



UNIVERSITA' DEGLI STUDI DEL MOLISE

Department of Biosciences and Territory

INTERNATIONAL PHD COURSE IN:

Management and Conservation Issues in Changing Landscapes

Cycle XXVI

**“EFFECTS OF UNDERSTORY LIGHT CONDITIONS
AND INTRASPECIFIC COMPETITION
ON DEVELOPMENT OF ESTABLISHED NATURAL REGENERATION IN A MIXED
MULTIAGED FOREST OF ITALIAN EASTERN ALPS”**

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ACADEMIC YEAR 2014/2015

Ai miei Genitori

a Claudio

a Gabriele

che mi hanno sempre supportato e sopportato

dedico questo lavoro, frutto di sacrifici e regalo di grandi soddisfazioni

EFFECTS OF UNDERSTORY LIGHT CONDITIONS AND INTRASPECIFIC COMPETITION ON DEVELOPMENT OF ESTABLISHED NATURAL REGENERATION IN A MIXED MULTIAGED FOREST OF ITALIAN EASTERN ALPS

Abstract

The current trend of silviculture aiming to manage forest as complex forest ecosystems, justified the attention researchers have devoted over the years to the characterization of light below canopy cover.

Explicit measurements of light gradients allowed to study the interactions between different canopy structures (e.g. heterogeneous vs homogeneous) and light transmittance providing managers with crucial information on how to control understory light availability by manipulating overstory and predict successional dynamics, such as natural regeneration processes.

On the other hand, the presence of natural regeneration represents one of the main conditions for promoting natural evolutionary process, providing continuity, enhancing resilience and resistance of forest ecosystems and maintaining heterogeneous conditions in terms of structure and light availability.

The objective of this P.h.D thesis is to improve the current knowledge on how the light affects two major processes involved in the natural regeneration of mixed multi-age forests (competition among recruited trees and their growth) as a function of structural attributes of the stands. A mixed silver fir (*Abies alba* Mill.) and Norway spruce (*Picea abies* L.) forest located in the mountain belt of eastern Italian Alps was used as a study case. Both species were considered and their behavior compared. Relationships between overstory canopy structure and radiance transmitted in the understory were also analyzed.

The following questions were addressed: i) which structural attributes mainly affect the light availability in the understory of a multi-aged mixed forest? ii) which understory light levels allow the coexistence of natural regeneration of Norway spruce and silver fir? iii) do the two species use the same growth strategies to access to the available light resource or do silver fir and Norway spruce seedlings differ in morphological responses to low light availability?

Results suggested that:

i) radiation below canopy in heterogeneous stands with continuous canopy cover depends more on the varying dendrometric attributes within the stands than their mean values. Vertical structure

exerts a clear effect on transmission of radiance. In particular, crown size characteristics, such as crown length (CL), crown base (CB) and height, and in particular their standard deviations are good proxy for light transmission, even more in mixed species forest stands.

iii) and iv) significant differences in terms of light availability characterize the site where the seedlings of the two species grow. Levels of radiance ranging from 20 to 30% of total transmittance allow the coexistence of fir and spruce seedlings. At those light conditions competition stimulate species to develop different growth strategies. While silver fir take advantage in terms of apical growth, increasing in light availability promote more effects in terms of radial growth in spruce. Neither light availability nor the competition indexes applied significantly affected the apical dominance ratio (ADR) and the live crown ratio (LCR) of the seedlings.

A careful overstory trees selection or a fine adjustment of light permeability of overstory is of particular importance for silver fir and Norway spruce regenerating in the understory of heterogeneous mixed forest. Both species apparently add to shade tolerance a rather good reactivity to light condition change.

Keywords: overstory structural attributes, natural regeneration, understory light, competition, growth, morphological parameter.

**EFFETTI DELLE CONDIZIONI DI LUCE NEL PIANO DOMINATO E DELLA
COMPETIZIONE INTRASPECIFICA SULLO SVILUPPO DELLA
RINNOVAZIONE NATURALE AFFERMATA
IN UNA FORESTA MISTA E DISETANEA DELLE ALPI ORIENTALI**

Riassunto

L'attuale tendenza della selvicoltura rivolta alla creazione di ecosistemi forestali complessi, giustifica l'attenzione che nel corso degli anni i ricercatori hanno dedicato alla determinazione della luce sotto copertura nei popolamenti forestali.

La caratterizzazione della luce nello strato dominato ha permesso di studiare le interazioni tra differenti tipologie di strutture forestali (ad esempio strutture eterogenee vs strutture omogenee) e la trasmittanza fornendo informazioni cruciali ai selvicoltori sul controllo della disponibilità di luce nel piano dominato attraverso la regolazione della struttura del piano dominante e consentendo di fare previsioni sulle dinamiche forestali di successione come il processo di rinnovazione naturale.

Dall'altra parte, la presenza di rinnovazione naturale rappresenta una condizione fondamentale per promuovere processi di evoluzione naturale, garantire la continuità del soprassuolo, aumentare la resistenza e resilienza dell'intero ecosistema forestale e mantenere un carattere eterogeneo sia in termini di struttura che di disponibilità di luce.

L'obiettivo della tesi è stato quello di incrementare le attuali conoscenze degli effetti della luce sui due principali processi coinvolti nella fase di rinnovazione naturale di un popolamento misto e disetaneo (competizione tra semenzali e crescita) in funzione degli attributi strutturali del popolamento. Come caso di studio è stato analizzato un bosco misto e disetaneo di abete bianco (*Abies alba* Mill.) e abete rosso (*Picea abies* L.) delle Alpi italiane orientali. In dettaglio è stato studiato e confrontato il comportamento di entrambe le specie. Inoltre sono state analizzate le relazioni tra gli attributi strutturali delle piante del piano dominante e luce trasmessa nello strato dominato.

Alla base dello studio sono state poste le seguenti domande: i) quali sono gli attributi strutturali che influenzano maggiormente la disponibilità di luce nel piano dominato di un popolamento forestale misto e eterogeneo come quello analizzato? ii) quali livello di luce consente alla rinnovazione di abete bianco e abete rosso di coesistere? iii) le due specie utilizzano le stesse

strategie di crescita per accedere alla luce disponibile o hanno differenti comportamenti tradotti in una diversa risposta morfologica dei semenzali?

I risultati hanno suggerito che:

i) in popolamenti eterogenei con copertura continua la radiazione nel piano dominato dipende più dalla variazione degli attributi dendrometrici nel popolamento piuttosto che dai loro valori medi. La struttura verticale esercita un chiaro effetto sulla trasmissione della luce. In particolare, le caratteristiche e le dimensioni delle chiome (profondità e inserzione) e delle altezze e la loro variazione (espressa nel nostro caso come deviazione standard) rappresentano dei buoni predittori della luce trasmessa nel piano dominato, soprattutto in popolamenti di specie miste.

ii), iii) le condizioni di luce in cui cresce la rinnovazione di abete bianco e abete rosso sono risultate significativamente diverse. Il livello di trasmittanza totale che permette la loro coesistenza è compresa tra il 20 e il 30%. E' probabile che a queste condizioni di luce, la competizione, mediamente più elevata, stimola un diverso comportamento nella crescita delle due specie. Infatti ad un aumento della luce disponibile mentre l'abete bianco si avvantaggia in termini di crescita apicale, l'abete rosso risponde positivamente con incrementi più evidenti nella crescita radiale. L'aumento di luce disponibile e del livello di competizione non produce invece nessuna risposta significativa sui parametri morfologici delle specie.

Comunque è evidente che entrambe le specie, nonostante la spiccata tolleranza all'ombra, hanno una buona reattività alla variazione delle condizioni di luce.

Complessivamente si può affermare che un'attenta selezione degli alberi e quindi una oculata regolazione della permeabilità della luce sul piano dominato risulta fondamentale per la rinnovazione naturale di abete bianco e abete rosso in popolamenti misti eterogenei.

Parole chiave: attributi strutturali del piano dominante, rinnovazione naturale, luce nel piano dominato, competizione, crescita, parametri morfologici.

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1. Introduction

The recognition of forest as complex system among scientists and communities (Levin 1998, Kuuluvainen 2009, Ciancio 2011, Nocentini 2011, Puettmann et al. 2013) has increasingly raised the necessity to develop new strategies for managing woodlands and make them more suited to face the challenges by global changes (Franklin et al. 2002, Larsen and Nielsen 2007, Millar et al. 2007, Puettmann 2011, O'Hara and Ramage 2013, Wagner et al. 2014). Multiple approaches, new tools and decision criteria on analyzing forest stands and designing silvicultural systems are being developed and improved (O'Hara 1998, Koch and Skovsgaard 1999, Gamborg and Larsen 2004, Pommerening and Murphy 2004, Meitner et al. 2005, Puettmann et al. 2009, Geldenhuys 2010; Messier and Puettmann 2011, Bradford and Kastendick 2010). Most - proposals aim to get multi-aged, mixed forests with heterogeneous structure consisting of a fine-scale mosaic of cohorts of trees, with different species, size, age and development stage and temporal continuity of natural regeneration of trees. Freestyle (Boncina 2011), single and group selection silvicultural systems with very variable retention of live and dead trees, emulating natural disturbance regimes, were proposed in order to modify overstory cover and create spatially differentiated microclimate conditions, particularly in terms of understory light availability. The level of visible light (380-710 nm) directly or indirectly affects other environmental parameters such as temperature, humidity, wind speed, soil condition, and can be even an effective indicator of the differences in stand structure across forests (Larcher 2003).

Foresters are aware that understory light availability plays a crucial role in driving forest dynamics, since it influences several aspects of plant regeneration and growth processes, such as seed germination, plant recruitment, early establishment of seedlings, young tree survival (Beaudet et al. 2011, Bartemucci et al. 2006). The benefits of managing light levels in the understory also include the control of shrub/herb layers growth either to suppress them as competitors or to promote their richness as source of biodiversity (Lieffers et al. 1999, McKenzie et al. 2000, Whigham et al. 2004, Royo and Carson 2006, Hart and Chen 2006, Gilliam et al. 2007, Molder et al. 2008, Tinya et al. 2009).

While above-canopy light cannot be regulated by managers, understory light and its spatial distribution can be manipulated, at least in part, by controlling the spatial arrangement of forest canopy structure and therefore by adjusting harvesting intensity and size, shape, location and

orientation of openings (Carlson and Groot, 1997; Lieffers et al 1999; Battaglia et al, 2002; Beaudet et al, 2011).

Numerous models have been developed over the years to predict understory light availability (Lieffers et al., 1999), although traditional forest ecology models were not designed to easily input forestry data or be readily used to address the management questions of foresters (Robinson and Monserud, 2002; Coates et al., 2003). In a context where exploring the impact of different type of harvesting is of interest, especially in structurally complex and species-diverse forests, spatially explicit, individual-tree models might be particularly appropriate (Canham et al. 1999, Beaudet et al. 2011).

Despite modeling tools are increasingly used by forest ecologists, who face the challenge of transferring knowledge to stakeholders and the general community, and managers, who benefit from the development of scenario-based supports for decision making (Vacchiano et al, 2012), the usefulness of those models is often limited by the large data requirements.

However, explicit characterizations of light gradients and of interactions between different canopy structures, such as heterogeneous vs homogeneous structures, and light transmittance would be useful for providing managers with crucial information on how to control understory light availability by manipulating overstory stand structures (Gersonde et al, 2004).

The efforts of silviculture in creating and managing complex forest ecosystems, justified the attention that researchers have devoted to the characterization of light below canopy cover (Lieffers et al 1999; Angelini et al 2014, in press) and confirmed the increasing interest in using understory light as predictive management tool, especially for predicting successional dynamics, such as natural regeneration processes.

2. Objectives of thesis

One of the main conditions promoting natural evolutionary processes and ecological integrity necessary to maintain variability in stand structure and services (Dorren et al 2004) is to guarantee the presence of a sufficient natural regeneration in the stand (Motta and Haudemand, 2000). The benefits of a permanent and multilayered canopy cover have direct consequences on improving forest ecosystems resistance and resilience and then also the continuity of functions requested from forests by society (Brang 2001, Drever and Lertzman 2006).

Natural regeneration is a crucial stage of the forest dynamics and the primary source for stand renewal (Dorren et al 2004). The whole phase, from seed germination to seedling establishment and growth, widely varies in duration depending on the ecological and physiological traits of species and the resources availability (Oliver and Larson, 1990; Franklin et al 2002).

An important role in the dynamics of the regeneration is played by light availability in the understory. The amount of radiation at disposal of seedlings highly depends on size, shape and orientation of gaps in the overstory cover (Dai Xiaobing 1996, Gray et al 2002, Albanesi et al 2008, Pretzsch H., 2014). However, in unevenaged mixed forests even vertical and horizontal structure of stands is important in determining how much radiation can reach the forest floor.

The objective of this P.h.D thesis is to improve the current knowledge on how the light affects two major processes involved in the natural regeneration of mixed multi-age forests (competition among recruited trees and their growth) as a function of structural attributes of the stands. A mixed silver fir (*Abies alba* Mill.) and Norway spruce (*Picea abies* L.) forest located in the mountain belt of eastern Italian Alps was used as a study case. Both species were considered and their behavior compared. The following assumptions were put at the base of the work:

- a) understory light availability in a multi-aged mixed forest vary sharply within the stand (Drever and Lertzman 2003);
- b) both vertical and horizontal structural attributes of stand affect understory light conditions in a mixed and multi-aged forest (Angelini et al 2014, in press);
- c) fir regeneration grows significantly better than spruce regeneration in low light conditions.

To prove these hypotheses, the following questions were tried to be answered:

- i) Which structural attributes mainly affect the light availability in the understory of a multi-aged mixed forest?

- ii) Which understory light levels allow the coexistence of natural regeneration of Norway spruce and silver fir?
- iii) Do the two species use the same growth strategies to access to the available light resource? Or do silver fir and Norway spruce seedlings differ in morphological responses to low light availability?

3. Structure of thesis

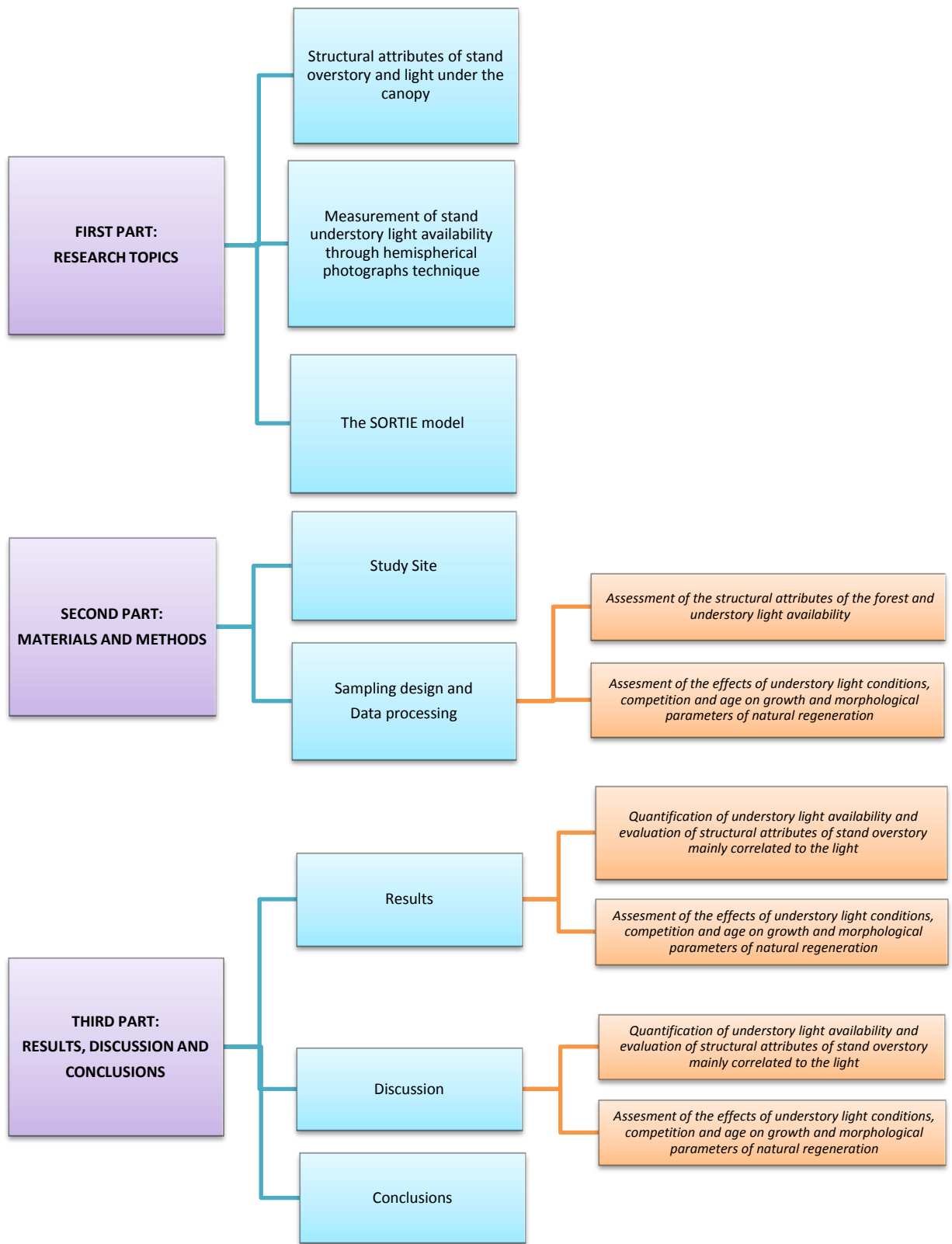


Fig 1: diagram showing the structure of thesis

The first part of the thesis (fig. 1) is composed of three chapters devoted to the deepening of three issues that were used to develop the main methodological aspects of the work. Each chapter is the results of bibliographic analysis, exchange of information with researchers working on the same topics, discussion with experts. They are also part of the output of the seven months of my PhD career I spent at the University of Quebec in Montréal in the laboratory of Professor Christian Messier, the summer school in “modeling forest complexity” and the training school in “studying mixed-forest dynamics and functioning: experimental and monitoring approaches” I attended,.

The three addressed topics are the following:

i) the “structural attributes of stand overstory better correlated to the light under the canopy”:

a detailed review of researches concerning the control of light through the manipulation of overstory structure was described. (Angelini et al 2014, in press).

ii) the “measurement of understory light availability through hemispherical photographs technique”: an overview about this technique was carried out since it was used during the sampling phase.

iii) the “SORTIE MODEL”: a spatially explicit forest model that makes population dynamic forecasts for juvenile and adult trees were; this part includes a description about model functioning, the potentiality and the tricky aspects of SORTIE, since some of the functions employed by the model, such as the allometric relationships describing the geometry of adult crowns and the growth-light function of regeneration were used in this work.

