UNIVERSITÀ
DEGLI STUDI
DEL MOLISE

FONDAZIONE
EDMUND
MACH

Influence of climatic variations and competitive interactions on the productivity of mountain forests in Italy

PhD in Biosciences and Territory

XXXII Cycle

THESIS

S.S.D AGR/05

Supervisor

Prof. Vittorio Garfì

Co-supervisor

Dott. Damiano Gianelle

Prof. Roberto Tognetti

Course coordinator

Prof. Giovanni Fabbrocino

Candidate

Soraya Versace

ACADEMIC YEAR 2019/2020

Index

Abstract IV

Riassunto V

GENERAL INTRODUCTION 1

- **Introduction** 2
- **Objectives and structure of thesis** 6
- **References** 7

CHAPTER 1 15

- **1.1. Introduction** 16
- **1.2 Materials and Methods** 19
  - **1.2.1 Study sites and plots** 19
  - **1.2.1.1 Sites description** 19
    - **1.2.1.2 Plot characteristics** 21
  - **1.2.2 Tree sampling and ring-width chronologies** 23
  - **1.2.3 Meteorological data** 24
  - **1.2.4 Drought indices** 24
  - **1.2.5 Identification of pointer years** 25
  - **1.2.6 Statistical analysis** 25
    - **1.2.6.1 Climate-growth** 25
    - **1.2.6.2 Growth and drought indices** 26
    - **1.2.6.3 Growth and extreme climatic events** 26
- **1.3. Results** 27
  - **1.3.1 Tree-ring width chronologies** 27
  - **1.3.2 Plot structure** 29
  - **1.3.3 Climate-growth relationships, and site- and stand-level differences** 30
  - **1.3.4 Temporal variability in climate-growth relationships** 34
  - **1.3.5 Growth-drought index relationship** 37
  - **1.3.6 Pointer years** 37
- **1.4. Discussion** 40
  - **1.4.1 Species-specific response to climate factors** 40
  - **1.4.2 Comparison of mixed-species vs. pure stands** 42
  - **1.4.3 Methodological considerations** 43
- **1.5. Conclusion** 44
- **1. Acknowledgements** 44
- **1. Supplementary material** 45

1. References 47

CHAPTER 2 55

Competition interaction in pure and mixed-species stands of silver fir and European beech in southern Italy 56

2.1. Introduction 56

2.2. Materials and methods 58

2.2.1 Study site 58

2.2.2 Field measurements 61

2.2.3 Individual-based competition indices 62

2.2.4 Modelling approach 63

2.2.5 Statistical analyses 65

2.3. Results 65

2.3.1 Stand structure 65

2.3.2 Individual-level competition of mixed-species versus pure stands 66

2.3.3 Growth models 67

2.4. Discussion 69

2.5. Conclusion 70

2. Acknowledgements 70

2. Supplementary material 71

2. References 72

CHAPTER 3 77

Prediction of Competition Indices in a Norway Spruce and Silver Fir-Dominated Forest using Lidar Data 78

Abstract 78

1. Introduction 78

2. Materials and Methods 80

2.1. Data Set Description 80

2.1.1. Study Area 80

2.1.2. Lidar Data 81

2.1.3. Field Data 81

2.2. Extraction of Competition Indices 81

2.3. ITCs Delineation 82

2.4. Lidar Metrics Extraction 83

2.5. Prediction 84

2.6. Relationship between AGB and Competition Indices 85

3. Results 86
3.1. ITC Crown Delineation 86
3.2. Prediction of Competition Indices 86
3.3. Relationship between Competition Indices and AGB 89
4. Discussion 90
5. Conclusions 92
References 92

GENERAL DISCUSSION AND CONCLUCIONS 96
Discussions and conclusions 97

Abstract

Tree growth is influenced by multiple factors including, climate and competition processes. Climate change has a strong impact on growth of trees and can cause negative impacts on forests, especially in the Mediterranean basin.

