greenwood 2011; Lachenbruch et al. 2011).

Interdependence between hydraulic and crown architectures may possibly exist, which means that hydraulic architecture also regulates the development of crown architecture as suggested by Nikinmaa et al. (2003), especially in unfavourable environmental conditions. Maximum tree height at least is suggested to be restricted by water economy (Woodward 2004). The latest research results suggest that there is an "intimate adaptive relationship between environment, stem size and vessel diameter" (Olson and Rosell 2012; see also Hölttä et al. 2011).

WBE is a universal model that postulates scaling in biological transport systems between conduit diameter and the size of the system in any environment, and thus simplicity is its strength whereas accuracy is not. WBE assumes systematic crown architecture with a democratic branching system, constant conduit tapering with transport distance, no conduit furcation and uniform biomechanical constraints within a tree. These

assumptions are usually not fulfilled in the case of real plants (McCulloh and Sperry 2005), leading to several open questions in the interpretations of the scaling results. We have shown that although tree-level conduit diameter of the studied species appeared to scale with transporting distance, various tree compartments and branching hierarchies showed different scaling patterns (see also Nygren and Pallardy 2008). We also found conduit furcation. Universal scaling models cannot explain the intra- and interspecies variation of hydraulic architectural designs, as this requires species-specific scaling functions and additional information of species-specific traits affecting water transportation (Sperry et al. 2012).

Utility and challenge of the thesis approach

The empirical field study produced a large data set including over 200 digitised trees grown in 17 stands, thus allowing statistical analyses of crown architecture and species-specific neighbour effects. This data set was powerful in showing the quantitative plastic changes that between-tree competition imposes on crown architecture.

Unlike in replacement or additive designs (Lappi-Seppälä 1930; Mielikäinen 1980), our focus was in the very close neighbourhood around the target trees, thus allowing us to study the smaller scale species disposition of mixed stands as these interactions are the underlying drivers of mixed species stand dynamics. Significant above-ground competitive stress in individual trees has been reported to be induced only by the ring of competitors immediately surrounding the subject tree crown (Cole and Lorimer 1994).

Empirical field studies always include several components affecting the results, a mixture of wanted and unwanted factors. We tried to control this mixture with the fractional factorial study design and multivariate statistical analysis. The use of fractional factorial design is based on a sufficient number of stands with sufficient coverage of the studied factor (Zaluski and Golaszewski 2006), i.e. a sufficient number of target and neighbour species identity combinations. This requirement was not satisfactorily fulfilled with *A. glutinosa* as a neighbour species, which may explain why the effect of *A. glutinosa* failed to gain statistically significant results in some of the analyses.

The empirical data set for hydraulic architecture was rather unique as it covered the whole tree, including below- and above-ground parts and different branching hierarchies (see also Atala and Lusk 2008; Nygren and Pallardy 2008; Sellin et al. 2008). Hydraulic architecture measurements were connected with detailed architectural measurements covering the branching topology, which enabled various inter-linkage analyses. Our study took one more step towards combining hydraulic and architectural modelling, with an aim towards more comprehensive future functional-structural tree modelling.

The empirically derived 3D crown models created in this thesis as tools to study crown architecture were shown to produce realistic tree-level biomass estimations for foliage and branches as well as a realistic within-crown variation of foliage and branch properties as described in IV (see Fig. 10). The model constructions were successfully compared to independent results of earlier studies. However, an independent data set for comparing various crown properties between constructed and empirically measured individuals together with an evaluation of these models against different competition statuses of trees would improve the reliability and applicability of the models. As the tree models are based on empirical submodels linking the structural features at different hierarchical levels, model

bias accumulates from one hierarchical level to another, which was not statistically considered during the model constructions.