The second part of the thesis is dedicated to the forest where the study was realized and the methodological aspects of the investigation.

The microclimatic and soil conditions, forest type and management history are described to characterize the study area.

After a brief introduction about the periods in which field data were collected the chapter concerning the “sampling design” and “data processing” was divided in two sections:

a) materials and methods applied to the analysis of relationships between overstory structure and understory light conditions;

b) procedure for studying the influence of understory light availability on regeneration process.

The most relevant results are showed in the third part of the thesis, separated in two sections corresponding to those of “materials and methods” and were commented in the “discussion” chapter. Concluding remarks, suggestion and proposals concerning future research on the

addressed topics and the management strategies of complex forests are discussed in the last chapter.

FIRST PART: RESEARCH TOPICS

4. Structural attributes of stand overstory and light under the canopy

Over the last two decades several articles have been dedicated to the relationship between light availability in the understory and the main qualitative and quantitative attributes of stand overstory usually considered in forest management and planning (e.g., species composition, density, tree sizes, etc.) as well as their changes as consequences of harvesting. We reviewed (Angelini et al, in press) such literature with the aim of putting into evidence which are the most significant stand traits and management features to build more practical models for predicting light regimes in any forest stand and, in more general terms, to support forest managers in planning and designing silvicultural treatments that retain structure in different way in order to meet different objectives.

This chapter is divided in three sections: the first one reviews studies which investigated the influence of species composition on understory light conditions; the second part examines the relationships among stand parameters determined from dendrometric field data and the radiation on understory layer. Discussion and concluding remarks will be described on the third section.

4.1 Forest composition and understory light

Silvicultural practices manipulate overstory tree species composition, which represent the primary attribute of forest ecosystems affecting the variation of transmittance (Barbier et al. 2008).

Light transmittance considerably varies among tree species (Montgomery and Chadzon 2001) so that the relative proportion of some categories of species (deciduous or coniferous, shade tolerant or intolerant) in mixed stands may explain, at least in part, the spatial and temporal variability of understory light availability (Hart and Chen 2006, Barbier et al. 2008).

Shade intolerant species (both deciduous and coniferous) transmit more light than shade tolerant species, presumably because of thinner crown and thus higher crown openness. Shade tolerant species showed larger canopy depth, and consequently smaller light transmittance, as stand grow older (Canham et al. 1994, Messier et al. 1998, Messier et al. 1999, Beaudet et al. 2002, Coates et al. 2003, Le Francois et al. 2008). For example in mixed spruce–aspen stands (*Populus tremuloides*, *Picea glauca*), the higher the percentage of the shade tolerant spruce in the

overstory, the less light is transmitted to the understory (Lieffer et al. 1999); in *Picea abies*–*Fagus sylvatica* forests, spruce is less tolerant than beech, thus total cover decreases and understory light increases with its percentage in the overstory composition (Barbier et al. 2008).

However, not all studies came to the same results: Drever and Lertzman (2003), in coastal Douglas-fir stands that varied in abundance and distribution of retained trees after partial cutting of different intensity, found that species composition was only weakly related to the amount of light in the understory. In that case the higher canopy openness than in intact forests dominated by different species (Canham et al. 1994, Hunter et al. 1999) highlighted that in managed forests other structural features affect light availability in the understory. Among the crown properties of tree species, spatial arrangement of leaves, leaf angle distribution and leaf orientation, leaf size and (or) optical properties of leaves, play an important role in affecting overstory transmittance (Valladares and Pearcy 1999, Falster and Westoby 2003, Hardy et al. 2004, Gendron et al. 2006, Barbier et al. 2008). Leaf angle distribution found different applications related to light transmittance, such as for LAI and clumping estimation (Nilson 1999, Pisek et al. 2013).

In particular, angular distribution influences the probability of the transmission of a beam of light through a canopy (Nilson 1999, Monsi and Saeki 2005). Pisek et al. (2013) demonstrated that a planophile rather than spherical leaf angle distribution appears to be a more appropriate assumption for temperate and boreal broadleaf stands.

Aussenac (2000) showed that the inclination angle of leaves with respect to canopy thickness, for *Fagus sylvatica* and *Quercus petraea*, follows Beer's law, and also that beech adapts better to excess and very low radiation than oak. This type of tropism can also be seen in conifers.

In plants of chaparral vegetation, Valladares and Pearcy (1999) highlighted the influence of leaf orientation on the heterogeneity of the light environments; upper, south-facing leaves intercepted greater daily light than leaves of any other orientation.

For many coniferous species (ponderosa pine, Douglas fir and western hemlock), the distribution and arrangement of foliage on shade shoots can greatly increase light interception, and therefore photosynthesis in the lower canopy (Bond et al. 1999). Needle clustering and penumbral effects of small size leaf also affect light penetration, interception, and photosynthesis (Stenberg et al. 1999).

Variation of light resources in the understory environment might also be observed in relation to the leaf phenology due to the seasonality that differs among species (Gendron et al. 1998, Hart

and Chen 2006). Before leaf expansion, and following leaf senescence, deciduous canopies have much higher light transmission than all other stand types (Ross et al. 1986). Even for that reason deciduous forests are considered to have a marked seasonal light variability than evergreen forests (Gendron et al. 2001, Yirdaw and Luukkanen 2004).

Komiyama et al. (2001a) reported that differential overstory leaf flushing patterns contributed to the formation of a patchy understory. Also Kato and Komiyama (2002) found that the heterogeneity of light conditions that occurred in a deciduous broad-leaved forest in late spring resulted from the different timing of leaf flushing by different tree species. In particular, heterogeneity is the main cause of the patchy distribution of understory plants. Effectively, direct spring sunlight penetrating should result in a positive correlation in terms of spatial distribution between late-flushing trees and understory plants in the plot (Komiyama et al. 2001a).

In general, we can sustain that species specific attributes, such as crown structure, determine significant effect on the amount, quality and spatial variation of light transmittance (Yirdaw and Luukkanen 2004, Pretzsh et al. 2014) and consequently a simple but profound effect on forest succession (Canham et al. 1994, Canham et al. 1999). Crown depth (Canham et al. 1994, Beaudet et al. 2002, Beaudet et al. 2011, Ametzegui et al. 2012) and crown width (Canham et al. 1999) for example, higher in shade tolerant species, influences the ratio of PAR to global radiation inside the canopy (Ross and Sulev 2000).

Nevertheless, size and spacing of the crowns, or rather canopy openness, regardless of species, was of primary importance to the interspecific variation in openness of individual crowns, (Canham et al. 1999, Beaudet et al. 2002), revealing a good predictor of the below-canopy transmitted diffuse and global solar radiation in old-growth and uneven-aged evergreen forest (Promis et al. 2009).

The crown structure of a tree is even more crucial in mixed stands where different species demonstrate their abilities to acclimate their structures in order to benefit of the resources more efficiently or obstruct the access of competitors to the same resources (Pretzsch 2009, Bayer and Pretzsch 2013). A morphological plasticity may results in crown and canopy structures in mixed stands which differ considerably from those observed in pure stands.

Effectively, whether in pure stands all individuals compete with similar behavior for the growing space and resources involving a homogenization of canopy structure with low canopy depth and size-asymmetric competition (Grams and Andersen 2007), in mixed stands the complementarity

of species in terms of light ecology allow trees to have more canopy space to occupy without mechanical abrasion or penetration of neighboring crowns (Pretzsch 2014). However, the ability of trees to intercept light decreases with environmental stress (Waring and Schlesinger 1985). In general, light transmission is higher for species of boreal forests with their cold conditions than for species in warmer and wetter temperate deciduous forests or conifer forests of the Pacific Northwest (Lieffers et al. 1999).

4.1 Dendrometric attributes of stands and understory light

Understory light availability, frequently expressed as canopy openness (the proportion of the sky hemisphere not obscured by vegetation when viewed from a single point) (Jenning et al. 1999), is a measure of great utility to foresters since it can be used to guide the level of canopy manipulation necessary for successful natural regeneration.

Actually, while above-canopy light cannot be regulated by managers, understory light and its spatial distribution can be manipulated, at least in part, by controlling and shaping harvesting according to the overstory structure of a forest stand (Battaglia et al. 2002, Beaudet et al. 2011). Therefore, knowing the interplay between stand structure and light is fundamental for managing forests. An accurate description of allometric functions and their relationships with radiance would provide foresters of precious information for silvicultural decisions.

Several dendrometric parameters proved statistically significant predictors of whole season light availability in the understory (Drever e Lertzman, 2003, Barbier et al. 2008).

The four structural attributes best able to forecast light at the centre of circular plots in a coastal Douglas fir forest in British Columbia were stem density, volume of retained trees, summed DBH and summed height. The statistically significant and negative nonlinear relationships between understory light and those structural attributes (summed variables, e.g., total height), provided better predictive capacity than averaged attributes (e.g., mean height) because involved also tree density thus reflecting the total amount of structure able to intercept light (Drever and Letzerman 2003). However, the predictive capacity of these variables was much better for high light levels (> 50 % of full sun) than for low light levels (< 20 % of full sun).

Among stand structural attributes determined from readily available field data, those descriptive of density, such as DBH, basal area and number of trees, are usually the most considered in similar studies. In mixed spruce-aspen forests, DBH affects indirectly the transmittance since,

although the value change by less than 30% (Astrup and Larson 2006), as DBH and crown size raise species-specific crown openness decreases increasing the probability that leaves would intercept light (Canham et al. 1999).

Comeau et al. (2001) observed that in white spruce-aspen dominated boreal mixedwood stands with high initial tree densities, the decline in understory light levels is likely to occur more rapidly, resulting in the potential for substantial reductions in growth and survival of understory spruce due to competition for light and physical damage to spruce as a consequence of aspen mortality by self-thinning.

For stands less than 40 year old, basal area provides a useful general predictor of understorey light levels, although these results should not be extrapolated to older stands without carefully evaluating the possible difference of overstory structure and site conditions (Comeau et al. 2001). Unpublished results mentioned by Comeau and Heineman (2003) indicated that in a mixed conifer stand understory light levels can be predicted from basal area if separate coefficients are developed for each species. Regression models that better predict light availability from broadleaf and conifer abundance of young (10–40-year-old) paper birch stands were based on broadleaf basal area and included either conifer cover or conifer basal area. Broadleaf density alone was a poor predictor of understory light, but in combination with broadleaf quadratic mean diameter or height of the tallest broadleaf the models improved.

Consistent relationships between understory light levels and broadleaf basal area were found also in aspen forests for four biogeoclimatic zones (Comeau et al. 2006). Conifer basal area was tested as an independent variable, but was not significant in this analysis. The difference is likely due to the lesser presence of conifers in the aspen than in the birch sample plots. In contrast to results presented by Comeau (2001) and Comeau and Heineman (2003), Comeau et al. (2006) indicated that a logarithmic relationship fit the data better than an exponential equation.

Sonohat et al. (2004), in even-aged stands of Douglas fir, Norway spruce, larch and Scots pine, found a negative exponential relationship between light transmittance and stand basal area, which explained between 56% and 80% of transmittance variation according to the species, and 82% for all species pooled data. However, other variables added to the basal area, such as tree height, crown height, crown length/total tree height, height of the first green whorl, etc., can improve the prediction of transmittance.

A strong and clear relationship between basal area and canopy transmittance was found in Sitka spruce plantation as the stand was thinned, although it is the percentage of the original basal area retained that affect the light in the understory rather than the actual value which could be found also in closed canopy stands (Hale 2003). These results are supported by other studies carried out in Sitka spruce stands (Hale 2001, Page et al. 2001, Malcom et al. 2001), suggesting that a basal area $< 30 \text{ m}^2/\text{ha}$ is necessary to provide the minimum light requirements, i.e. 15% of incident light, for the growth of sitka spruce seedlings. However, some authors (Beaudet et al. 2011, Battaglia et al. 2002, Sprugel et al., 2009), showed that harvesting in a stand does not necessarily increase light transmission proportional to the reduction in basal area. In effect, the spatial arrangement of the residual trees (and hence the spatial pattern of harvest) also plays a very important role. Battaglia et al. (2002) demonstrated that increasing the aggregation of residual basal area, not only increases the mean stand level understory light availability but also increases the variation of light resulting in more heterogeneous understory light environments.

In old growth and second growth forests in lowland Costa Rica, Montgomery and Chadzon (2001) did not find strong relationships between measures of forest structure and light availability, although the strength of these relationships differed between forest types. In both the studied forests, understory light availability at 0.75 m decreased with increased sapling and shrub density, but was not significantly influenced by local tree density or basal area. Similar trends were found in an old-growth and uneven-aged forest of *Nothofagus betuloides* (Promis et al. 2009). However, by combining basal area, crown projection, crown volume, and stand volume, it was possible to explain a large amount of the variability of the below-canopy transmitted, diffuse and global radiation.

A study carried out by Valladares et al. (2006) in the holm oak (*Quercus ilex*) woodlands of the Western Mediterranean basin, characterized by low mean canopy height (2.4 m), high stem density ($14,500 \text{ stems ha}^{-1}$) and intermediate basal area, showed that canopy height exhibited a more significant correlation with understory light (particularly with indirect light), than stem density and basal area although only in the tree-dominated zone of the plot. However, since the potential of canopy height as a predictor of understory light was low due to the large fraction of unexplained variance, the incorporation of other canopy features (e.g. leaf angle distribution, leaf and branch clustering) would likely increase significantly the accuracy of the estimation of understory light based on canopy structure.

Results from a study by Heithecker and Halpern (2007) suggested that levels of light at the forest floor within aggregate retained trees can be surprisingly similar to those inside the forest; the aggregates significantly reduced PPFD (Photosynthetic Photon Flux Density) in the adjacent harvested area to distances of 10-30 m.

Therefore, it is evident that spatial aggregation or rather the spatial distribution of stem density for retained trees strongly regulates the abundance and spatial variation of light in the understory (Coates et al. 2003). Changes concern the quantity and quality of light, as well as its directionality, so that more of the forest floor receives direct solar radiation and sunflecks become longer and more intense (Lieffers et al. 1999; Gendron et al. 2001).

4.2 Discussion and conclusions

The numerous studies concerning the relationships between transmittance and structural attributes in forest stands carried out over the last two decades confirmed the great interest in predicting understory light conditions by using attributes readily available from field data. Different bioclimatic zones (boreal vs tropical), stands structure (plantation vs natural, even-aged vs uneven-aged, young vs old growth), species composition (pure vs mixed), and silvicultural treatments (clearcutting vs partial cutting) were taken into account in these studies. However, most of the research was carried out in boreal forests, likely because light was considered one of the most critical factors for successional dynamics in this environment.

On the whole, the results of the examined studies highlighted that different traits of forest overstory affect light intensity in the understory, even more in heterogeneous stands with continuous canopy cover. Composition, density and structure of overstory are the characteristics mainly correlated to light transmittance (Fig. 2).

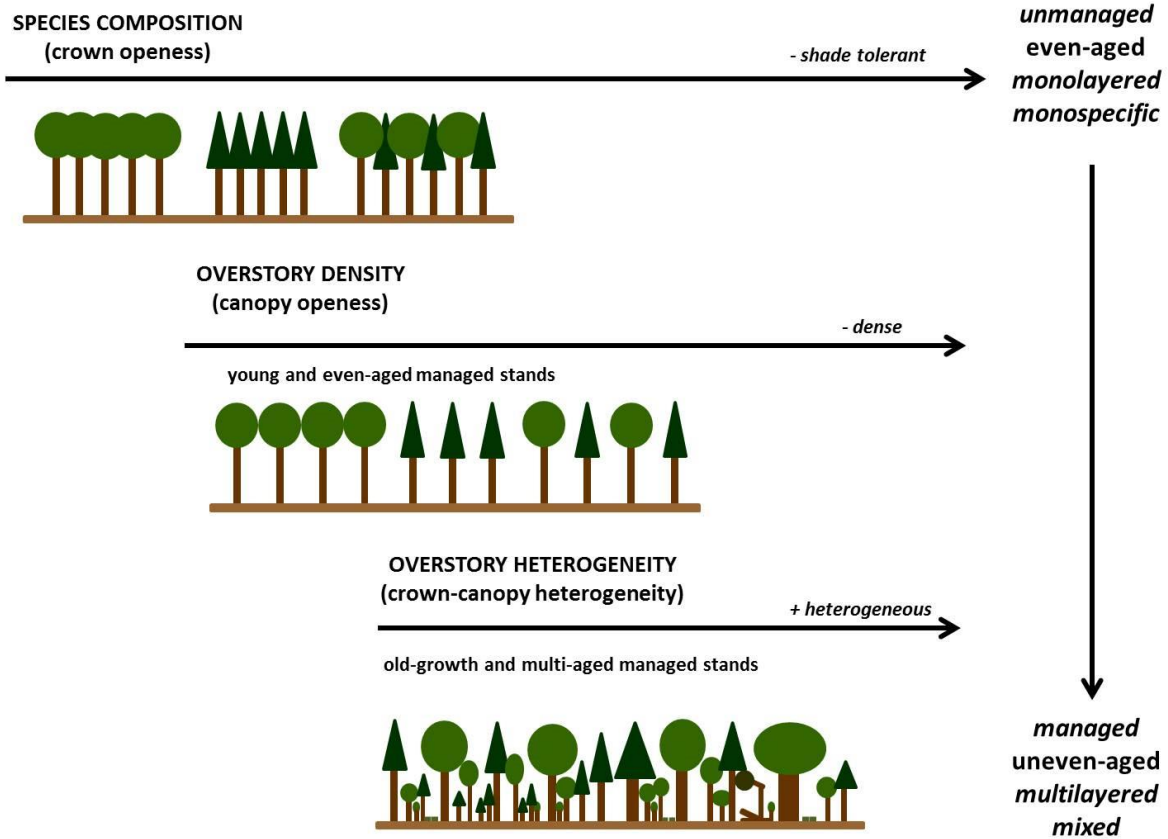


Fig. 2: main overstory characteristics affecting understory light of a forest stand according to the type of management and then the complexity of structure

The weight of each of them seems to depend on the degree of complexity of the stand. In even-aged, unthinned and monospecific stands with homogeneous canopy covers and regular spatial distribution of trees, understory light conditions much depend on species composition, or rather on specific traits of species such as shade-tolerance, which in turn is strictly linked with crown properties (depth, width, leaf angle distribution, etc.). In regular mixed forests, tree composition controls the amount of radiance under the canopy and the spatial and temporal distribution of light especially if evergreen and deciduous species or deciduous species with different phenology are a significant part of the mixture. In managed forests, canopy openness can be manipulated by cuttings changing stand density attributes. Among the latter, basal area demonstrated a prominent role in predicting light as long as understory radiation fall above 20% and especially in young stands. It is the percentage of the original basal area retained rather than the actual value which effectively influence light availability in the understory (Hale 2003, Coates et al. 2003),

highlighting that harvesting does not necessarily increase light transmission proportional to the reduction in basal area and that spatial arrangement of the residual trees plays a very important role (Beaudet et al. 2011, Battaglia et al. 2002, Sprugel et al. 2009).