However, tree growth can also be influenced by competitive interactions, through the use and absorption of resources within tree communities. To quantify the level of competition between trees, competition indices are used, which are normally computed over small areas. Predicting competitive interactions over larger areas can be very important and light detection and ranging (lidar) data, could be the suitable tool. Based on these considerations, the main objective of the thesis was to identify and study the influence of climatic variations and competitive interactions on the growth of three important forest species, European beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* L.) and silver fir (*Abies alba* Mill.). The work is structured into three chapters, in which the first analyzes the influence of climate and extreme events on the radial growth of beech and silver fir in mixed and pure plots along a latitudinal gradient in Italy. In the second chapter the competitive interactions in mixed and pure populations of European beech and silver fir, located at the limits of their distribution range (southern Italy) are analyzed. In the third chapter, instead, was to estimate the competition dynamics for individual trees of Norway spruce and silver fir, located in the municipality of Lavarone (Trentino), and to identify the relationship between competitive interactions and tree aboveground biomass. Overall, results highlighted the response of trees under to climate and competition processes in mountain forests in Italy. In particular, the results of the first work showed a different response only at the regional level for the maximum temperatures. In Trentino the temperatures in winter, for silver fir, and summer, for both species, had a lesser negative impact on radial growth of trees compared to southern sites. Despite this, the results obtained from the correlations (radial growth-drought indices) and from principal component analysis have shown that no plot was sensitive to summer drought. Results are important to implement operational techniques that increase species adaptation to climate change. In the second work showed that the basal area increment, under the negative influence of high competition levels and slope terrains, varied between stands. In this sense, higher competitive interactions have been observed in Molise than in Calabria. Finally, in the third work showed that lidar metrics could be used to predict the competition indices of individual trees. In addition, biomass was observed to decrease as competition increased. The results of the three works showed that for the choice of sustainable forestry options it is necessary to consider the conditions of the site where these species are found and the structure of the forest stands, in terms of density and arrangement of the trees. Furthermore, it has been found that the use of remote sensing techniques (e.g. lidar) can be very useful in the forestry field, since they can provide information on larger areas.

Riassunto

La crescita degli alberi è influenzata da molteplici fattori tra cui, il clima e i processi di competizione. I cambiamenti climatici hanno un forte impatto sulla crescita degli alberi e possono causare impatti negativi sulle foreste, soprattutto nel bacino del Mediterraneo. Tuttavia, la crescita degli alberi è influenzata anche dalle interazioni competitive. Per quantificare le interazioni competitive tra gli alberi vengono utilizzati indici di competizione, che normalmente sono calcolati su aree di piccole dimensioni. Prevedere le interazioni competitive su aree più estese può essere molto importante e i dati LIDAR (*light detection and ranging*) potrebbero essere lo strumento adatto. Sulla base di tali considerazioni, l'obiettivo principale della tesi è stato quello di individuare l'influenza delle variazioni climatiche e delle interazioni competitive sulla crescita di tre importanti specie forestali, faggio (*Fagus sylvatica* L.), abete rosso (*Picea abies* L.) e abete bianco (*Abies alba* Mill.). Il lavoro è strutturato in tre capitoli. Nel primo viene analizzata l'influenza del clima e degli eventi estremi sulla crescita del faggio e dell'abete bianco in plot misti e puri lungo un gradiente latitudinale in Italia. Nel secondo capitolo vengono analizzate le interazioni competitive in popolamenti misti e puri di faggio e abete bianco, situati ai limiti del loro areale di distribuzione (Italia meridionale). Nel terzo capitolo, invece, sono state stimate le dinamiche di competizione di abete bianco e abete rosso, situati nel comune di Lavarone (Trentino), e individuata la relazione tra le interazioni competitive e la biomassa degli alberi. Nel complesso, i risultati hanno evidenziato le risposte di accrescimento degli alberi alle variazioni climatiche e ai processi di competizione in foreste montane in Italia. In particolare, il primo lavoro ha evidenziato una risposta diversa solo a livello regionale per le temperature massime. In Trentino le temperature invernali, per l'abete bianco, ed estive, per entrambe le specie, hanno avuto un minor impatto negativo sulla crescita radiale degli alberi rispetto ai siti meridionali. Nonostante ciò, i risultati ottenuti dalle correlazioni (crescita radiale-indici di siccità) e dall'analisi delle componenti principali hanno evidenziato che nessun popolamento era sensibile alla siccità estiva. Nel secondo lavoro è stato osservato come l'incremento dell'area basimetrica, sotto l'influenza negativa di alti livelli di competizione e alta pendenza del terreno, variava tra i popolamenti. In tal senso sono state osservate interazioni competitive più elevate in Molise rispetto alla Calabria. Infine, nel terzo lavoro, è stato dimostrato che le metriche lidar possono essere utilizzate per prevedere gli indici di competizione. Inoltre, è stato osservato che la biomassa diminuiva all'aumentare della competizione. I risultati dei tre lavori hanno evidenziato che per la scelta di opzioni forestali sostenibili è necessario considerare le condizioni del sito in cui tali specie si trovano e la struttura dei popolamenti forestali, in termini di densità e disposizione degli alberi. Inoltre, è stato constatato che l'utilizzo di tecniche di telerilevamento (es. lidar) possono essere molto utili in campo forestale, poiché possono fornire informazioni su aree più estese.