Crown architecture models can be used with caution to study the within-crown variation of crown components in trees of varying sizes and competitive pressures, as in this summary. Another important utility for the created crown models is their possible further usage in dynamic functional-structural growth models, e.g. to produce the initial crown architecture in a dynamic model or to test model predictions. Hovi and Korpela (2013) used the 3D crown model created for *B. pendula* in this thesis to simulate small footprint airborne light detection and ranging (LiDAR). They compared real LiDAR waveforms extracted from young *B. pendula* crowns against simulated LiDAR. The simulation was based on the 3D crown model supplemented with measurements of optical leaf properties of *B. pendula* (Lukeš et al. 2013) and the Monte Carlo ray tracing method. It was concluded that such ray tracing simulation is a useful tool for developing new interpretation techniques and for testing hypotheses considering the interpretation of LiDAR data (Hovi and Korpela 2013).
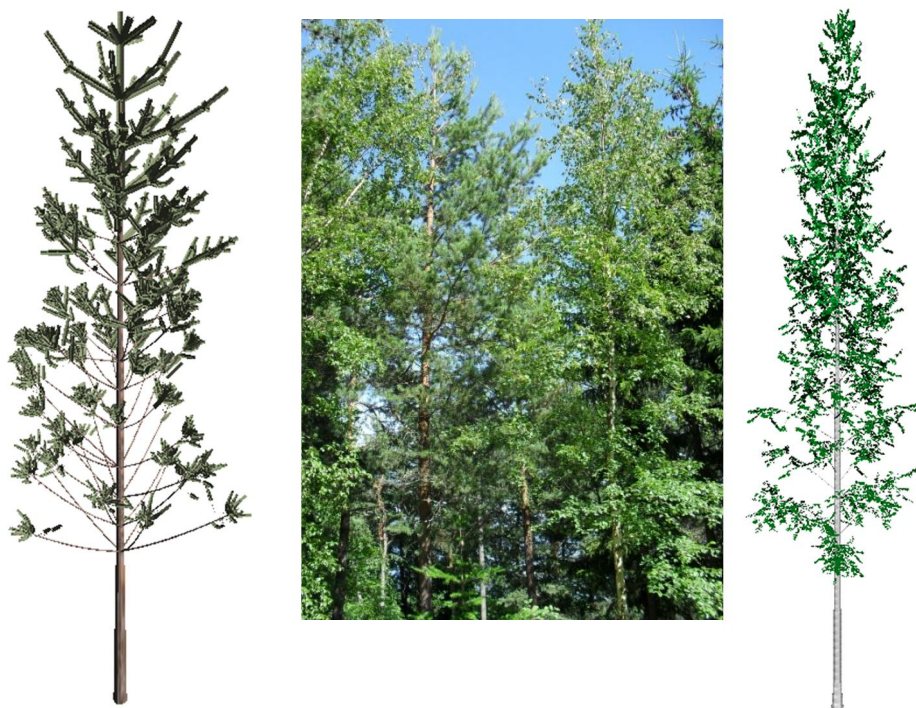

Figure 10. The middle picture represent a *Pinus sylvestris* and *Betula pendula* tree in the field with their simulations on the left- and right-hand sides. Only measured tree-level input information along with competition indices have been used for the simulations: height (H) = 1100 cm, diameter at breast height (DBH) = 15.6 cm, crown height (CH) = 300 cm for *Pinus sylvestris* and H = 900 cm, DBH = 8 cm, CH = 200 cm for *Betula pendula*.

Crown architecture models were utilised in this thesis for simulating light climates in even-aged forests with different species-mixtures to study species-specific differences of light transmission that is one basic driver of stand development. With explicit 3D models it was possible to assess the precise role of species-specific crown architecture in light transmission at forest stands by keeping the stand characteristics, including location and size of each neighbouring tree, constant in the species comparison, which is challenging in field studies. Light simulations showed interesting differences in species-specific light transmission properties and the simulation results were compared with preliminary field measurements. However, further evaluation of the simulations is needed. Models are always simplifications of reality, and especially the assumption of symmetric crowns, thus ignoring the ability of real trees to fill in canopy spaces by directing branches to available light (Stoll and Schmid 1998) should be taken into consideration in the application of the results, i.e. no local spatial dynamics can be analysed. Such approach would require that stands are first grown to specific spatial composition or whole crown level measurements of asymmetry would be available. Crown asymmetry affects dense, irregular stands the most (Umeki 1997). The assumption of symmetric crowns in combination with random tree placement likely led to a slight overestimation of crown overlapping and spatial variation within the stand (Oker-Blom and Kellomäki 1983) and between repeated simulations (see Umeki 1997), although the error was reduced with the minimum between-tree distance restriction.