For low average light levels typical of uneven-aged and old-growth forests, horizontal and vertical stand structure attributes need to be considered for increasing the accuracy of prediction. In such conditions, light transmission through canopy and the occurrence of patchy or homogeneous understory is controlled by the complex interplay of overstory composition, density and structure.

In conclusion, basal area can be viewed as the preferable light predictor for managing young stands with homogeneous structure. The experiences suggested considering additional parameters descriptive of tree size, such as DBH, height and volume, in order to increase the accuracy of light predictions in case of older stand or in presence of a layer of suppressed trees.

A different and more complex task is providing a significant estimate of radiation below canopy in stands characterized by heterogeneous vertical and horizontal structures. The few studies carried out until now didn't provide a clear overview of appropriate attributes for an accurate prediction of understory light in these types of forest structure. Therefore, considering the increasing importance of creating and maintaining stand structure heterogeneity through silvicultural treatments in order to enhance the resilience of forest ecosystems facing the global change, more research would be necessary to deepen this topic.

The continuous development of technologies is increasingly allowing their access to researchers and forest managers with relative low costs. The use of aerial and terrestrial LIDAR technologies (Aschoff et al. 2004; Danson et al. 2007; Maas et al. 2008) which is already extensively used for three-D analysis of forest stand structure, could represent in the future a valid solution for improving this type of studies and integrating field data with a more detailed information of canopy structure.

5. Measurement of stand understory light availability through hemispherical photographs technique

Several direct and indirect techniques, were developed for measuring light conditions within forest environments. While direct methods that measure light through use of quantum sensors or chemical techniques (Lieffers et al 1999) are rather labor intensive, time-consuming, destructive, and practical only in small areas (Bréda, 2003; Macfarlane et al., 2007c), indirect techniques measure light transmission through an estimation of canopy properties or gap fraction using optical ground-based instruments (Bréda, 2003; Cutini et al., 1998; Dufrêne and Bréda, 1995; Welles, 1990).

Among indirect methods, hemispherical photography has received an increasing attention over the last years. Since the 1970s, photography has been used to quantitatively describe the architecture and radiative regime of forest canopies. Hemispherical canopy photography traditionally has relied upon analog black and white or color films, and scanners to produce digital images for analysis (Frazer, 1997).

The change from traditional to digital hemispherical photography not only allowed to simplify image capture and time-processing (Macfarlane 2011), but also offered remarkable opportunities to improve image quality and contrast (Jonckheere et al. 2004) providing forest scientists with a practical alternative to traditional film photography (Frazer et al., 2001).

Nowadays hemispherical photography represents an inexpensive and widely used technique for characterizing plant canopies using upward looking photographs taken through an extremely wide-angle lens (fisheye lens) (Rich, 1990; Gendron et al., 1998). Photographs, provide estimates of near-ground solar radiation (Zou et al. 2007), leaf area index (Zhang et al. 2005), and microclimate below canopy (Van Pelt & Franklin 2000) by measuring the gap fraction (or its complementary: canopy closure).

After the image acquisition, which requires also ability for a correct exposure (Macfarlane et al 2011), the processing of photographs consists on more steps. Firstly the photographs need to be pre-processed, or rather converted into binary images comprising just “sky” and “non-sky” pixels.

The following phase, called “thresholding”, allows to correctly separate “sky” from “non-sky” selecting a radiometric threshold value. Because the “thresholding” process could be a source of

errors, some authors tried to identify an “optimal threshold” either through automatic (Nobis & Hunziker 2005, Macfarlane 2011) or manual approaches (Frazer et al. 2001).

Several commercial software packages have been developed and were used in a broad range of applications for processing hemispherical images: WinSCANOPY (Regent Instruments, Québec, Canada, Rich et al., 1993), SOLARCALC (e.g. Ackerly and Bazzaz, 1995), Winphot (ter Steege, 1997), HemiView (Delta-T Device, Cambridge, UK, e.g. Battaglia et al., 2002), Gap Light Analyzer (GLA) (Frazer et al., 1997; Frazer) and CIMES (Walter et al., 2003).

Some of the disadvantages of these software packages (GLA, HemiView) are based on the manual application of a visually selected threshold for the whole image, which has proven to be a source of inconsistency and error with variations dependent on the observer subjectivity, and time-consuming to apply to large numbers of images (Jokneere et al 2005).

A relative new fast, inexpensive, and simple to use, procedure for monitoring forests is a digital cover photography which in some situations could be an efficient substitute of digital hemispherical photography (Macfarlane et al 2007a, 2007b, Chianucci & Cutini, 2013). However, exposure and threshold settings continue to constitute the main sources of variation of such photographs. A promising alternative to digital cover and hemispherical photography, to overcome these problems seems to be the thermal canopy photography (Nolke et al 2014).

6. The SORTIE Model

In a context where exploring the impact of different type harvesting is of interest, especially in structurally complex and species-diverse forests, spatially explicit, individual-tree models are particularly appropriate (Canham et al., 1999; Beaudet et al, 2010).

Since the remarkably small amount of input data, SORTIE-ND (Pacala et al., 1993, 1996), a spatially explicit, mixed-species forest model that makes population dynamic forecasts for juvenile and adult trees and was used to explore and explain the consequences of a wide range of silvicultural strategies on forest dynamics (Coates et al 2003).

It was developed in the early 1990s for transitional oak-northern hardwood forests in the northeastern United States (Pacala et al., 1993, 1996). Afterwards, SORTIE has been parameterized and extensively modified to be adapted to the ecological conditions and species compositions of forests of different geographical areas such as Northern British Columbia (SORTIE-BC, Coates et al. 2003), Southern New Zealand (Kunstler et al., 2009) Spanish Pyrenees (Ameztegui and Coll 2011; Ameztegui et al. 2012). Basically, SORTIE consists of four sub-models (Fig. 3): light, growth, mortality and recruitment sub-model. The spatial distribution of trees in the forests determines both the spatial distribution of light (light sub-model) and the spatial distribution of new seedlings (recruitment sub-model). Spatial variation in light levels determines growth (growth sub-model), and growth rates are used to predict mortality rates (mortality sub-model), which in turn determine the distribution of trees at the beginning of the next time step (Coates et al, 2003).

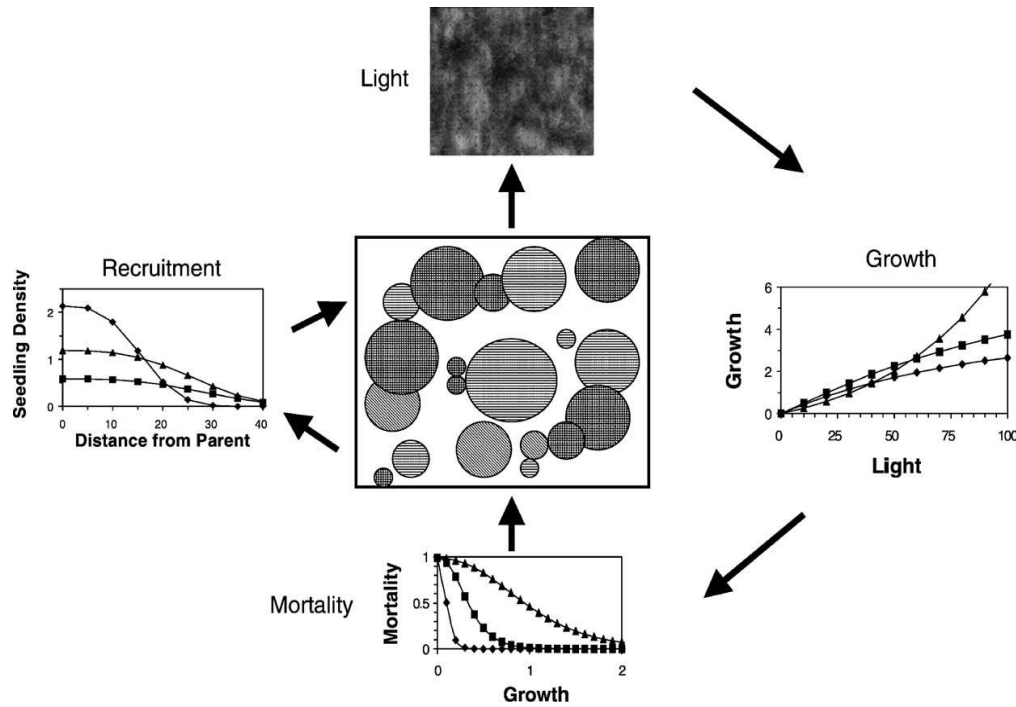


Fig. 3: Schematic diagram of the SORTIE-BC model (Coates et al, 2003).

I analyzed SORTIE-ND model version 7.01 (www.sortie-nd.org), which is based on the earliest SORTIE model (Pacala et al., 1996); SORTIE-ND is individual-based (the basic unit of data is a tree), spatially explicit (each tree has a unique location), dynamic (the model shows how a forest changes during a certain time span) and empirical (the model functions are fitted based on field data) (Tremblay et al., 2005). SORTIE can be used to simulate different silvicultural scenarios and to explore and explain the consequences of different resultant light conditions on the established regeneration growth and mortality. For the aim of this study light, growth and mortality sub-models were parametrized using data from the study area, while the recruitment phase (Ribbens et al, 1994) will be not considered.

6.1 Light model

Predicting light availability in forest understory is a key step in the modeling of forest dynamics. In SORTIE-ND, individual crowns of all the neighboring trees are modeled as cylinders and light are attenuated by a given factor for each crown it encounters (Boivin et al., 2011). Therefore, each tree must be defined by its location, DBH, crown geometry and Crown Openness (CO).

To define crown geometry for each species the following allometric relationships are used:

- tree height as a function of DBH:

$$\text{Tree height} = 1 + (\text{Max height} - 1.3) \left[1 - e^{(-b \text{ DBH})} \right] \quad (\text{eq. 1})$$

where DBH is in centimeters and tree height in meters; the Maximum height was determined as the average height of the 5% tallest trees for each species (Ameztegui et al, 2012); b is an estimated parameter.

- crown radius as a function of DBH and crown height as a function of tree height

$$\text{Crown radius} = c \text{ DBH}^d \quad (\text{eq. 2})$$

$$\text{Crown height} = f \text{ TH}^g \quad (\text{eq. 3})$$

where crown radius, crown length and TH (tree height) are expressed in meters and DBH in cm. c, d, f and g are estimated parameters (Beaudet et al., 2002).

Thus, all of the empirical functions needed to specify the dimensions of the crown can be estimated from readily available field data (e.g., Canham et al. 1994). Light interception by tree boles below the live crown is neglected (Canham C. D. et al, 1999).

Crowns of each species are assumed to have a species-specific canopy openness (i.e., fraction of sky visible through the crown).

Crown openness (CO) varies substantially among species (Beaudet et al., 2002; Le Francois et al, 2008). In general, shade-tolerant species present lower CO than shade-intolerant ones, which in part may explain their reported higher ability to intercept light (Valladares and Niinemets, 2008).

To determinate CO as described by Canham et al. (1999) it is necessary take pictures of the crown of every measured adult tree, selecting only undamaged individuals with regular crowns and with no signs of having developed free from competition (Boivin et al, 2011). The acquisition and determination of crown openness represent one of the main tricky process, although according to some authors CO has a low influence in forest understory light availability (Ameztegui et al 2012), while size, distribution and geometry of tree crowns are the most

important factors regulating spatial variation of understory light (Canham et al. 1999, and Beaudet et al. 2002).

For each individual, SORTIE simulates a hemispherical photograph and uses this simulated photograph to calculate GLI, i.e., the percentage of full light received by the tree (Canham et al 1988). The region-specific light parameters (Beam Fraction of Global Radiation; First and Last Day of Growing Season; Clear Sky Transmission Coefficient) that determine the local sky brightness and the seasonality to the local situation are adjusted.

The calculated light availability is subsequently used to determine the growth of the subject tree.

6.2 Growth Model

Growth is strongly influenced by light availability. Knowledge of the effects of variation in light on seedling and sapling growth has long been considered fundamental for understanding the successional dynamics of the forest and to calibrate models of forest dynamics (Pacala et al, 1994; Wright et al, 1998; Wright et al, 2000). The gradient of light conditions is obtained by selecting seedlings/saplings under a range of different regimes of light.

The growth sub-model consists of species-specific equations that predict radial growth from diameter and GLI (Pacala et al, 1994; Wright et al, 1998; Wright et al, 2000). Diameter is included as an independent variable simply because trees grow geometrically when are small (annual diameter growth increases linearly with diameter), and grow progressively slower than geometrically as they become large (Pacala et al, 1995). Obviously, GLI is included because of light limitation.

Both radial and apical growth might be modelled against light availability.

The relationship between growth and light availability was established using a Michaelis–Menten function, which is widely used for modelling tree growth (Pacala et al. 1994; Wright et al. 1998; Lin et al. 2002; Kunstler et al. 2005). According to this function, growth can be expressed as:

$$G = \frac{a*GLI}{\frac{a}{s}+GLI} size^d$$

where G is the growth of an individual of a given size at a light level GLI , while a and s are the parameters of the Michaelis–Menten function, which can be interpreted as asymptotic growth rate and slope at zero light, respectively. Size was defined as radius (in mm) in the case of radial

growth and as tree height (in cm) in the case of length growth, and d is a parameter that describes the changes in growth rate with tree size. To estimate the maximum likelihood parameter values, we used simulated annealing (Goffe et al. 1994).

6.3 Mortality model

The mortality sub-model includes an equation for each species that gives an individual's probability of mortality as a function of its rate of growth over the previous three years (Kobe et al 1995; Kobe et al, 1996; Kobe et al 1997; Wyckoff & Clark, 2002). Implementing this method requires the growth rates of live and recently dead saplings, together with an estimation of annual mortality rate. Growth rates of living saplings are obtained from the sample collected for growth–light relationships. To obtain the growth rate of dead saplings, the recently dead saplings of each species are randomly harvested from transects, and growth rate was obtained using the method given above for living saplings.

6.4 Recruitment model

Recruitment, the addition of new individuals into a community, is an important factor that can substantially affect community composition and dynamics (Ribbens et al 1994). Spatial distributions of recruits in SORTIE are predicted using the species-specific functions based on parent tree proximity, size and abundance and on the abundance and suitability of seedbed substrates. The equation is characterized by three components: the seed production, dispersal and establishment. Seed production is a function of both seed size (mean mass per seed) and plant size (basal area or leaf mass) (Ribbens et al 1994; Greene and Johnson 1998); in particular seed production is highly and inversely correlated with the mean seed mass and directly proportional to tree size. Clearly seed dispersal patterns, although poorly documented because hard to track (Hirsch et al 2012), are a critical component of spatial variation in plant seedling recruitment.

There are a number of methods available for determining individual dispersal curves (Greene & Calogeropoulos 2002), but SORTIE conventionally consider a wind dispersal assuming a Weibull distribution of seeds, which also depend on parent trees proximity.

To complete the recruitment phases, fundamental is the survivorship of seeds which depend on the proportion of seeds that survive on favourable substrate and those that survive on a no-favourable substrate (Greene and Johnson 1998).

SORTIE-ND model could be a good support to explore and explain the consequences of a wide range of silvicultural strategies on light distribution and then on established regeneration growth (Coates et al 2003).

SECOND PART: MATERIAL AND METHODS

7. Study site

The study was performed in the Italian eastern Alps (Cinte Tesino, Trentino, 46°3'0"N, 11°37'0"E) (fig. 4) in a mixed multi-aged forest dominated by silver fir (*Abies alba* Mill.) and Norway spruce (*Picea abies* L.) with an underlayer of beech (*Fagus sylvatica* L.). Natural regeneration of fir and spruce was abundant and well spread in patches. Two forest compartments (ID 29 and 31) have been selected, the first one East oriented and the second one North-East oriented, both on average at 1100 m above sea level. The parent rocks are calcareous with midly deep and “podzolic black” soils. Mean annual temperature ranges between 8,9° C and 7,3°C and the average annual rainfall ranges between 1100 and 1400 mm, with high snow permanence during the winter until the spring time.

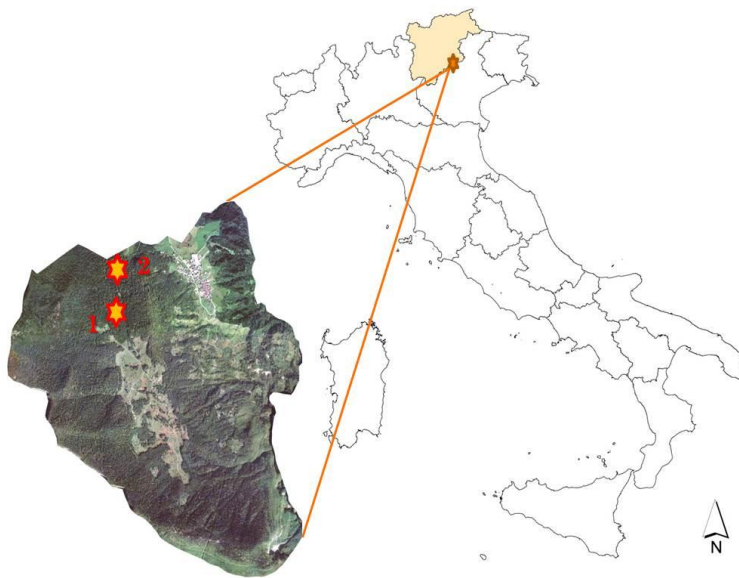


Fig. 4: localization of study area

Until the end of Second World War, the whole area was intensely exploited to face the high demand of wood from local community. Management based on clearcuts with brief rotations had strongly damaged and depleted these forests, since harvested volume was higher than the ability of forest to supply wood. Since the fifties, forest planning strategy have changed aiming at gradually increasing the growing stock of stands by reducing the allowable cut under the increment of volume. Thus, during the past 50 years, the area has been managed with silvicultural

systems ranging from irregular shelterwood to single-tree or group selection cutting. Beech, instead, has been managed as coppice to produce firewood for the local communities until recent years when conversion of beech stumps into high forests has started.

Currently, the structure is characterized by vertical and horizontal heterogeneity with small and large gaps and a fine scale mosaic of cohorts of trees. The low browsing pressure of ungulates and the favorable site conditions allows the natural regeneration to establish and grow-up.