GENERAL INTRODUCTION

Introduction

Tree growth is influenced by several factors, such as climate, site conditions and competition processes (Jucker et al. 2016; Liang et al. 2019). The climate has a strong impact on the growth, structure, composition and distribution of forests (Mund et al. 2002; Mueller et al. 2005; Zhang et al. 2018). Continuously rising temperatures and decreasing precipitation are causing substantial impacts on forests in many parts of the world, threatening the provision of ecosystem services (Boer et al. 2020; Hubau et al. 2020). One of the areas where climate change is most pronounced is the Mediterranean basin (Scarascia-Mugnozza et al. 2000). In fact, according to the IPCC 2017 in the coming decades, a greater increase in temperatures and higher inter-annual rainfall variability are expected, as well as increasing extreme drought events. The progressive decrease in water availability and the increase in evaporative demand may have dramatic implications for the future of these forest ecosystems.

The Mediterranean basin has a complex and heterogeneous climatology, composed of a northern temperate climate and the semi-arid climate in the south (Sangüesa-Barreda et al. 2019). In the majority of Mediterranean areas, water is abundant in winter, but during the summer the absence of precipitation can significantly limit the growth of trees, thus becoming a limiting resource. Therefore, precipitation and soil water availability, especially in these environments, can play an important role in the cambial activity of species (Cherubini et al. 2003). Water shortage can lead to drops in productivity, as well as mortality and decline in tree growth (Bussotti and Pollastrini 2017). According to Breshears et al. 2005, the decline in tree growth is linked not only to poor water supply, but also to rising temperatures, which cause an increase in evapotranspiration. However, there is conflicting evidence on the warming effects on tree growth. For example, Büntgen et al. 2019 and Pretzsch et al. 2014a found that the increase in temperatures determines a higer growth of trees. Moreover, understanding the population-level response of trees to climate and assessing of geographical range changes is complicated due to the longevity of trees (Jump et al. 2006). Trees of many species can survive for hundreds of years and persist at the edges of species distribution long after the climate has become unsuitable for their growth and reproduction (LaMarche 1973; Pigott and Huntley 1978). These changes in tree growth cause variations in the width of the annual growth rings that are recorded during each growing season (Jump et al. 2006).