The results are best applicable at similar stands as where data collection took place, mainly involving rather young, medium fertile sites. Trees above 20 m in height were poorly represented in the data and are thus not accurately described by the results presented in this thesis. The effect of neighbour species identity might be different in dry, nutrient poor or highly fertile sites, where the competitive status of the studied species is clearly unequal. Also linkage between hydraulic and crown architectures may be different in growth habitats that differ clearly in water or nutrient status (Nikinmaa et al. 2003). The geographical area covered by this thesis was the southern half of Finland, but regarding the studied species I consider the results to be generalisable to the whole boreal zone. Responses of shade-tolerant species to neighbour competition may be completely different (see Messier at al. 1999).

The results offer practical information applicable to forest management and planning in terms of the competitive effects and responses of *B. pendula* and *Pinus sylvestris*, but most of all, indicate a method how to analyse and simulate mixed species stand development. New information is provided, especially on the effects that neighbour species identity have on competition. Within-stand competition is a precursor needed for growing valuable timber, as has been known for centuries. However, it seems that despite *B. pendula* growing taller and bearing less and shorter branches with competitive pressure, the proportional biomass distribution to the stem, at least within the living crown, decreases in favour of the main branches and foliage. The same is not true for *Pinus sylvestris*. This result gives us new insight to the current recommendations of growing *B. pendula* in sparser spacing compared to *Pinus sylvestris*. The practical conclusion from these results in terms of species mixture depends on the favoured species and preference between high biomass production and high-quality timber production. Results suggest that the more *Pinus sylvestris* individuals within a stand are surrounded by *B. pendula*, the more height and the less biomass is gained by them, and vice versa. If there is no preference between the species, a 50% mixture seems to lead to the highest average tree height.

Crown architecture analyses also give practical information concerning the properties and within-crown variation of crown characteristics in different-sized tree individuals growing under varying competitive stress. This tree-level information can be achieved from field measurements or tree-level growth simulations, and crown details then estimated based on the results presented here. Crown properties and detailed tree models can further be used for estimating wood biomass and log quality based on branch characteristics and wood density.

I consider the most value part of this thesis to be the comprehensive examination of the above-ground responses of *B. pendula* and *Pinus sylvestris* to neighbour competition at various hierarchical structure levels and including identification between light competition intensity and neighbour species identity.

CONCLUSIONS

Crown architecture plays a major role in between-tree crown interactions by shaping the competitive effect and competitive response of a tree. Crown architecture of the studied boreal tree species showed plastic responses to the species identity of neighbour trees in addition to their size and proximity. It seems that the control of growth responses in the studied species ranged from the level of individual branches and shoots, reflecting e.g. local light condition variations within the crown, to the whole-tree level.

Measurements of crown architecture can be changed into a dynamic analysis with proper modelling. It is possible to empirically analyse competition effects and responses between tree individuals in complex systems like mixed species stands. Even causal relationships behind the crown interactions can be studied as done in this thesis by modelling light transmission through simulated stands.

Crown architecture, competitive crown interactions and hydraulic architecture of *Betula pendula* and *Pinus sylvestris* were characterised and compared with novel detail. Crown architecture of these species was characterised by vertically and hierarchically varying number and size of shoots and branches within crown. This variation was evident in both species, but the scale of vertical variation was smaller for *Pinus sylvestris*.

Competitive responses of *B. pendula* and *Pinus sylvestris* seemed similar in terms of e.g. decreased number and size of branches and decreased probability of having foliage in a branch section, but different in terms of biomass distribution. Proportional biomass distribution to foliage and main branches over the stem increased in young *B. pendula* with increasing competition intensity, whereas *Pinus sylvestris* used the opposite strategy. Growth vigour of *B. pendula* and *Pinus sylvestris* was higher when surrounded with intraspecific neighbours, whereas height growth was increased when surrounded with interspecific neighbours.

Results showed that the diameter and frequency of water conducting cells vary within the crown and are linked to tree architecture, thus reflecting the plastic responses of crown architecture. The scaling of conduit size with distance from the apex is in accordance with the WBE model, but we showed here that conduit anatomy is also linked to other crown characteristics.

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