8. Sampling design and data processing

8.1 Assessment of the structural attributes of the forest and the understory light availability within the stands

- *Field survey*

In each forest compartment understory light availability and stand attributes were sampled in a square plot of 50x50 m (Plot 1 and Plot 2) (fig.5a).



Fig. 5: delimitation of square plots (a) and measurement of stand attributes by field-map (b).

The topographic position of all trees higher than 40 cm was recorded through a FIELD-MAP instrument (fig. 5b). The following attributes were measured on each mapped tree with diameter at breast height (DBH) larger than 10 cm: DBH, total height (H), crown base (CB), crown depth (distance between the top of the tree and the base of the crown, being the base of the crown defined as the lowest point where foliage is found on non-epicormic branches, CL) and crown radius (CR). A core was extracted at an height of 1.30 m above ground from 30 adult trees (15 from silver fir and 15 from Norway spruce) to determine the age.

Light availability was measured by hemispherical photographs taken at 1 m above-ground by a systematic sampling along the 2 diagonals of each plot, for a total of 12 light measurement points for each plot. Circular subplots with radius equal to 8 m and centered on each light measurement point were extracted from the stand map layer by using ArcGIS 10.0 software.

- *Data processing*

The stand structural attributes, such as species composition, number of trees for DBH classes, basal area, were estimated.

Age of the adult stand was determined by the cores using the microscope connected to the *Computer Aided Tree Ring Analysis System* software (CATRAS) (R. W. Aniol, 1983).

Three allometric equations were used to define crown geometry for each overstory species: (i) tree height as a function of DBH (eq. 1), (ii) crown length as a function of tree height and (eq. 2) (iii) crown radius as a function of DBH (eq. 3) (see chapter 6). To predict tree height as a function of DBH was used a nonlinear exponential curve that saturates at a maximum height (Canham et al., 1999; Beaudet et al., 2002). All trees sampled within the two plots were used for building up the equations.

Total transmittance expressed as a percentage of full light, was computed by analyzing the hemispherical photographs through Gap Light Analyzer 2.0 software (Frazer et al., 2000) (fig.6).



Fig. 6: phases of hemispherical photographs analysis

A pairwise comparison of each measured structural attributes and light was performed to test the differences between the two plots, using the Mann-Whitney *U-test* (Harding 1984), a non-parametric test suitable for non-normal or unknown distributions and for small samples.

Relationships between understory light availability and forest structure has been firstly examined by using a linear pairwise correlation analysis among each structural attributes and total transmittance. The following structural attributes were considered: number of trees (N), DBH, basal area (BA), total height (H), CB, CL, distance from trees to measurement light point (Distance), normalized standard deviations of height (Std H), crown base (Std CB) and crown length (Std CL). Besides the classic attributes usually available from inventory data (N, DBH,

BA, H) and applied in many researches to predict light in the understory (see chapter 6; Angelini et al., in press) other parameters expressing crown geometry and the vertical variability of overstory were taken into account.

Since a simple pairwise correlation is not able to consider the influence on understory light availability of the whole set of the structural attributes, a Principal Component analysis (PCA) was also performed to exclude eventual intrinsic interactions among attributes and for studying them simultaneously.

Principal Components (PCs) were then correlated with transmittance.

8.2 Assessment of the effects of understory light conditions, competition and age on growth and morphological parameters of natural regeneration

8.2.1 Determination of radial growth, slenderness index and understory light availability (seedlings sample 2012)

- *Field survey*

For the aim of this study, I considered as established regeneration the trees with height ranging from 30 cm to 200 cm.

The effect of light on radial growth was estimated for 104 individuals of silver fir and 50 of Norway spruce chosen within the 2 forest compartments. The samples were selected (fig 7a) taking into account the following criteria:

- i. keeping a different understory light gradient as well as different overstories crown canopy cover;
- ii. keeping all height classes of seedlings (from 30 cm to 200 cm);
- iii. favouring the easy accessibility of the measurement points. The ground should not be rugged to allow the easy positioning of the hemispherical camera tripod.



Fig. 7: seedlings selection (a) and measurement of light availability above seedlings (b)

Light conditions (total transmittance %) above the top of seedlings were assessed taking hemispherical photographs (fig. 7b) in three different periods of summer 2012 (July, August and

September). Measurements of light availability on 50 recently dead individuals of Norway spruce (the criterion used to consider an individual as “recently dead” was twig suppleness and the maintenance of some needles), were also collected to investigate the range of light conditions where that species can survived or died. Any sample of dead silver fir was not instead found. The selected seedlings (live and dead) were harvested at the end of the growing season (October 2012) and a cross section of stem at height of 10 cm was cut (fig. 8a).

- *Data processing*

The width of the three most recent annual rings was measured on each cross section using the microscope connected to the *Computer Aided Tree Ring Analysis System* software (CATRAS) (R.W. Aniol, 1983) (fig. 8b). After that, the effect of light availability on radial growth (see chapter 8.2.2) and slenderness index was estimated.



Fig. 8: seedlings harvesting (a) and measurement of annual rings width on cross section of seedlings (b)

8.2.2 Determination of growth, crown morphology, intraspecific competition and understory light availability (seedlings sample 2014)

- *Field survey*

To study the possible interaction between light availability and competition on growth and crown and shoot morphological parameters (Grassi and Giannini 2005) in summer 2014, 59 individuals (30 Norway spruce and 29 silver fir), ranging in height from 35 to 200 cm and chosen with the same criteria indicated in the previous paragraph but considering only subjects having healthy leaders.

Light above the top of individuals (total transmittance %) was detected with the same procedure of the 2012 survey.

Also in this case, the selected seedlings were harvested at the end of the growing season a stem cross section at 10 cm height was cut.

Competition within natural regeneration was estimated using a method similar to that developed by (Duchesneau et al 2001). A circular area 1.13 m radius surrounding the sample tree was delimited and only competing individuals located inside were taken into account. After dividing the circular area in four quadrants, the following parameters were measured: the total height of the selected seedling (H_s), the percent surface covered by competing saplings in quadrant j (C_j), the mean height of competing saplings in quadrant j (H_j) and the mean distance between the competing saplings in quadrant j and the sample tree (D_j).

- *Data processing*

Growth of the selected individuals was assessed by: a) the radial growth (the width of three most recent annual rings); b) the relative height growth (RHG, length of the apical leader divided by total height). Crown morphology was estimated by calculating the apical dominance ratio (ADR, length of the apical leader divided by the mean length of the healthy lateral shoots at the last node) and the live crown ratio (LCR, live crown depth divided by total height express in percentage) (Williams et al 1999, Grassi and Giannini 2005).

The width of the 3 most recent annual rings and the age of a sample of seedlings were estimated by using the microscope connected to the *Computer Aided Tree Ring Analysis System* software (CATRAS) (R. W. Aniol, 1983). The number annual rings were also counted to estimate the age of each sampled tree.

The competition index was determined, as follows (Duchesneau et al. 2001):

$$I = \frac{1}{H_s} \frac{1}{4} \sum_{j=1}^4 \frac{C_j H_j}{D_j}$$

where:

H_s represents the total height of the selected seedling, C_j the percent surface covered by competing saplings in quadrant j , H_j the mean height of competing saplings in quadrant j , and D_j the mean distance between the competing saplings in quadrant j and the sample tree.

A *t-test* was performed to test the differences in terms of growth, morphological parameters, light and competition index between the two species.

- *Effect of light availability on growth and slenderness index*

The relationship between growth and light availability was established using a Michaelis–Menten function, which is widely used for modelling tree growth (Pacala et al. 1994; Wright et al. 1998; Lin et al. 2002; Kunstler et al. 2005).

According to this function, growth can be expressed as:

$$G = \frac{a \times L}{a + L} \text{size}^d$$

where G is the growth (radial or height) of an individual of a given size at a light level L (% of total transmittance), while a and s are the parameters of the Michaelis–Menten function, which can be interpreted as asymptotic growth rate and slope at zero light, respectively. Size was defined as radius (in mm) in the case of radial growth and as tree height (in cm) in the case of length growth, and d is a parameter that describes the changes in growth rate with tree size. To estimate the maximum likelihood parameter values, we used simulated annealing (Goffe et al. 1994). A series of alternate models were fitted to each data set. The simplest model (null model) only considered the effect of size on tree growth, and was used to assess the influence of light availability on growth. We also fitted a linear model to the data available for each species. The R^2 of the observed versus predicted regression was used as a measure of goodness of fit of each model, and alternative models were compared using ΔAICc , the difference in corrected Akaike information criterion (Burnham & Anderson 2002).

The effect of light was also assessed for the slenderness index (ratio between height express in cm and diameter express in mm)

To highlight possible influence of tree size, the linear and non-linear functions were applied also to sub-datasets characterized by seedlings with height greater than 1 meter and those with height lower or equal to 1 meter.

- *Effect of light, competition and age, on growth and crown morphology*

The relationships of radial growth, relative radial growth, height growth, relative height growth (RHG), ADR, LCR with light availability, the competition index and age were analyzed.

Furthermore, a relationship between light availability, competition index and age was performed.

THIRD PART:
RESULTS, DISCUSSION AND CONCLUSION

9. Results

9.2 Quantification of understory light availability and evaluation of structural attributes of stand overstory mainly correlated to the light

9.1.1 Stand structure and understory light conditions

- Dendrochronological history of overstory trees

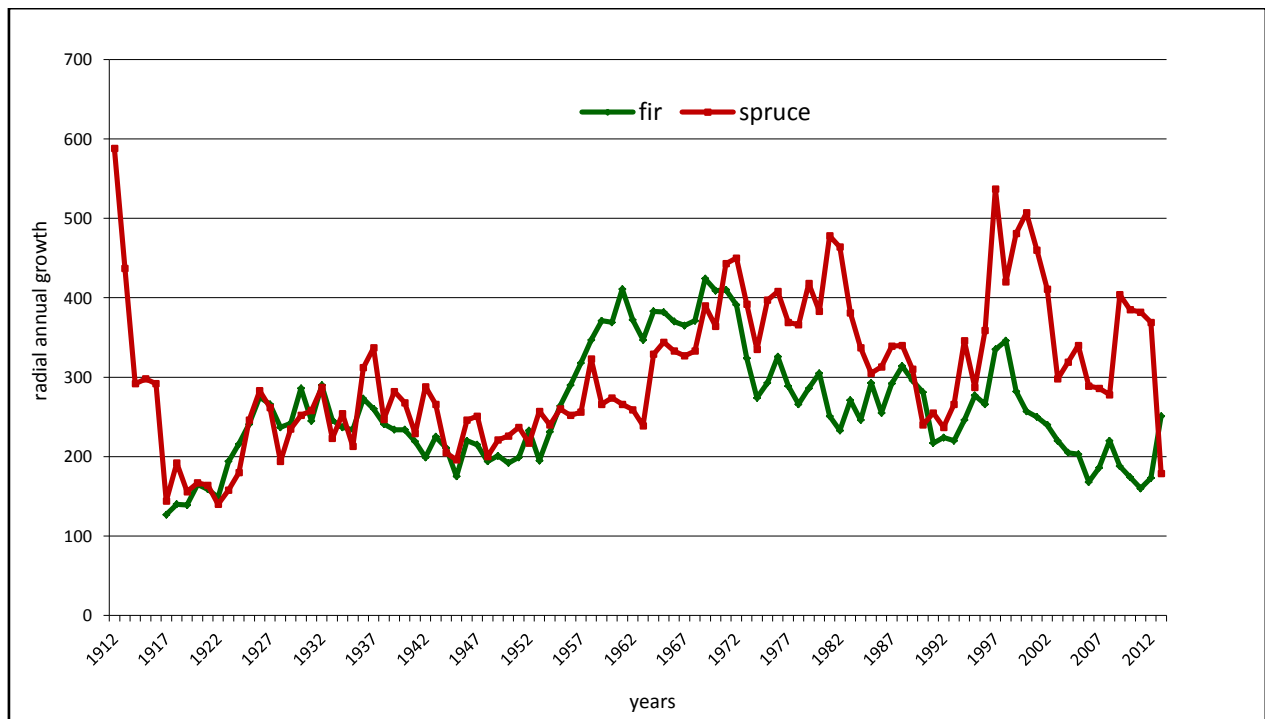


Fig. 9: Annual radial growth trend (express as millimeter*100) of adult trees of silver fir and Norway spruce

Adult stand of silver fir and Norway spruce showed significant similar annual growth tendency over the time (fig. 9), although with different age. On average spruce is 100 years old and is 5 years older than fir.

- **Stand structure, crown geometry and understory light conditions**

Table 4 lists the main stand attributes.

The total number of trees is 396 per hectare for plot 1 and 420 per hectare for plot 2 and the total basal area is 50.14 m² and 53.75 m², respectively, for plot 1 and plot 2. The bar graphs (fig. 11) show the dominance of Norway spruce in term of basal area. Two stories could be basically identified in both plots (fig. 12): beech and Norway spruce characterize, respectively, the understory and the over-story of the adult stand; whereas, silver fir covers almost all tree size classes.

The Mann-Whitney *U*-test (*MW*) showed no significant differences between the two plots for stand attributes except for the crown base (CB) (table 5).

Nevertheless, examining species by species significant differences ($p < 0.05$) between plots were found in silver fir for crown length and height, in Norway spruce for crown radius, DBH, H and crown base, and in beech for crown length, and crown base.

The prevalence of spruce regeneration in the plot 1 (fig. 13a) and fir regeneration in the plot 2 (fig. 13b) doesn't coincide with the adult dominance of the same species expressed above.

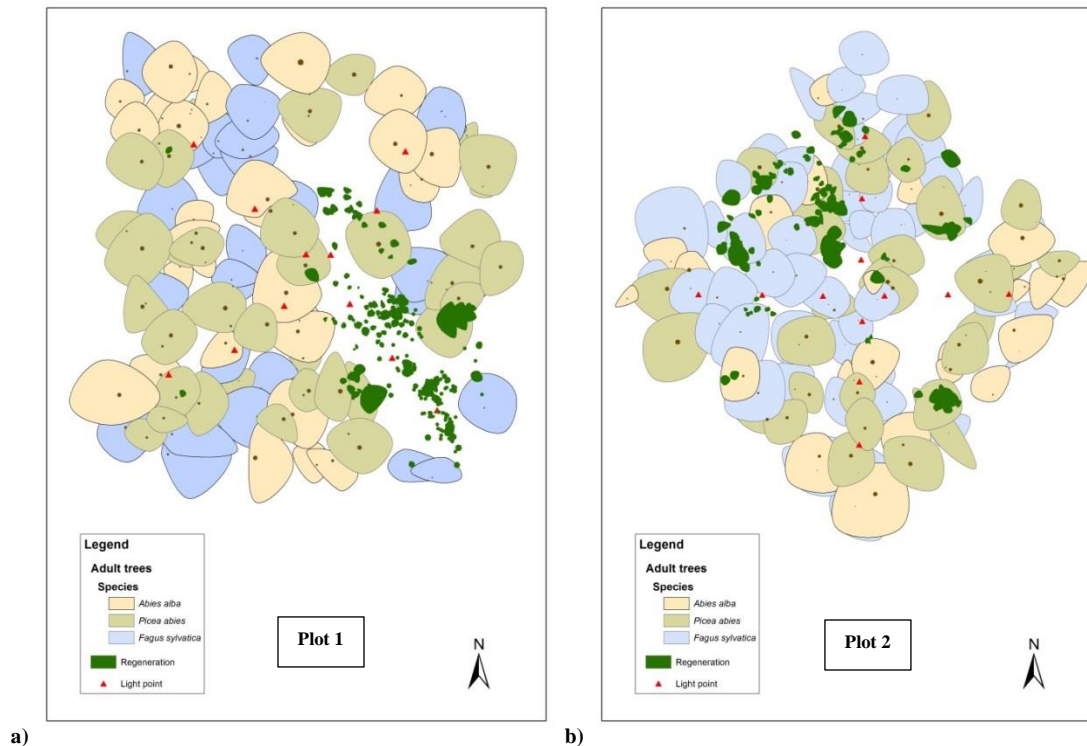


Fig. 10: Tree position and crown projection map of plot 1 (a) and 2 (b)

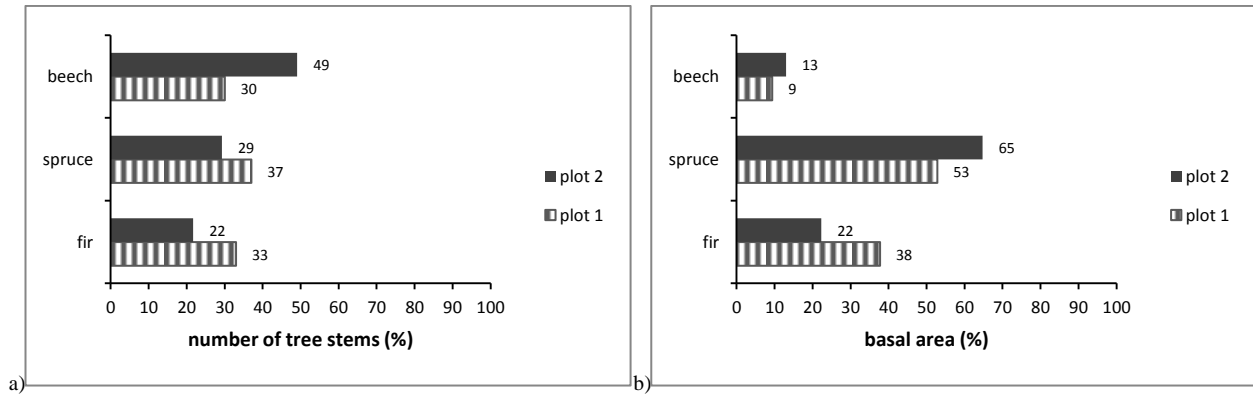


Fig. 11: Percent distribution by species of number of tree (a) and basal area (b).