One of the most used methods to study variations of the width of the annual growth rings and tree species responses to the climate is through dendrochronology. Dendrochronology is the science that deals with the dating of annual tree rings and allows us to reconstruct past tree behaviour at annual resolution (Fritts 2001). Most dendrochronological studies are based on isolated or dominant trees, as they are more sensitive to climate than smaller trees. This increased sensitivity could be linked to tree age and size increase (Mencuccini et al. 2005; Rossi et al. 2008). The increase in size and age can affect stomatal conductance (i.e. water-use efficiency) (Hubbard et al. 1999; Bert et al. 1997) and photosynthetic performance causing a reduction light capture efficiency (Niinemets 2010). Furthermore, tree sensitivity to climate can vary in time and space due to phenotypic plasticity and genetic variability (e.g. Voltas et al. 2008; de Luis et al. 2013), altitudinal gradient (Liang et al. 2019), community structure and local environmental conditions (Martín-Benito et al. 2011; Moreno-Gutiérrez et al. 2012).

However, tree responses to climate can be different from species to species, due to their adaptive capacities and environmental requirements (Nicoll et al. 2006). For example, the association of different tree species could respond differently to the climate, due to the different functional traits (e.g. genetic diversity and physiological characteristics) (Lebourgeois et al. 2013). According to Hisano et al. (2018), diversity of tree species in a defined habitat show positive responses, in terms of radial growth, even when the effects of climate variables are negative. This suggests that systems with greater diversity are more suitable and resistant to the impacts of climate change. In fact, several studies have shown that higher tree species richness may lead to greater forest stand productivity (e.g. Liang et al. 2016), higher degree of resistance and resilience to biotic and abiotic disturbances (e.g. Seidl et al. 2016) and an improvement in the provision of ecosystem services (Gamfeldt et al. 2013).

However, overyielding effects in mixed forests could be masked by other factors (e.g. varying soil conditions, management practices, competitive interactions) (Pretzsch et al. 2015b) that can vary across plots and change with stand age (Lu et al. 2016).

The interactions between trees are important mechanisms for forest community dynamics, and the result of these interactions can vary depending on the environmental gradient and tree growth stages (Fichtner et al. 2012; Coates et al. 2013; Forrester, 2014). Interactions can be attributed to competition or facilitation effects occurring in forest stands (del Río et al. 2014a; García-Cervigón et al. 2013). Generally, positive interactions occur when trees can interact with each other, improving the availability or uptake of a given limiting resource (He et al. 2013; Forrester 2014). Divergent crown architectures, crown phenology and root distribution can play an important role in the complementary use of resources (Forrester and Albrecht 2014; Pretzsch et al. 2014b, 2015a). For example, in mixed forests with divergent architectures and differences in shade tolerance between species, different space occupation and light irradiance partition (Lu et al. 2016). The partitioning of light could improve even when the species in mixtures differ in their crown phenology.

Furthermore, different depths between root systems can improve the acquisition of nutrients and water (Forrester et al. 2010; Reyer et al. 2010; Brassard et al. 2013; Pretzsch et al. 2013). Several studies (e.g., Coates et al. 2013; Mölder and Leuschner 2014; Forrester 2014) have shown that competitive interactions in mixed stands are less severe than in corresponding monocultures. However, the positive effects that occur in mixed forests can also depend on stand density (Condés et al. 2013), site quality (Pretzsch et al. 2010) and changes in growth conditions (del Río et al. 2014b) and the spatial arrangement of trees (Fraver et al. 2014). Fraver et al. (2014) and Fichtner et al. (2015) have shown that the spatial arrangement of trees, especially in uneven-aged and uneven-structured stands (Weber et al. 2008), can regulate and modify the intensity and strength of competitive interactions, strongly influencing the radial growth of trees.

Studying and understanding the interactions that occur between species, especially in mixed forests, is very complicated. The interactions between trees are often dynamic and this dynamism can lead to a change in the resources availability or climatic conditions that do not always turn into positive interactions for species (Pretzsch et al. 2010; Forrester et al. 2011; Bouillet et al. 2013).

One way to study and identify the interactions between trees is through the use of competition indices (Bosela et al. 2015). The competition indices are classified into two main groups: distance-independent indices and distance-dependent indices (Metz et al. 2013; Sun et al. 2019). Distance-independent indexes use only data based on the size distribution of trees within a given area (Wimberly and Bare 1996). The distance-dependent indices, on the other hand, are based on spatial data incorporating both the size and the spatial distribution of trees (Biging and Dobbertin 1995; Tomé and Burkhart 1989).

However, to calculate competitive interactions and study the effect they have on forest populations, it is essential to obtain information regarding the spatial distribution of individual trees, and their height, diameter, crown projection, and biomass. Generally, this information is taken from methods based on field measurements. These conventional techniques provide reasonably accurate estimates, but they require labor-intensive and time-consuming measurements and inspections. In addition, these methods based on field measurements are generally limited to small areas while in many cases, it is necessary to have measurements over large areas. Therefore, the use of remote sensing, in particular of light detection and ranging (lidar) remote sensing technology, partially overcomes these limitations. Lidar (detection and light beam) is an active remote sensing technique that uses laser light. Lidar instruments measure the roundtrip time of a laser pulse between the sensor and a target (Dubayah and Drake 2000). The travel time of the pulse (usually with a near infrared wavelength for vegetation studies), provides a distance or a radius from the instrument to the object (Dubayah and Drake 2000). ALS (Vierling et al. 2008) and HS (Asner et al. 2015) data are a very promising tool for studies related to forest ecology and territorial mapping, offering a better estimate of the structure of forests. In fact, several studies (e.g. Popescu et al. 2004; Simonson et al. 2016) have used lidar metrics for the estimation of forest biomass and volume and other forest characteristics.

Therefore, determining how or when interactions between species occur and understanding how climate affects tree radial growth is essential for developing adaptive forest management strategies. Forest management can mitigate the impacts of climate change by maintaining or improving the provision of ecosystem services (e.g. carbon sequestration), soil conservation, water regulation and biodiversity prevention (Albert et al. 2015; Körner 2017; Nabuurs et al. 2017; Hisano et al. 2018). Stand density and thinning can change tree responses to climate (Cotillas et al. 2009; Martin-Benito et al. 2010) and modulate climate sensitivity (Linares et al. 2010; Mérian and Lebourgeois 2011). Stand density may also change over time due to the growth and mortality of the trees related to the mixing effects (Reyes-Hernandez et al. 2013; Pretzsch and Zenner 2017). Therefore, it is necessary that forest management is adapted to reduce competition for resources within the stands (Hemery 2008; Doley 2010; Lindner et al. 2010) and that silvicultural regimes are modified and developed considering particular structural characteristics of particular species on certain sites (Forrester, 2019). Another way to deal with environmental changes could be the selection of tree species that are more resistant to drought (Bréda et al. 2006) or increase tree diversity within stands (Hooper et al. 2005). Diversity in tree species could have positive effects on long-term productivity (Isbell et al. 2019), as different systems could lead to an improvement in tackling climate change (Hooper et al. 2005). However, increasing diversity is not always a good predictor of the water stress response of species. According to Forrester et al. (2016) it is necessary to have more detailed information on the combinations of species, sites, climatic conditions, age and stand structures to reduce the water stress of the forests. Although recently the focus of forest research has shifted toward mixed-species forests, there is contrasting evidence about the ability of tree species mixture to better withstand climatic variations (Bouillet et al. 2013; Epron et al. 2013). Additional insights on the functions of mixed-species stands and the causes of their overyielding is required for implementing efficient management strategies.

Objectives and structure of thesis

The study and identification of factors that can influence the radial growth of trees is fundamental to implement sustainable forest management practices and to understand the dynamics of forest development. In this context, the research activity carried out during the three-year doctorate focused on growth-climate relationships in mixed-species vs. corresponding monocoltures.

The main objective of this thesis was to study and understand the influence of climatic variations and competitive interactions on trees radial growth, in particular of three important forest species: European beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* L.) and silver fir (*Abies alba* Mill.). The thesis is linked with activities conducted within the COST (European Cooperation in Science and Technology) Action CLIMO (Climate-Smart Forestry in Mountain Regions - CA15226), financially supported by the EU Framework Program for Research and Innovation HORIZON 2020.