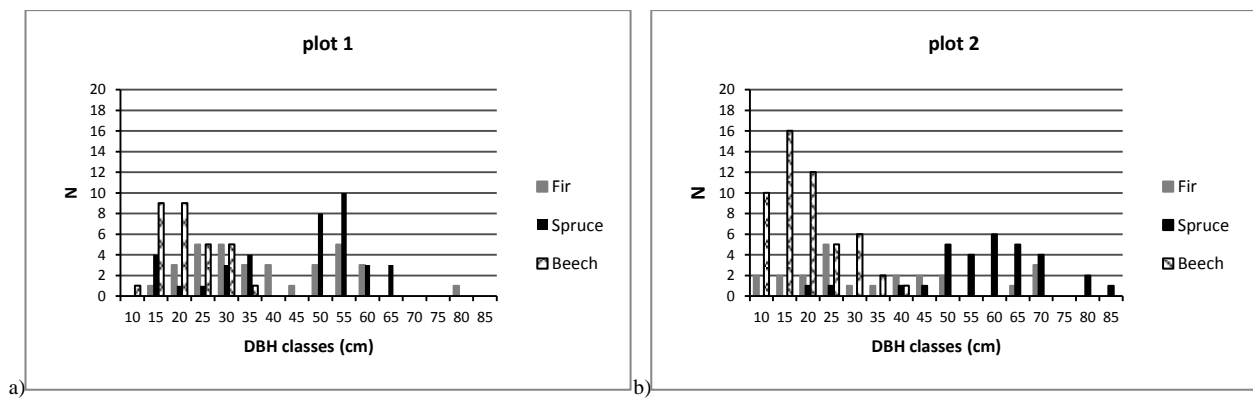


Fig. 12: Frequency distribution of trees (N ha ha⁻¹) by diameter class and species.

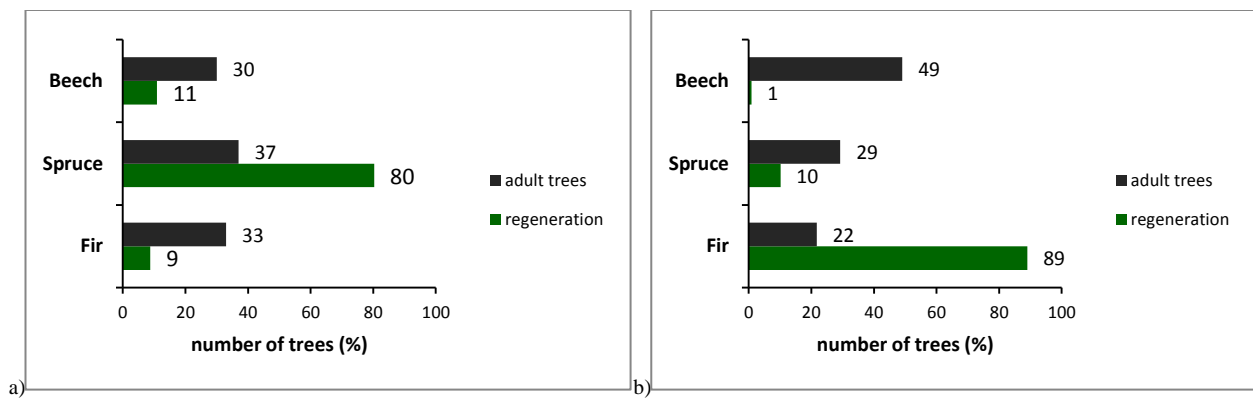
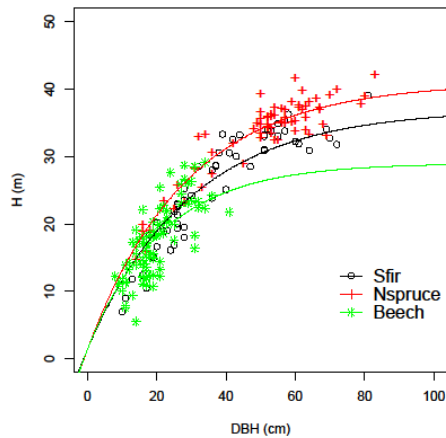


Fig. 13: Percentage of number of adult trees and regeneration by species in plot 1(a) and plot 2 (b).

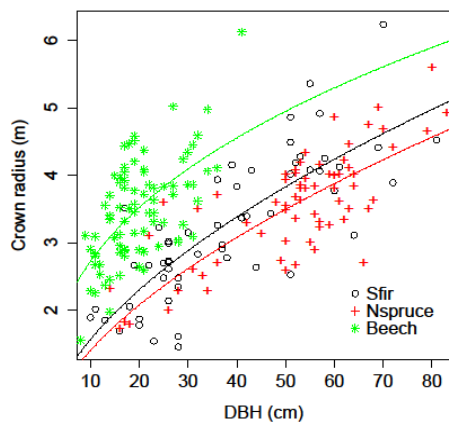
As shown in the figure 14 and table 1 spruce had the highest predicted height and beech and spruce rapidly reach the asymptotic maximum height (highest b value), whereas fir had the lower slope. Moreover, beech and fir have wider and deeper crowns than spruce (fig. 15 and tab. 2; fig 16 and tab. 3).

Differences between the two conifers were weak and no significant, nevertheless silver fir showed on average the higher value of crown length for tree height lower than around 35 meters.



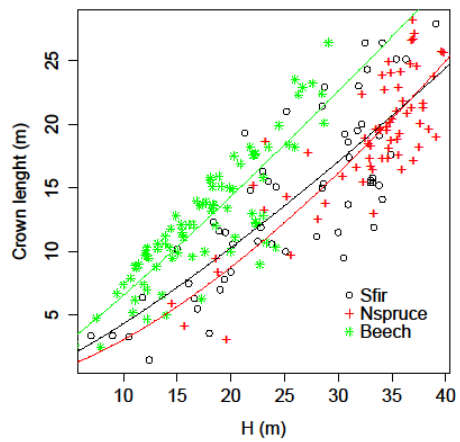
Species	n	par	estimate	Std. Error	p	R ²
fir	56	<i>b</i>	0,0339	0,0011	<2e-16	0,87
spruce	68	<i>b</i>	0,0349	0,0008	<2e-16	0,87
beech	82	<i>b</i>	0,0466	0,0019	<2e-16	0,57

Fig. 14 and tab. 1: Tree height as a function of dbh: estimate of parameters (par) of equation 1



Species	n	par	estimate	Std. Error	p	R ²
fir	56	<i>d</i>	0,4315	0,1017	8,75E-05	0,63
		<i>e</i>	0,5577	0,0622	2,83E-12	
spruce	68	<i>d</i>	0,3759	0,0968	0,00024	0,62
		<i>e</i>	0,5697	0,0642	7,29E-13	
beech	82	<i>d</i>	1,1499	0,1965	1,03E-07	0,36
		<i>e</i>	0,3728	0,0560	3,22E-09	

Fig. 15 and tab. 2: Crown radius as a function of dbh: estimate of parameters (par) of equation 2.



Species	n	par	estimate	Std. Error	p	R ²
fir	56	<i>f</i>	0,2489	0,1388	0,0785	0,64
		<i>g</i>	1,2436	0,1641	4,77E-10	
spruce	68	<i>f</i>	0,0964	0,0550	0,084	0,70
		<i>g</i>	1,5068	0,1599	7,81E-14	
beech	82	<i>f</i>	0,4976	0,1223	0,00011	0,74
		<i>g</i>	1,1224	0,0812	<2e-16	

Fig. 16 and tab. 3: Crown length as a function of Height (H): estimate of parameters (par) of equation 3

Species	Structural attribute	Plot 1				Plot 2			
		mean	min	max	std dev	mean	min	max	std dev
spruce	N	37				31			
	DBH (cm)	45.2	14	67	15.7	58.3	22	83	13.6
	Height (m)	31.2	14.5	37.3	6.7	35.3	23.2	41.9	4.2
	CrownBase (m)	13.2	7	19.6	3.1	15.1	4.7	20.4	3.5
	Crown_Lenght (m)	18.0	3	28.1	6.1	20.3	9.6	32.7	5.0
fir	N	33				23			
	DBH (cm)	39.8	13	81	15.8	36.0	10	72	19.4
	Height (m)	27.7	11.8	39.1	6.7	22.7	7	34.1	8.7
	CrownBase (m)	10.9	2	21	4.9	12.0	3.6	21.4	4.6
	Crown_Lenght (m)	16.8	6.4	27.9	5.9	10.7	1.5	24.3	6.0
beech	N	30				52			
	DBH (cm)	21.4	8	36	6.7	19.4	9	41	7.2
	Height (m)	17.7	9.4	26	4.7	17.5	5.5	29.1	5.9
	CrownBase (m)	6.6	2.1	13.9	3.3	4.2	1.9	10	2.0
	Crown_Lenght (m)	11.1	4.7	19.9	3.9	13.4	2.5	26.4	5.4
whole stand	N	100				106			
	DBH (cm)	36.3	8	81	16.9	34.4	9	83	20.9
	Height (m)	26.0	9.4	39.1	8.3	23.9	5.5	41.9	9.8
	CrownBase (m)	10.5	2	21	4.7	9.1	1.9	21.4	5.8
	Crown_Lenght (m)	15.5	3	28.1	6.2	14.8	1.5	32.7	6.5

Tab. 4: Statistics of the stand attributes

Plot 1 (n=100)	Statistics	CR	DBH	H	CB	CL	BA	Plot 1 (n=12)	Statistics	Total Transmit
vs	U	1.0 10 ⁴	1.1 10 ⁴	1.1 10 ⁴	1.110 ⁴	1.1 10 ⁴	0.9 10 ⁴	vs	U	198
Plot 2 (n=106)	P	>0.05	>0.05	>0.05	0.023	>0.05	>0.05	Plot 2 (n=12)	p	0.006

Tab. 5: Mann Whitney U test (U) between plots for structural attributes and total transmittance.

Transmittance resulted significantly different between plots (tab. 5). Plot 1 showed higher mean light conditions, as well as the maximum light variability (fig. 17) ranging between 4.4 and 52 %. Weaker variation of understory light conditions in plot 2 (from 8.5 to 25%) is likely due to the

absence of as much gaps as in plot 1 (fig. 10a) and to the more diffuse intermediate layer of beech (fig. 12b), which ensure a more homogeneous transmittance.

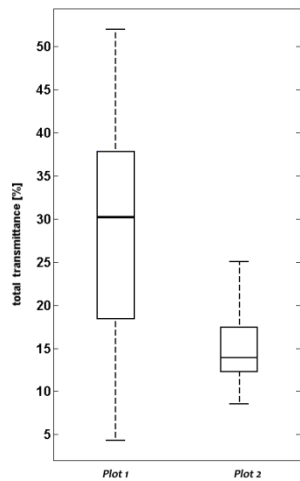


Fig. 17: Box plots of light transmittance in the two plots

- *Relations among understory light and forest structure*

Some attributes of forest structure proved to be statistically associated with light availability in the understory (fig. 18). According to the pairwise correlations, N ($r=-0.79$) and BA ($r=-0.65$) are the dendrometric attributes with the closest association with the light, although the single plots showed evident differences in Pearson coefficients. Standard deviations of crown length, of crown base and of tree height also are significantly associated with transmittance (respectively, $r=-0.51$, $r=-0.57$ and $r=-0.47$). However, three subplots fell in points of the stand where only regeneration layer or only one tree were present, then structural attributes and standard deviations were equal to zero, so those correlations resulted strongly affected by those subplots.

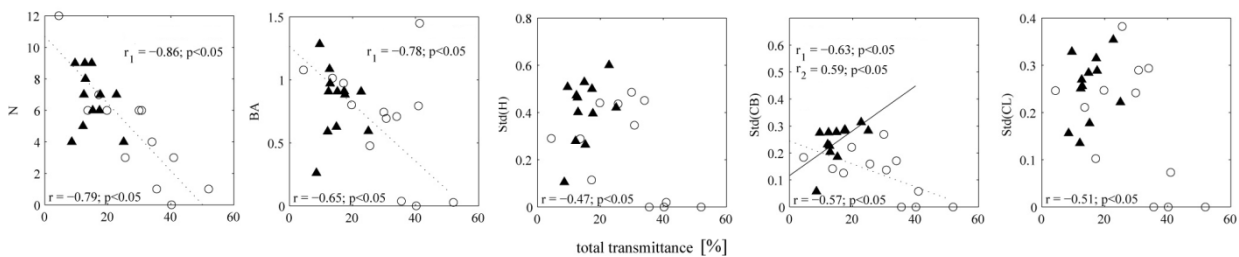


Fig. 18: relationships between structural attributes and total transmittance. White circles and dotted line: data and regression line of subplots 1; black triangles and black line: data and regression line of subplots 2. r : Pearson correlation coefficient of the whole dataset (subplots 1 plus subplots 2). r_1 and r_2 : Pearson correlation coefficients of subplots 1 subplots 2

According to the PCA, the first 2 components explained the 80.7% of the total variance, a high percentage of the whole system. Since PC3 explained less than 10% of the variance, only PC1 and PC2 can be taken into account. Figure 19 shows how attribute vectors are displayed on the two dimensional space, their reciprocal influence (according to the parallelism/perpendicularity and the direction of the lines) and the influence on the two first components, as confirmed by the listed coefficients in the table 6.

ATTRIBUTES	PC1 w	PC2 w
N	0.30	-0.03
DBH	0.17	0.42
CB	0.24	0.34
H	0.19	0.44
CL	0.13	0.44
BA	0.38	0.18
D	0.01	0.25
Std(H)	0.46	-0.34
Std(CB)	0.47	-0.26
Std(CL)	0.43	-0.18
% of explained variance	63.4	18.4
% Cumulative variance	63.4	80.7

Tab. 6: Coefficients, explained variance and cumulative variance of the two first components of PCA

PC1 explains more than half of the variance of the system. The structural attributes better correlated with PC1 were the three standard deviations (StdCL, StdCB, StdH). BA and N show only a moderate correlation.

Correlation between the PC1 and total transmittance (fig. 20) shows a good Pearson coefficient (-0.63). These results highlight that standard deviations of H, CL and CB, expressive of the variability of stand profile, play a significant role in determining understory light availability, more than N and BA, attributes that in similar studies carried out in even-aged and more homogeneous forest stands resulted highly significant.

DBH, CL and H show higher correlation with PC2. Furthermore, the strong relationships and vectors proximity of these parameters (fig. 19), particularly DBH and H, confirmed by their Pearson coefficient, suggest these attributes might be interchangeable in this kind of analysis. Subplots 1.11, 1.12 and 1.11 show an abnormal behavior with respect to the others, more uniformly clustered (fig. 19); these subplots fell in those points of the stand where only regeneration layer or only one tree was present, therefore structural attributes and standard deviations were equal to zero and we can suppose the total transmittance was affected by nearby trees just outside the subplots.

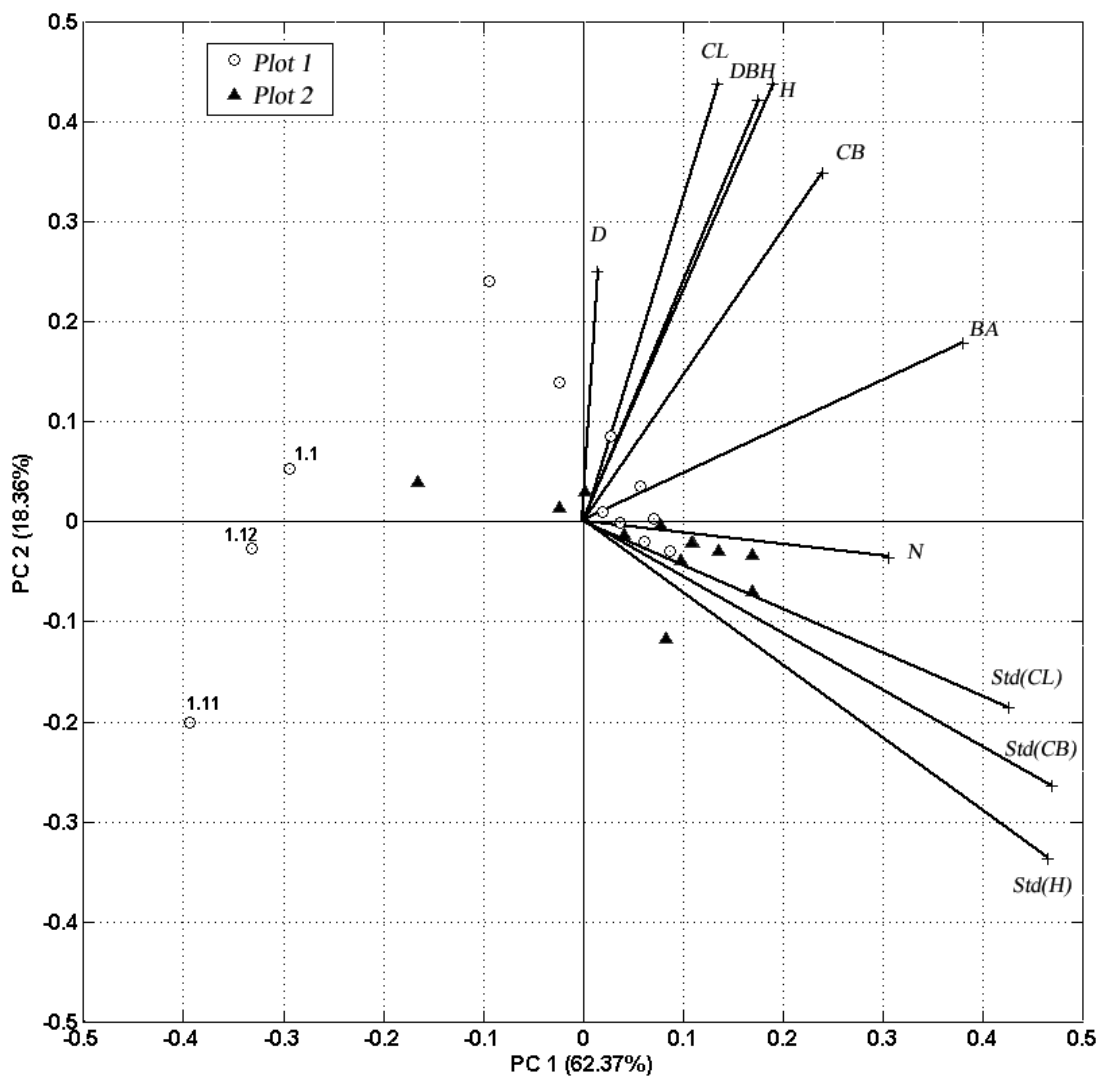


Fig. 19: PCA analysis: the direction and length of vectors indicate how each parameter contributes to the first two PCs. Parallel vectors are positively (same sign) or inversely (opposite sign) correlated to each other, orthogonal vectors are uncorrelated; scatter points: the transformed variable values. Symbols and color as in fig. 18

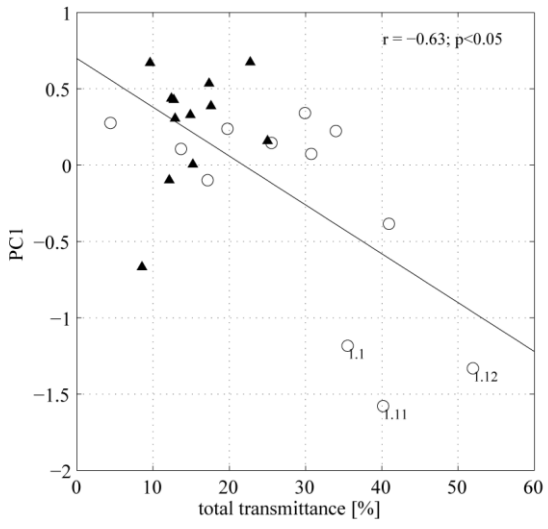


Fig. 20: Relationships between principal component 1 and light transmittance. White circles: subplots 1; black triangles: subplots 2

9.2 Assessment of the effects of understory light conditions, competition and age on growth and morphological parameters of natural regeneration

9.2.1 Effect of understory light availability on radial growth and slenderness index (seedlings sample 2012)

- *Light and growth estimation*

Significant ($p < 0.05$) differences between the two species were found for light conditions of sampled seedlings. Spruce on average grows at higher light conditions than fir (tab. 7). While fir is able to survive at low light conditions, seedlings of spruce are inclined to die for light levels lower than 20% of total transmittance (fig. 21). Significant differences ($p < 0.05$) between species were also found in term of radial growth and on average spruce showed greater growth rate than fir (tab. 7).