The work is structured into three chapters. In detail, the first chapter is being reviewed by the European Journal of Forest Research; the second work is close to submitting iForest - Biogeosciences and Forestry and the third work was published to Remote Sensing. The work described in the first chapter, aims to understand how climatic variables and extreme events influence European beech and silver fir growth along a latitudinal gradient of the Italian peninsula (Trentino, Molise and Calabria).

In this context, the second work, described in chapter 2, aims to analyze the interactions between European beech and silver fir and the influence these interactions have on the growth of trees in mixed and pure stands located in two regions (Molise and Calabria) in southern Italy at the limits of the distribution area of these two forest species. In particular, it was assessed whether the competitive interactions in mixed stands were lower than the corresponding monocultures and whether intra- and inter-specific competition favored the radial growth of silver fir compared to beech in mixed stands. The interactions between trees have been identified through the calculation of the competition indices at the individual level.

In line with the second work, the research activities continued with a further deepening of the competition processes. In detail, the third work, described in chapter 3, aims to test the efficiency of light detection and ranging (lidar) remote sensing technology in predicting competition indices. In particular, the aim was to estimate the competition dynamics for individual trees of Norway spruce and silver fir in an area of approximately 4 km^2 in the municipality of Lavarone (Trentino) and to identify the relationship between competitive interactions and tree aboveground biomass (AGB).

References

Albert, M., Hansen, J., Nagel, J., Schmidt, M., and Spellmann, H. (2015). Assessing risks and uncertainties in forest dynamics under different management scenarios and climate change. Forest Ecosystems, 2(1), 14.

Asner, G. P., Martin, R. E., Anderson, C. B., and Knapp, D. E. (2015). Quantifying forest canopy traits: Imaging spectroscopy versus field survey. Remote Sensing of Environment, 158, 15-27.

Bert, D., Leavitt, S.W., and Dupouey, J.L. (1997). Variations of wood δ13C and water-use efficiency of Abies alba during the last century. Ecology, 78(5), 1588-1596.

Biging, G.S., Dobbertin, M. (1995). Evaluation of Competition Indices in Individual Tree Growth Models. Forest science, 41, 360–377.

Boer, M.M., Resco de Dios, V. and Bradstock, R.A. (2020). Unprecedented burn area of Australian mega forest fires. Nat. Clim. Chang. 10, 171–172.

Bošeľa, M., Tobin, B., Šebeň, V., Petráš, R., and Larocque, G.R. 2015. Different mixtures of Norway spruce, silver fir, and European beech modify competitive interactions in central European mature mixed forests. Canadian Journal of Forest Research, 45(11): 1577-1586.

Bouillet, J.P., Laclau, J.P., de Moraes Gonçalves, J.L., Voigtlaender, M., Gava, J.L., Leite, F.P., Hakamadar, R., Mareschal, L., Mabiala, A., Tardy, F., Levillaing, J., Deleporte, P., Eprona, D., Nouvellon, Y. (2013). Eucalyptus and Acacia tree growth over entire rotation in single-and mixed-species plantations across five sites in Brazil and Congo. Forest Ecology and Management, 301, 89-101.

Brassard, B.W., Chen, H.Y., Cavard, X., Laganière, J., Reich, P.B., Bergeron, Y., Paré, D., and Yuan, Z. (2013). Tree species diversity increases fine root productivity through increased soil volume filling. Journal of Ecology, 101(1): 210-219.

Bréda, N., Huc, R., Granier, A., and Dreyer, E. (2006). Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. Annals of Forest Science, 63(6), 625-644.

Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G., Romme W.H., Kastens, J.H., Floy, M.L., Belnap, J., Anderson, J.J., Myers, O.B., and Meyer, C.W. (2005). Regional vegetation die-off in response to global-change-type drought. Proceedings of the National Academy of Sciences, 102(42), 15144-15148.

Büntgen, U., Krusic, P.J., Piermattei, A. et al. (2019) Limited capacity of tree growth to mitigate the global greenhouse effect under predicted warming. Nat Commun 10, 2171.

Bussotti, F., and Pollastrini, M. (2017). Observing climate change impacts on European forests: what works and what does not in ongoing long-term monitoring networks. Frontiers in plant science, 8, 629.

Cherubini, P., Gartner, B.L., Tognetti, R., Braeker, O.U., Schoch, W., and Innes, J.L. (2003). Identification, measurement and interpretation of tree rings in woody species from Mediterranean climates. Biological Reviews, 78(1), 119-148.

Coates, K.D., Lilles, E.B., and Astrup, R. (2013). Competitive interactions across a soil fertility gradient in a multispecies forest. Journal of Ecology, 101(3), 806-81.

Condés, S., Del Río, M., and Sterba, H. 2013. Mixing effect on volume growth of *Fagus sylvatica* and *Pinus sylvestris* is modulated by stand density. For. Ecol. Manag. 292: 86-95.

Cotillas, M., Sabate, S., Gracia, C., and Espelta, J.M. (2009). Growth response of mixed Mediterranean oak coppices to rainfall reduction: could selective thinning have any influence on it?. Forest Ecology and Management, 258(7), 1677-1683.

de Luis, M., Cufar, K., Filippo, I.A., Ovak, K., Apadopoulos, A., Iovesan, G., Athgeber, C.B., Aventós, J., Az, M.A., and Mith, K.T. (2013) Plasticity in dendroclimatic response across the distribution range of Aleppo pine (*Pinus halepensis*). PLoS One 8:e83550

Del Río, M., Schütze, G., and Pretzsch, H. (2014a). Temporal variation of competition and facilitation in mixed species forests in Central Europe. Plant Biology, 16(1), 166-176.

Del Río, M., Condés, S., and Pretzsch, H. (2014b). Analyzing size-symmetric vs. size-asymmetric and intra-vs. inter-specific competition in beech (*Fagus sylvatica* L.) mixed stands. Forest Ecology and Management, 325: 90-98.

Doley, D. (2010). The response of forests to climate change: the role of silviculture in conserving threatened species. Australian forestry, 73(2), 115-125.

Dubayah, R. O., and Drake, J. B. (2000). Lidar remote sensing for forestry. Journal of Forestry, 98(6), 44-46.

Epron, D., Nouvellon, Y., Mareschal, L., e Moreira, R.M., Koutika, L.S., Geneste, B., Delgado-Rojas, J.S., Laclau, J-P., Sola, G., de Moraes Gonçalves, J.L., and Bouillet, J.P. (2013). Partitioning of net primary production in Eucalyptus and Acacia stands and in mixed-species plantations: two case-studies in contrasting tropical environments. Forest Ecology and Management, 301, 102-111.

Fichtner, A., Forrester, D.I., Härdtle, W., Sturm, K., and von Oheimb, G. (2015). Facilitative-competitive interactions in an old-growth forest: the importance of large-diameter trees as benefactors and stimulators for forest community assembly. PloS one, 10(3), e0120335.

Fichtner, A., Sturm, K., Rickert, C., Härdtle, W., and Schrautzer, J. (2012). Competition response of European beech *Fagus sylvatica* L. varies with tree size and abiotic stress: minimizing anthropogenic disturbances in forests. Journal of Applied Ecology, 49(6), 1306-1315.

Forrester, D. I. (2019). Linking forest growth with stand structure: Tree size inequality, tree growth or resource partitioning and the asymmetry of competition. Forest Ecology and Management, 447, 139-157.

Forrester, D. I., Bonal, D., Dawud, S., Gessler, A., Granier, A., Pollastrini, M., and Grossiord, C. (2016). Drought responses by individual tree species are not often correlated with tree species diversity in E uropean forests. Journal of Applied Ecology, 53(6), 1725-1734.