Species	N	min	max	mean	std. dev
Total Transmittance (%)					
fir	104	3,9	36,9	14,0	6,5
spruce	56	8,5	37,0	23,9	8,8
spruce (dead)	105	5,5	37,2	13,4	5,4
Radial Growth(mm*year⁻¹)					
fir	104	0,025	0,995	0,296	0,231
spruce	56	0,025	1,845	0,463	0,373
spruce (dead)	105	0,025	0,280	0,111	0,058

Tab. 7: Statistics (minimum, maximum, mean and standard deviation of values) of total transmittance and radial growth distinguished by species

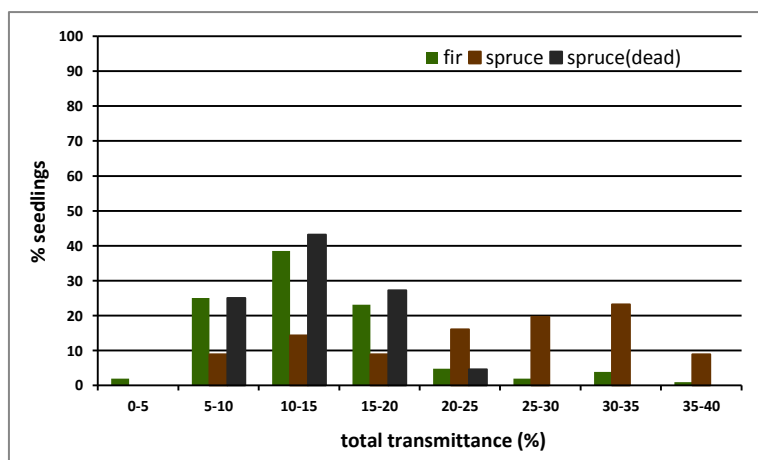


Fig. 21: Frequency of live fir, live spruce and dead spruce seedlings by class of total transmittance (%)

Differences statistically significant ($p < 0.05$) between species were also found in the sub-dataset; in particular for seedlings with height smaller than 1 meter growth and transmittance are on average greater in spruce than in fir (fig. 22a and 22b).

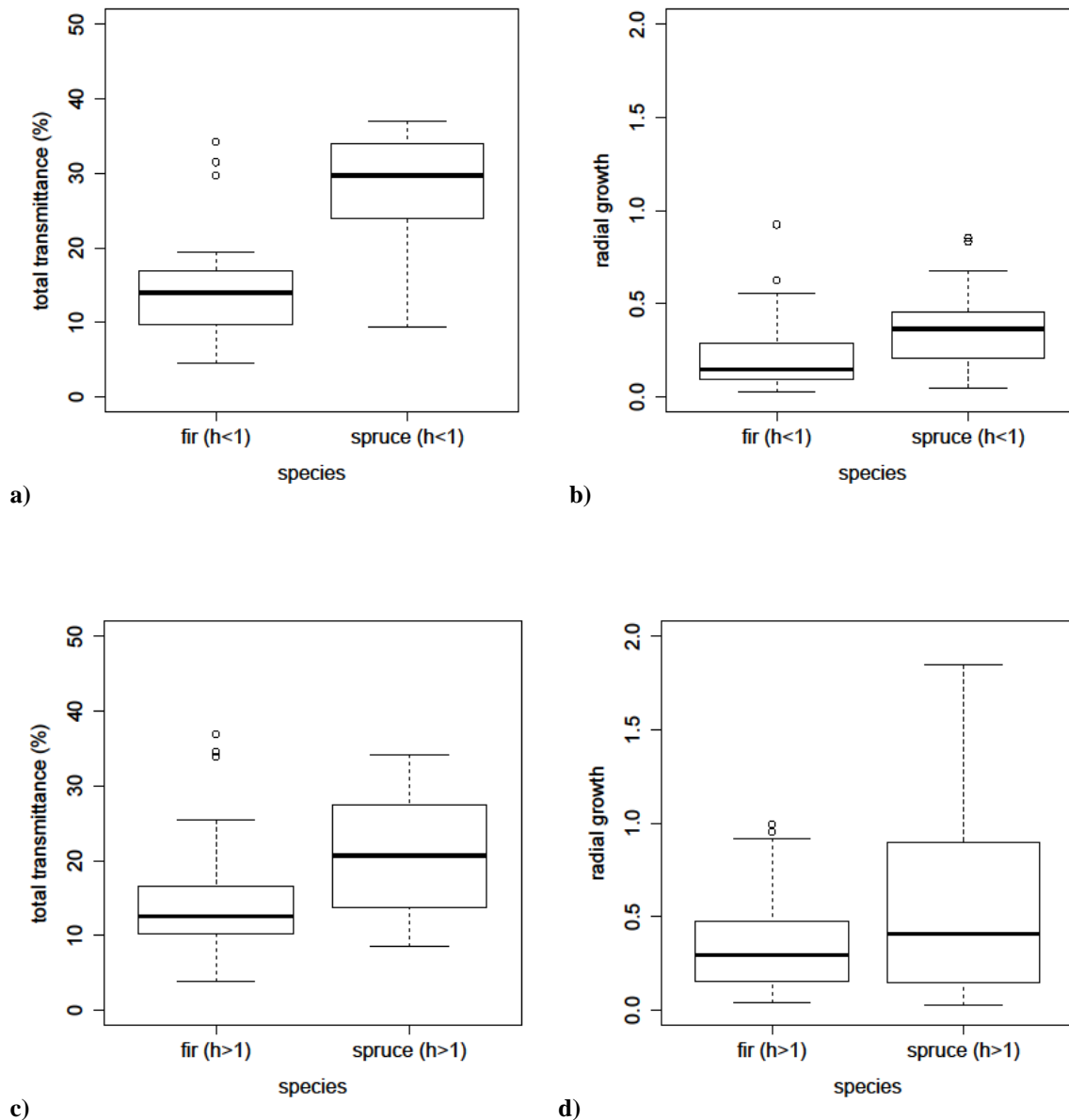


Fig. 22: Boxplots of total light transmittance and annual radial growth by species: (a) and b) seedlings with height < 1 m; (c) and d) seedlings with height > 1 m

Differences between species were also investigated for classes of transmittance: from 0 to 20%, from 10 to 20%, from 20 to 30% and from 20 to 40% (tab. 8). The frequency of seedlings for each class varied and was higher for the intermediate level of radiance (from 20 to 30%).

However, significant differences were found for high light levels (20-40 % of total transmittance) in the relative radial growth and in the slenderness index, while for low light levels (<20% and 10-20%) species were different only in terms of slenderness index. In the intermediate level of radiance no significant difference were found.

For seedling higher 1 meter only the height/diameter was significant different between species (tab. 8).

For samples with height lower than 1 meter, it was not possible testing the differences between specie because of the lack of the simultaneous presence of spruce and fir on the same classes of transmittance.

Total transmittance (%)	Statistics	radius	H	H/D	RADG	Relat. RADG
All seedlings						
0-20	H:	1	1	1	0	0
	p value:	0.001	0.007	<2.2e-16	0.90	0.26
10-20	H:	1	0	1	0	0
	p value:	0.04	0.14	<2.2e-16	0.89	0.52
20-30	H:	1	0	0	0	0
	p value:	0.04	0.14	0.97	0.89	0.16
20-40	H:	0	0	1	0	1
	p value:	0.15	0.08	1.284e-09	0.70	0.02
Seedlings h>1 meter						
0-20	H:	0	0	1	0	0
	p value:	0.11	0.84	<2.2e-16	0.66	0.56
10-20	H:	0	0	1	0	0
	p value:	0.41	0.64	<2.2e-16	0.69	0.70
20-30	H:	0	0	1	0	0
	p value:	0.74	0.58	8.426E-06	0.51	0.69
20-40	H:	0	0	1	0	0
	p value:	0.22	0.95	2.304e-08	0.12	0.22

Tab. 8: T-test between species for radius, height, height/diameter ratio (H/D), radial growth (RADG) and relative radial growth (relat. RADG) of seedlings

- *Effect of light availability on radial growth*

A linear and Michaelis-Menten models were compared with the null model in which no influence of light was supposed. The second function (Michaelis-Menten) which considers radial growth as function of light and size presented a much lower AICc value (tab. 9 and fig. 23a). An alternate third model which considered the relative radial growth (radial growth/radius) as a linear function of light was performed and the results were showed respectively in the tab. 9 and fig. 23b.

The positive linear correlation implied that irradiance promoted a higher relative radial growth.

The higher (almost double) angular coefficient “b”, and thus the steeper trend of Norway spruce straight line, highlighted differences in growth rate between spruce and fir seedling in the studied range of light conditions. Only for spruce increases on radiance availability explained at least the 50% of growth variance (tab. 9)

Michaelis–Menten function (fig. 23a) provided further elements for understanding the behavior of the species.

Below 10% of the total transmittance conditions, both species showed a clear and linear response to the light; as light availability increased above 10% fir rapidly reached asymptotic growth and thus spruce outgrew fir.

The 37% and 46% of the variance of radial growth respectively for silver fir and Norway spruce was explained by understory light availability.

MICHAELIS MENTEN model – radial growth							
Species	N	a	s	d	R ²	AICc	ΔAICc
fir	104	0.1275	0.01076	0.5947	0.40	-98.27	16.8
		[0.1120-0.1487]	[0.0095-0.0126]	[0.5650-0.6254]	2.674e-13		
spruce	56	0.4636	0.0036	0.7330	0.53	1.12	-0.53
		[0.2777-1.1405]	[0.0032-0.0041]	[0.6890-0.7774]	1.043e-10		

LINEAR model – relative radial growth									
Species	N	a	b	Std. Err. (a)	Std. Err. (b)	r	R ²	AICc	ΔAICc
fir	104	0.0138	0.0010	0.0038	0.0002	0.38	0.14	-558.31	-
	p value	0.0004	6.5e-05			6.5e-05	6.673e-05		
spruce	56	0.0131	0.0025	0.0083	0.0003	0.71	0.51	-267.29	-
	p value	0.121	5.9e-10			5.9e-10	6.585e-10		

Tab. 9: Estimate of parameters of linear models (a,b) and Michaelis Menten (a,s,d), coefficient of correlation (r), the regression coefficient of the observed versus predicted equation (R²), akaike information criterion corrected (AICc), the decrease in AICc for the selected Michaelis–Menten model as compared with a null model, in which no light effect on growth is considered (ΔAICc). Values in brackets are the two-unit support intervals for the parameter estimates

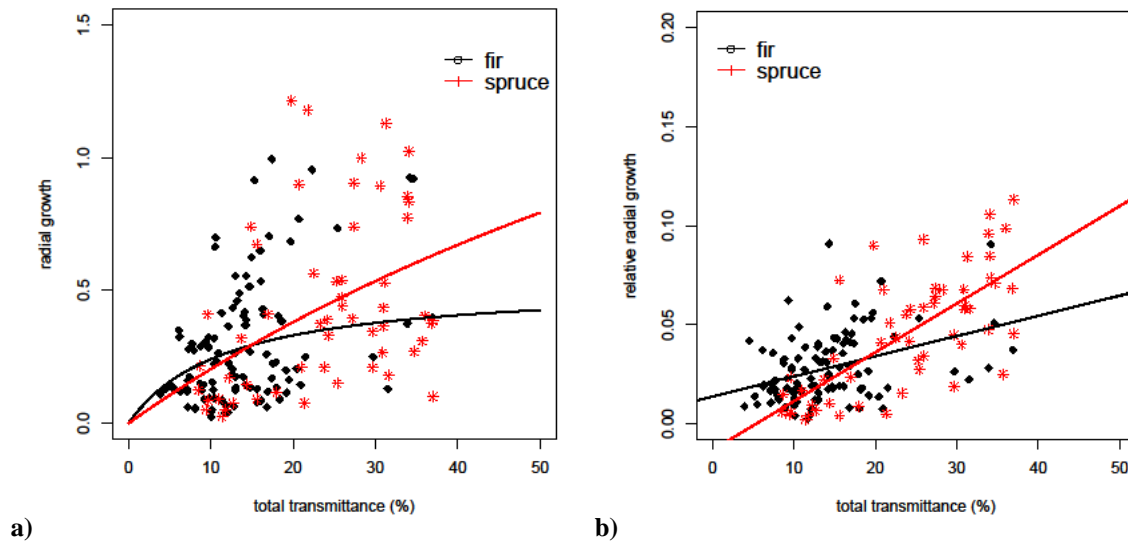


Fig. 23: Michaelis-Menten a) and linear b) responses of radial growth and relative relative radial growth to increases in light availability

Similar trends were found also considering the sub-datasets. Michaelis-Menten model better fitted the growth response to light increment than the linear function (tab. 10).

<i>MICHAELIS MENTEN model – radial growth</i>									
Species	N	a	s	d	R ²	AICc	ΔAICc		
fir (h>1)	56	0.1868	0.0114	0.5280	0.35	-26.03	-24.04		
		[0.1563-0.2387]	[0.0099-0.0137]	[0.4963-0.5659]	1.625e-06				
spruce(h>1)	29	0.5111	0.0039	0.7032	0.59	24.86	-14.86		
		[0.2486-15.7431]	[0.0033-0.0046]	[0.6469-0.7474]	9.857e-07				
fir (h<1)	48	0.0515	0.01254	0.8776	0.50	-70.23	-17.35		
		[0.0455-0.0611]	[0.0092-0.0225]	[0.8249-0.9411]	1.609e-08				
spruce(h<1)	27	0.1440	0.0056	0.8479	0.30	-15.46	-11.81		
		[0.1135-0.1800]	[0.0043-0.0071]	[0.7801-0.9113]	0.003				
<i>LINEAR model – relative radial growth</i>									
Species	N	a	b	Std. Err. (a)	Std. Err. (b)	r	R ²	AICc	ΔAICc
fir (h>1)	56	0.0095	0.0011	0.0041	0.0003	0.48	0.23	-318.14	-316.15
	p value	0.02	0.0002			0.0002	0.0002		
spruce(h>1)	29	-0.0151	0.0024	0.0101	0.0004	0.71	0.51	-140.48	-180.27
	p value	0.144	1.52e-05			1.52e-05	1.52e-05		
fir (h<1)	48	0.0193	0.0009	0.0067	0.0004	0.29	0.08	-244.18	-191.3
	p value	0.006	0.043			0.043	0.043		
spruce(h<1)	27	-4.079e-05	2.134e-03	1.565e-02	5.494e-04	0.61	0.37	-123.55	-119.9
	p value	0.99	0.001			0.001	0.001		

Tab. 10: Estimate of parameters of linear models (a,b) and Michaelis Menten (a,s,d), coefficient of correlation (r), the regression coefficient of the observed versus predicted equation (R²), akaike information criterion corrected (AICc), the decrease in AICc for the selected Michaelis–Menten model as compared with a null model, in which no light effect on growth is considered (ΔAICc). Values in brackets are the two-unit support intervals for the parameter estimates.

- *Effect of light availability on slenderness index*

Height to diameter ratio of regeneration decreased globally with increasing light conditions (fig. 24a) and decreasing size (diameter) class (fig. 24b). This relationship was significant ($r=-0.31$, $p<0.05$) for silver fir seedlings with height lower than 1m.

A comparison of the two species showed that on average spruce had smaller height to diameter ratio than fir, but the differences were not significant ($p>0.05$). Otherwise, significant differences ($p<0.05$) between species were found only for seedlings higher than 1 meter.

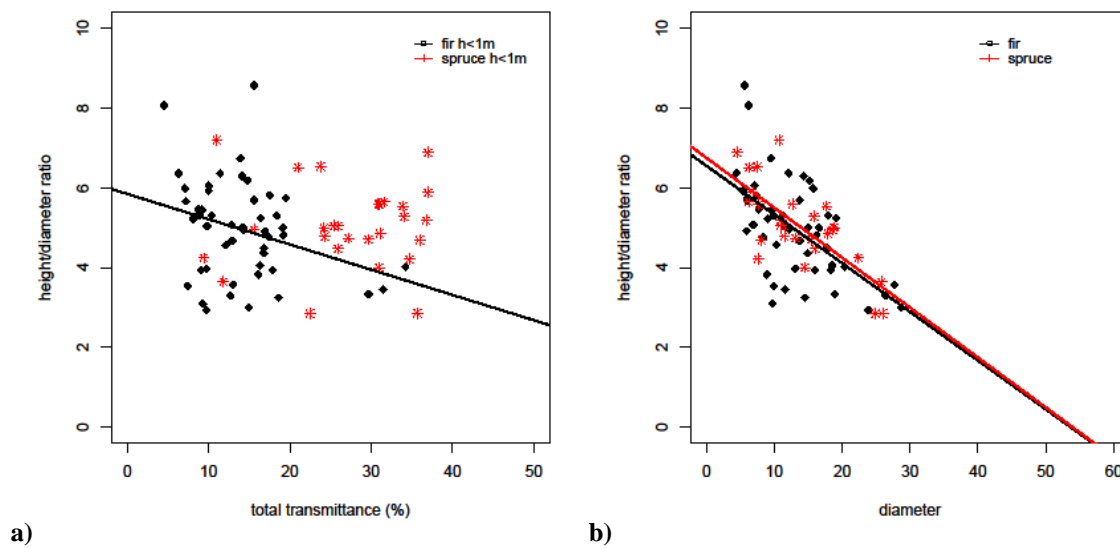


Fig. 24: Height/diameter ratio vs light (fir $r=-0.31$, $R^2=0.09$, $p<0.05$) (a) and height/diameter ratio vs diameter (spruce: $r=-0.74$, $R^2=0.55$, $p<0.05$; fir: $r=-0.58$, $R^2=0.35$, $p<0.05$) (b)

9.2.2 Effect of understory light availability, competition index and age on growth and morphological parameters (sample of 2014)

Significant differences between species ($p < 0.05$) were found for: slenderness index (H/D), length of last shoot (apical leader), relative height growth (RHG), radial growth (RADG), relative radial growth (relative RADG), age and light availability (tot. trans.) (tab.11). Live crown ratio (LCR) and apical dominance (ADR) were at the limits of confidence interval. On average spruce grows with radial increment and light availability greater than fir, which conversely showed height growth rate higher than spruce. Seedling of fir were older and on average with a double age than spruce. The species did not showed significant differences in terms of intraspecific competition, although on average higher in spruce.

	Statistics	H	H/D	CL	Apical leader	LCR	ADR	RHG	RADG	Relative RADG	Age	Comp. Index	Tot. trans
	H:	0	1	0	1	0	0	1	1	1	1	0	1
	p value:	0.946	0.030	0.570	0.001	0.062	0.053	0.021	0.0003	0.0001	0.0005	0.088	0.0004
fir	mean	104.1	6.4	71.6	7.5	66.9	0.7	0.09	0.5	0.057	27	0.22	26.4
	min	35.0	4.0	20.0	1.2	40.7	0.1	0.02	0.1	0.025	14	0.00	10.1
	max	189.0	4.6	155.0	18.3	95.7	2.2	0.24	1.2	0.063	39	0.67	48.0
	std dev	41.4	0.4	37.6	3.5	14.4	0.4	0.05	0.3	0.030	6.6	0.18	9.1
spruce	mean	102.4	5.1	75.9	4.9	73.0	0.9	0.06	0.7	0.075	16	0.33	34.5
	min	48.0	5.7	30.0	2.3	51.2	0.1	0.01	0.2	0.041	7	0.02	17.8
	max	170.0	6.2	140.0	10.0	90.3	2.5	0.16	1.6	0.058	40	0.91	52.4
	std dev	38.8	0.3	34.0	1.9	9.1	0.5	0.03	0.3	0.012	7.2	0.25	8.1

Tab. 11: Results of t-test between species and statistics (mean, minimum, maximum and standard deviation) for growth, morphological parameters and age, competition index and total transmittance

Also in this case, differences between species were investigated even for classes of transmittance: from 0 to 20%, from 10 to 20%, from 20 to 30% and from 20 to 40% (tab. 12).

For classes of low (<20%) and high (>40%) light levels it was not possible testing the differences between specie because of the insufficient simultaneous presence of sample of spruce and fir on those classes of transmittance

The frequency of seedlings for each class varied and was higher for the intermediate level of radiance (from 20 to 30%).

However, significant differences were found for high light levels (20-40 % of total transmittance) in radial growth (RADG), relative height growth (RHG), apical leader, slenderness index

(h/diameter) and age, while for intermediate light levels (20-30%) species were different only in age and h/diameter ratio.

Tot. Trans. (%)	Statistics	radius	H	H/D	CL	Apical lenght	LCR	ADR	RHG	RADG	Relat. RADG	Age	Comp. Index
20-30	H:	0	0	1	0	1	0	0	0	0	0	1	0
	p value:	0.73	0.97	1.133e-05	0.93	0.04	0.67	0.16	0.94	0.94	0.54	0.002	0.23
20-40	H:	0	0	1	0	1	0	0	1	1	0	1	0
	p value:	0.22	0.58	9.685e-07	0.42	0.02	0.06	0.15	0.02	0.02	0.92	0.02	0.33

Tab 12: T-test between species for growth, morphological parameters and age, competition index for interval of total transmittance

- *Effect of light availability on competition index*

As the light availability increased, the level of competition grow in both species, with a linear trend in silver fir ($r=0.40$, $p<0.05$) (fig. 25). For high light conditions (>30% of total transmittance), the trend of competition of spruce seedlings was not really clear.

However, light explained less than 20% of variability of competition in silver fir seedlings.

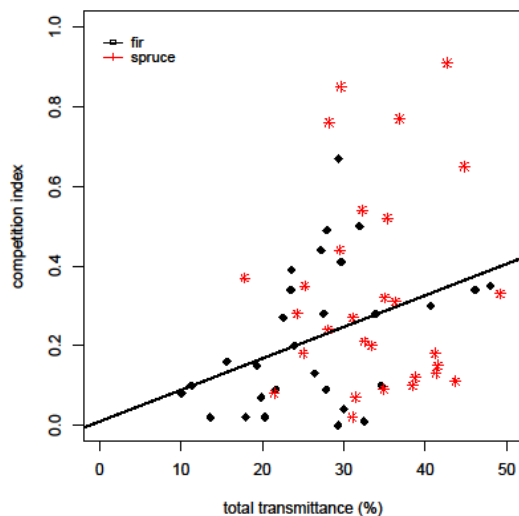


Fig. 25: Relationships between competition index of seedlings and light availability

- *Effect of light availability and competition index on growth and morphological parameters*

Also for data collected in the 2014, the best fitness was found with Michaelis-Menten model (fig. 26a and tab. 13). The third model performed (relative radial growth vs light) was not showed because of not significant trend was found. However, only for spruce the correlation with radiance was significant. However, light availability explained less than 20% of radial growth. No relationships were found between radial growth and competition index although on average spruce showed higher growth rate than fir for the same level of competition (fig. 26b).

MICHAELIS MENTEN model - relative radial growth							
Species	N	a	s	d	R ²	AICc	ΔAICc
fir	29	0.5817	0.0927	7.43e-09	0.034	10.70	3.45
	p value	[0.5182-0.6869]	[0.0630-0.2256]	[0-0.0614]	0.3		
spruce	30	0.3167	0.0507	0.3725	0.64	-0.30	4.73
	p value	[0.2977-0.3461]	[0.0375-0.0947]	[0.3502-0.4030]	8.111e-08		

Tab.13: Parameter estimates for linear and Michaelis–Menten growth–light function for radial growth. R² is the regression coefficient of the observed versus predicted equation and the AICc for the selected Michaelis–Menten model as compared with a null model, in which no light effect on growth is considered.

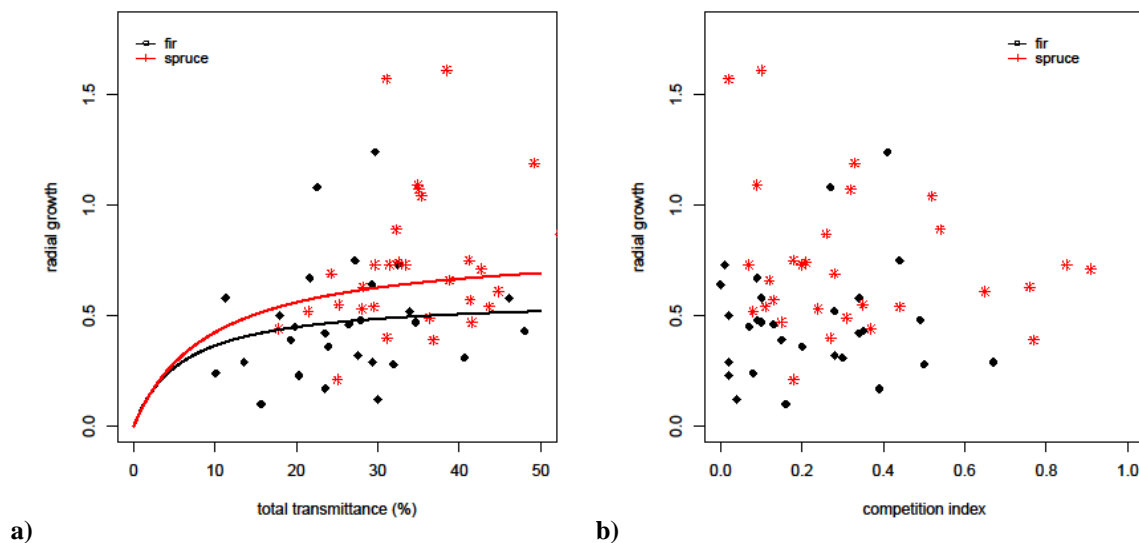


Fig. 26: Michaelis-Menten responses of radial growth to increases in light availability (a) and responses of radial growth to increases in competition (b)

Michaelis-Menten was also the model that better fitted the relationships between height growth and light (tab. 14) while the linear function was not statistically significant. Model was stronger

in fir with 0.63 of the growth variance explained by the light variability. The slope of the function is higher in Norway spruce seedlings, which reached the asymptotic growth at low light conditions (around 5% of the available total transmittance) and before the seedlings of silver fir (fig. 27a).

Figure 26b and 27b highlighted the higher frequency of spruce at high levels of competition. No significant relationships were found between height growth and competition index. Nevertheless, figure 19b showed that for low competition levels the height growth was higher.

MICHAELIS-MENTEN							
Species	N	a	s	d	R ²	AICc	ΔAICc
fir	29	0.1525	0.0142	0.9204	0.63	132.46	-4,84
		[0.1326-0.1761]	[0.0105-0.0202]	[0.9020-0.9385]	2.538e-07		
spruce	30	0.2553	0.0999	0.6554	0.32	121.19	1,9
		[0.2271-0.2901]	[0.0390-0.1000]	[0.6358-0.6807]	0.001		

Tab. 14: Parameter estimates for Michaelis–Menten growth–light function for radial growth. R² is the regression coefficient of the observed versus predicted equation and ΔAICc is the decrease in AICc for the selected Michaelis–Menten model as compared with a null model, in which no light effect on growth is considered

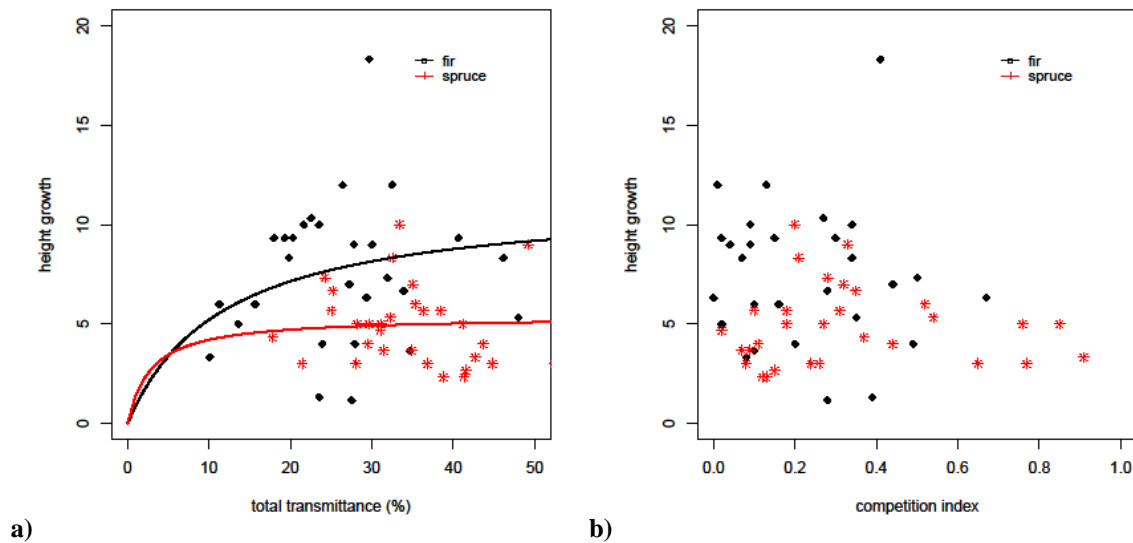


Fig. 27: Michaelis-Menten responses of height growth to increases in light availability (a) and responses of height growth to increases in competition (b)

In both examined species irradiance promoted a higher apical dominance ratio (ADR) and a deeper live crown (LCR) although these increments were not significantly evident (fig. 28a and 28c).

Because of the high scatter of data, particularly evident for ADR, it was not possible to define the type of relationship between morphological parameters and light, as well between those parameters and competition index. Competition didn't produce strong variation on morphological parameters (fig. 28b and 28d).

The effect of seedling size (height) was more significant than light, in particular for ADR of silver fir ($r=0.39$), although height explained only the 15% of the ADR variability (fig. 29a). LCR showed positive increment as the height increased and the significance was at the limit of the confidence interval (fir: $p=0.06$ and spruce: $p=0.05$) (fig. 29b).

However, as confirmed by Mann U Whitney test (tab. 11), no significant differences between species were found for ADR and LCR.

If we consider light stressed seedlings with $ADR < 1$ and $LCR < 60\%$ (as suggested by Duchesneau et al 2001, Grassi et al 2005), it is evident that silver fir survives on average, in more light stressed conditions than spruce. Furthermore, results indicate that higher values of ADR or LCR higher were found in correspondence of levels of light conditions ranged between 20 and 30% for silver fir and 30-40% for Norway spruce.

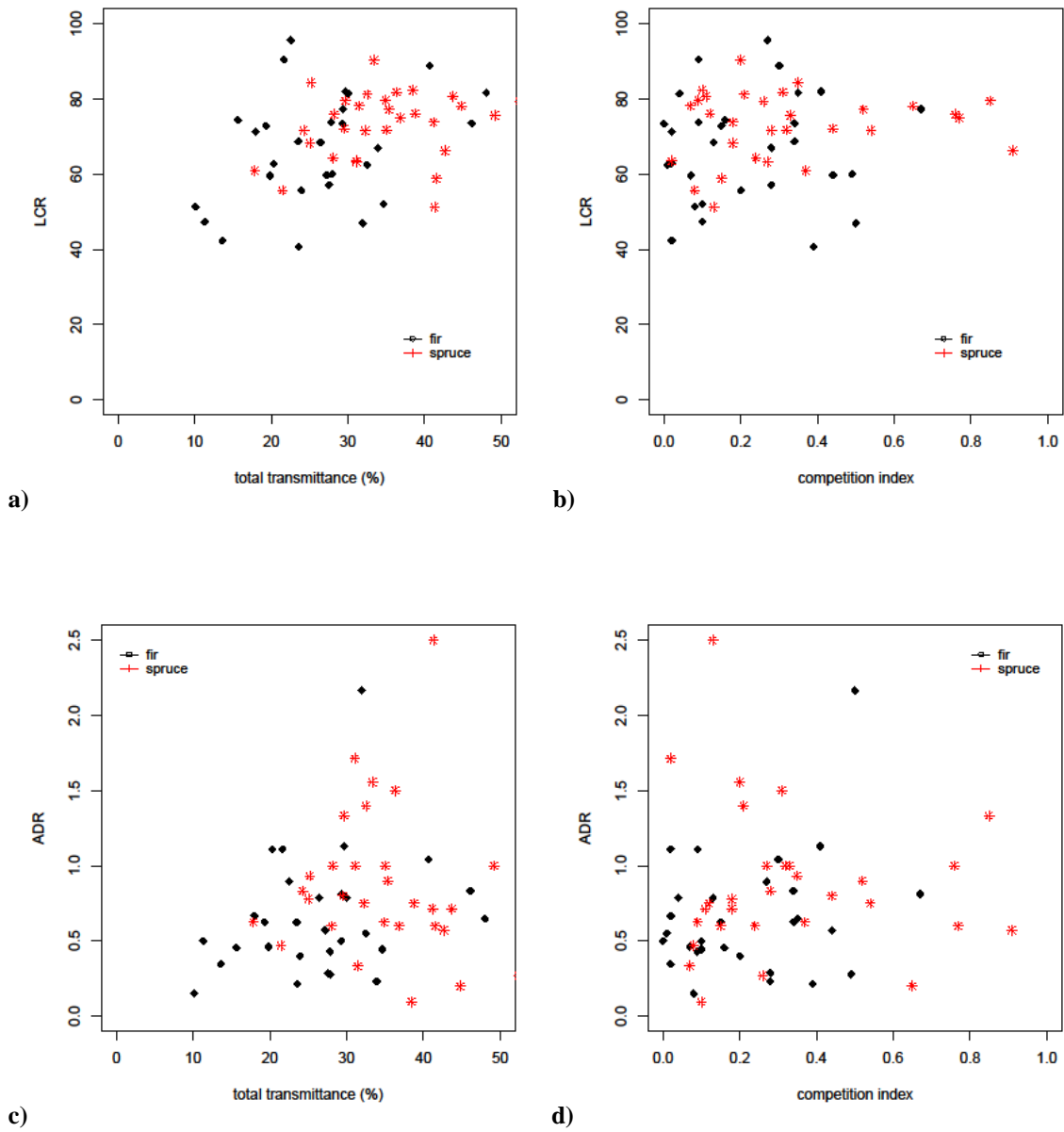
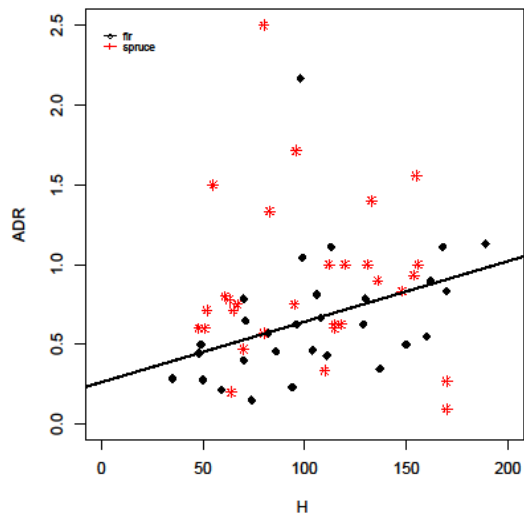


Fig. 28: Relationships between total transmittance and percentage of live crown ratio (LCR) (a) and and apical dominance ratio (ADR) (c) and between competition index and LCR (b) and ADR (d)



a)

b)

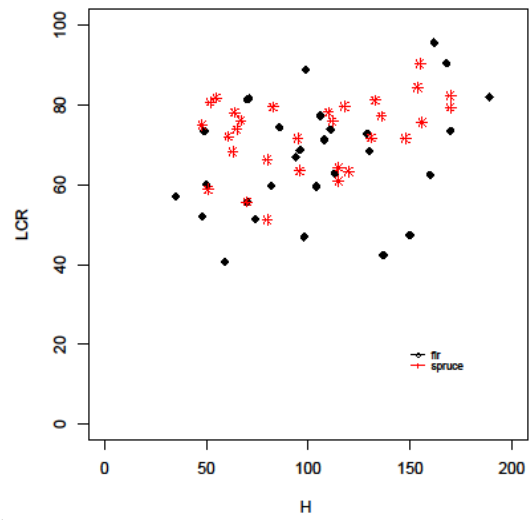


Fig. 29: response of ADR (a) and LCR (b) to height increases

- *Effects of age on growth and morphological parameters*

Few studies took into account age, mainly for the time consuming required for being estimated. Effectively, age cannot be considered the cause for determining variation on growth and morphology. In this study, it was interesting analyzed if species so similar in height and diameter differed in age and if morphological and growth parameters varied with the variation of the age. Figure 30 showed that older seedlings of both species were found in the lowest light conditions, although the relationship was more significant in silver fir ($r=-0.46$, $R^2=0.21$, $p<0.05$).

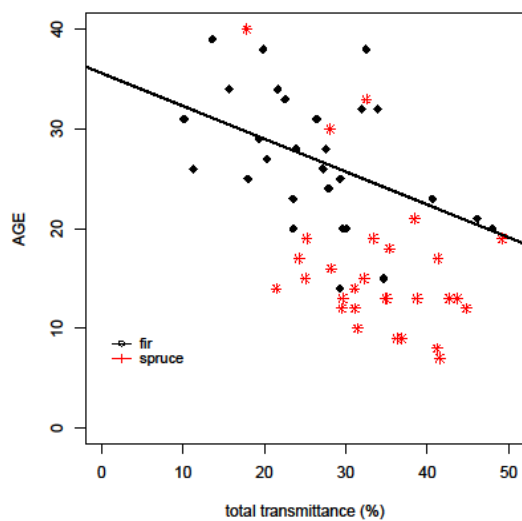
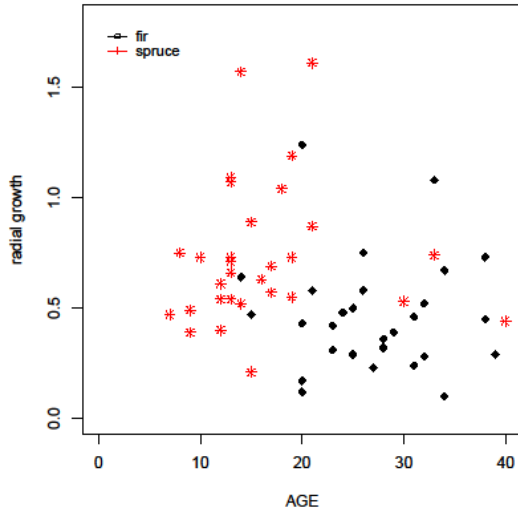
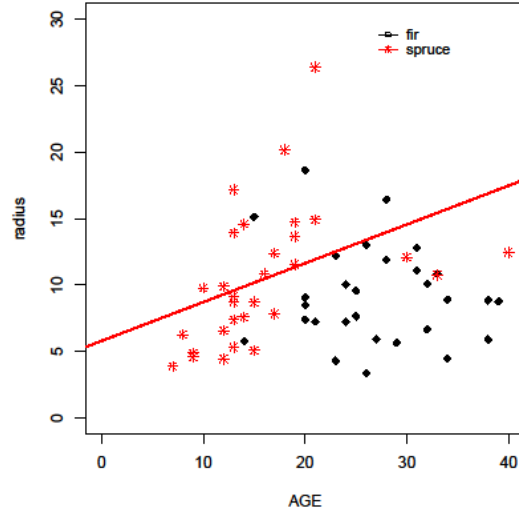


Fig. 30: Relationships between age of seedlings and light availability

Any significant correlations between radial growth ($p>0.05$) and age were obtained (fig. 31a), while a positive trend of radius in relation to the age was found for spruce seedlings ($r=0.42$, $p<0.05$) (fig. 31b).



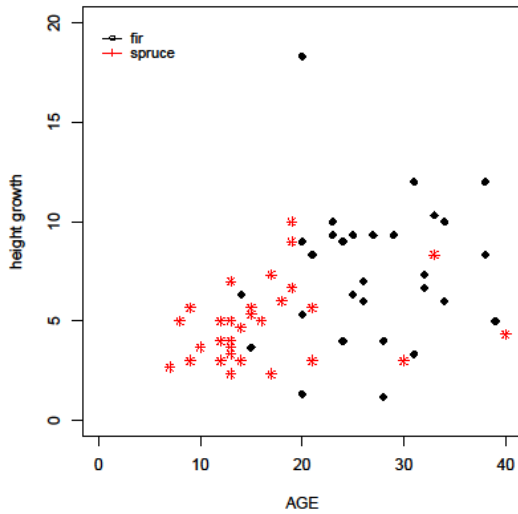
a)



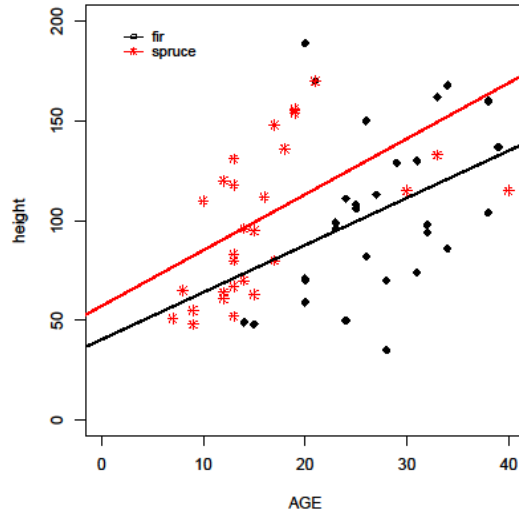
b)

Fig. 31: relationships between age and radial growth (a) and between age and radius (b)

Also for height growth were not found any relationships with age (fig. 32a), although height of both species showed positive correlations ($r=0.38$ for fir and $r=0.52$ for spruce, $p<0.05$) in as the age increased (fig. 32b).



a)



b)

Fig. 32: Relationships between age and height growth (a) and between age and height (b)

Any significant correlations were found between morphological parameters and age (fig. 33a and 33b). Despite apical dominance and live crown ratio were on average lower for older seedlings and therefore for silver fir, the age didn't produce strong effects on those parameters.

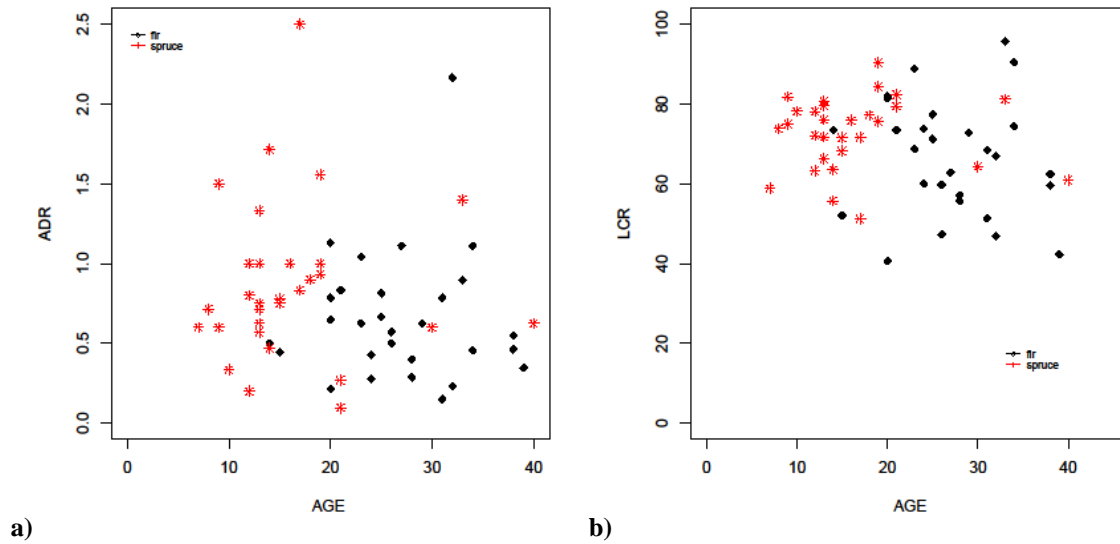


Fig. 33: Relationships between age and apical dominance ratio (ADR) (a) and between age and percentage of live crown ratio (LCR) (b)

10. Discussion

10.1 Quantification of the understory light availability and evaluation of the structural attributes of stand overstory mainly correlated to the light

Allometric functions demonstrated that stand overstory is characterized by shade-tolerant species, with deep (*Canham et al 1994*) and wide crowns. The differences between the two conifers were weak and the values of estimated parameters of silver fir were comparable to those found in *Ameztegui et al 2012*. Except for the height of live crown insertion (crown base), no significant differences were found between plots for structural attributes of stand overstory.

Clearly, the significantly diverse understory light conditions between plots might be explained by the diversity within species, in particular in terms of crown structure (*Pretzsh et al. 2014*). Also spatial arrangement of trees might play an important role in the understory light environments (*Battaglia et al. 2002*).

Differences in transmittance, between and within plots, proved the high degree of variability over short distances of below canopy radiance in multi-aged mixed forests. Values of radiance reported in this study are comparable to those recorded in similar type of forests (*Grassi and Giannini, 2005*). Strong linear correlations with transmittance are observed N and BA. However, the highest Pearson coefficients were provided by the plot 1, where in most subplots understory light condition exceeded 20% of total transmittance and were greater than in subplots of plot 2. *Drever and Lerztman (2003)* and *Comeau and Heineman (2003)* found the predictive capacity of structural attributes related to stand density was better for relative high light levels (>20% full sun).

On the other hand, the overall effect of standard deviation of CL, CB and H, as expressed by PC1, showed a close association with total transmittance. In stands with continuous canopy cover and high heterogeneity structural and crown profile, transmittance is primarily regulated by crown geometry variability, and secondly by tree density. The complementarity of different species in terms of light ecology allows trees to acclimate in the specific case their crown structures, to benefit of the resources more efficiently and to increase the heterogeneity of canopy structure reducing competition among crowns (*Grams and Andersen, 2007; Pretzsch 2009, Bayer and Pretzsch, 2013*).

The negative correlation (-0.63) between PC1 and transmittance proves that greater is the heterogeneity of vertical stand structure, lesser radiation can go through the crowns and reach the

understory layer, especially if tree density is high, and therefore crown are close each other and easily overlap.

Although density (N or BA) is the main feature used in many similar studies to model understory light, as well by forest managers to quantify level of harvesting, in this research they prove to have weaker association with light conditions compared to the standard deviations of height and crown structure.

10.2 Assessment of the effects of understory light conditions, competition and age on growth and morphological parameters of natural regeneration

Overstory canopy structure and its manipulation generate a variability of understory light conditions which affects growth processes of tree seedlings and is fundamental for understanding the diverse regeneration niches.



Fig. 34: example of understory light availability for seedlings

The study underlined significant differences in terms of light availability between species (fig. 34).

Levels of radiance ranging between 20 and 30% represent the suitable interval for the coexistence and survival of both species.

In those conditions silver fir and Norway spruce develop diverse strategies which seem to be in part attributable to the differences in the apical leader growth (tab 12).

Also the higher frequencies of fir and spruce seedlings respectively in low (lower than 20%) or high (higher than 30%) radiance conditions highlighted different abilities of fir and spruce regeneration in light resource exploitation, confirming the better ability of *Picea abies* seedlings to exploit high radiance availability (Grassi and Bagnaresi 2001). The confirmation of these outcomes was also found in the growth versus transmittance functions. In effect, Michaelis-Menten model which demonstrated to best fit our dataset (Ametzegui et al 2011) showing positive radial and height growth responses to light availability increase, described a different behavior of the two species: while spruce benefits in terms of radial growth, silver fir take advantage in height growth as the light increases. Similar results were also found for seedlings with height either higher and lower than 1 meter. The greater height growth rate in fir than spruce was consistent with the results of Grassi et al 2005.

However also the relative radial growth well explained the positive responses of species to light availability, especially for spruce seedlings since, as observed in Michaelis-Menten model, the trend of radial growth was closer to linearity.

Height/diameter ratio was larger on average in silver fir than spruce. It confirms the opportunistic behavior of *Abies alba* (Robakowsky et al 2004), which combines high shade tolerance with pronounced responsiveness to light in terms of apical growth.

Any significant effect was not promoted by transmittance on morphological parameters (LCR and ADR) of regeneration although positive tendencies were identified from data. Differences for ADR and LCR between species were not significant. Nevertheless some considerations might be discussed. The apical dominance (ADR) which reflects the impact of irradiance in crown shape were characterized by lower mean values in silver fir (although the difference with spruce was not significant), indicating more accentuate crown flattening than larger horizontal growth and possibility of intercepting light, typical traits of this and other similar species (Williams et al 1999, Robakowsky et al 2003). Furthermore, such results demonstrated that on average fir was more light stressed and this condition decreased with the increasing of light availability. This behavior, similar to other shade tolerant conifers (Parent and Messier 1995, Messier et al 1999),

highlighted a higher morphological plasticity of *A. alba* than *P. abies* in responses to different light availability (Messier et al 1999, Robakowsky et al 2003, Robakowsky et al 2004). Further evidence was found in the greater frequency of spruce seedlings for levels of transmittance higher than 20% and their tendency to die for lower levels of transmittance. In general, spruce resulted less light stressed when total transmittance cross over 30%.

However, the high scattering of data that characterize almost all the relationships between transmittance, growth and morphology, demonstrated that current light conditions are not able to totally explain the variability of data. The current conditions of growth and above all morphological parameters might reflect past radiance conditions in which seedlings grew.

The fact that older seedlings were found in the lowest light conditions demonstrated that seedlings, in particular silver fir, can survive for long time in light stressed conditions reducing at the minimum the radial growth and on the other hand increasing the growth of lateral branches (Walters et al 1996, Williams et al 1999).

Light availability promoted higher levels of competition (Grassi et al 2005), but while silver fir followed a linear trend, in spruce the relationship was not well defined, in particular for light conditions higher than 30%. However increasing in competition levels didn't generate significant responses in radial and height growth (Duchesneau et al 2001, Grassi et al 2005).

Intraspecific competition didn't produce strong responses not even in morphological parameters (Grassi et al 2005) in the range of radiance examined, even analyzing only seedlings responses to total transmittance higher than 15% (Grassi et al 2005). Rather, in contrast to the findings of Messier and Nikinmaa 2000 and Kneewshaw et al 2006, which sustained that shade tolerance species might lose their crown plasticity (a species trait that allows to be more shade tolerant) as they grow taller, the apical dominance of silver fir seems positively affected by height, confirming the findings of Claveau et al 2002 for North-American species with similar traits, such as balsam fir and white fir. Height however was not significantly correlated with the percentage of live crown (LCR) in contrast to Claveau et al 2002, but in agreement with Duchesneau et al 2001 for balsam fir.

11. Conclusions

This work has contributed to improve knowledge about the behavior of silver fir and Norway spruce in the forest stand conditions analyzed, highlighting some differences with studies carried out for similar species. Considering the role of natural regeneration in maintaining heterogeneous conditions, providing continuity and enhancing resilience and resistance of forest ecosystems (Drever et al. 2006, Franklin et al 2002, Deal et al 2012), this study could be the starting point for extend this type of analysis to other Alpine forest stands, since natural regeneration process is still a topic to be explored from several points of view.

Concluding remarks related to the stated hypotheses and questions, are summarized here below:

i) PCA analysis allowed to explore the role of structural attributes generally not taken into account in similar studies and, to deduce some hypotheses worth to be tested on a larger set of conditions. Radiation below canopy in heterogeneous stands with continuous canopy cover depends more on the variability of dendrometric attributes than their mean values. Vertical structure exerts a clear effect on transmission of radiance. In particular, crown size characteristics, such as CL, CB and height, and in particular their standard deviations are good proxy for light transmission, even more in mixed species forest stands (Pretzsch 2013). Stand attributes as DBH, H, N and BA are not the best predictor of understory light conditions in a multi-aged and mixed forest. On the other hand, it is clear that a single attribute cannot explain the whole variability of radiance (Promis et al, 2009), even more if the mosaic of cohorts of trees is fine-grained (Grassi et al 2003) like in this case-study.

ii), iii) significant differences in terms of light availability characterize seedlings of the two species. Those differences underline the abilities of both species to grow in low light conditions (<15- 20% of total transmittance) for seedlings of fir or in higher light conditions (>30 % of total transmittance) for seedlings of spruce. In particular, silver fir seedlings demonstrated to be able surviving in suppressed conditions for long time, minimizing growth efforts. Radiance ranging from 20 to 30% of total transmittance allow the coexistence of fir and spruce seedlings. However, higher levels of competition at those light conditions stimulate species to develop different growth strategies. While silver fir take advantage in terms of apical growth, increasing in light availability promote more effects in terms of radial growth in spruce. This result seems to confirm the opportunistic behavior of *Abies alba* (Robakowsky et al 2004), combining high shade

tolerance with pronounced responsiveness to light in terms of apical growth. Although neither light availability nor competition index produce significant responses in the apical dominance ratio (ADR) and live crown ratio (LCR), the values of these morphological parameters underlined high level of light stress conditions (Grassi et al 2005) which was confirmed also by crown flattening in silver fir, a typical behavior of other shade tolerant conifers (Williams et al 1999, Parent and Messier 1995, Messier et al 1999, Robakowsky et al 2003).

Results from this study provide knowledge for better understanding and predicting development of complex forests, and the design of silvicultural treatment in multiaged forests.

Canopy structure affects light transmittance into understory and its attributes can slow or favoring successional dynamics and growth of natural regeneration. Canopy is also the main element that might be manipulated by forest managers, then understanding the role of stand attributes in determining certain light conditions below canopy is fundamental for planning appropriate silvicultural strategies. A careful overstory trees selection or a fine adjustment of light permeability of overstory is of particular importance for the regeneration of species like silver fir and Norway spruce, which add to shade tolerance a rather good reactivity to light condition change.

This study represents a first step towards a parametrization of the growth sub-model of SORTIE, which provided important knowledge about the behavior of two species characterizing a significant part of Alpine forests. However, results might be considered efficient only for the analyzed forest stand. More efforts in terms of time and economic resources would be required for completing the parametrization of the growth sub-model or rather of the whole SORTIE model for the Alpine forests.

Aknowledgements

I thank Professor Luigi Portoghesi for driving me during the whole academic career and for being my advisor during the PhD period.

I thank Professor Piermaria Corona for giving me the possibility to carry out this working experience and for his precious suggestions during these four years.

I thank the University of Molise, the University of Tuscia and the Center of study of Pieve Tesino for giving me the possibility to develop the project.

I thank Professor Christian Messier for hosting me in the laboratory of Université du Quebec à Montreal and for giving me the possibility to meet and discuss with researches and experts working on the same topics of my project (Alain Paquette, Lluís Coll, Aitor Ametzegui, Marilou Beaudet, Fred Boivin).

Finally, I thank my colleagues of University of Tuscia and all foreign and italian people that I meet during this phase of my life for having upgraded my knowledge and make meaningful this experience.

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