Forrester, D.I. (2014). The spatial and temporal dynamics of species interactions in mixed-species forests: from pattern to process. Forest Ecology and Management, 312, 282-292.

Forrester, D.I., and Albrecht, A.T. (2014). Light absorption and light-use efficiency in mixtures of *Abies alba* and *Picea abies* along a productivity gradient. Forest Ecology and Management, 328, 94-102.

Forrester, D.I., Theiveyanathan, S., Collopy, J.J., and Marcar, N.E. (2010). Enhanced water use efficiency in a mixed *Eucalyptus globulus* and *Acacia mearnsii* plantation. Forest Ecology and Management, 259(9), 1761-1770.

Forrester, D.I., Vanclay, J.K., and Forrester, R.I. (2011). The balance between facilitation and competition in mixtures of Eucalyptus and Acacia changes as stands develop. Oecologia, 166(1), 265-272.

Fraver, S., D'Amato, A.W., Bradford, J.B., Jonsson, B.G., Jönsson, M., and Esseen, P.A. (2014). Tree growth and competition in an old-growth *Picea abies* forest of boreal Sweden: influence of tree spatial patterning. Journal of Vegetation Science, 25(2): 374-385.

Fritts, H.C. (2001). Tree Rings and Climate. The Blackburn Press, London.

Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., Riuz-Jaen, M.C., Fröberg, M., Stendahl, J., Philipson, C.D., Mikusiński, G., Andersson, E., Westerlund, B., Andrén, H., Moen, J., and Bengtsson, J. 2013. Higher levels of multiple ecosystem services are found in forests with more tree species. Nature Communications, 4: 1340.

García-Cervigón, A.I., Gazol, A., Sanz, V., Camarero, J.J., and Olano, J.M. (2013). Intraspecific competition replaces interspecific facilitation as abiotic stress decreases: The shifting nature of plant–plant interactions. Perspectives in Plant Ecology, Evolution and Systematics, 15(4), 226-236.

He, Q., Bertness, M.D., and Altieri, A.H. (2013). Global shifts towards positive species interactions with increasing environmental stress. Ecology letters, 16(5), 695-706.

Hemery, G. E. (2008). Forest management and silvicultural responses to projected climate change impacts on European broadleaved trees and forests. International Forestry Review, 10(4), 591-607.

Hisano M., Searle E.B., and Chen H.Y. (2018). Biodiversity as a solution to mitigate climate change impacts on the functioning of forest ecosystems. Biological Reviews, 93, 439-456. doi: 10.1111/brv.12351

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., Wardle D.A. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological monographs, 75, 3-35.

Hubau, W., Lewis, S.L., Phillips, O.L. et al. (2020) Asynchronous carbon sink saturation in African and Amazonian tropical forests. Nature 579, 80–87.

Hubbard, R.M., Bond, B.J., and Ryan, M.G. (1999). Evidence that hydraulic conductance limits photosynthesis in old *Pinus ponderosa* trees. Tree Physiology, 19(3), 165-172.

Isbell, F., Tilman, D., Reich, P.B., and Clark, A.T. (2019). Deficits of biodiversity and productivity linger a century after agricultural abandonment. Nature ecology and evolution, 3(11), 1533-1538.

Jucker, T., Avăcăriţei, D., Bărnoaiea, I., Duduman, G., Bouriaud, O., Coomes, D.A. (2016). Climate modulates the effects of tree diversity on forest productivity. Journal of Ecology, 104, 388–398.

Jump, A.S., Hunt, J.M., and Penuelas, J. (2006). Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. Global Change Biology, 12(11), 2163-2174.

Körner, C. (2017). A matter of tree longevity. Science, 355(6321), 130-131.

LaMarche, V. C. (1973). Holocene climatic variations inferred from treeline fluctuations in the White Mountains, California. Quaternary Research, 3(4), 632-660.

Lebourgeois, F., Gomez, N., Pinto, P., and Mérian, P. (2013). Mixed stands reduce *Abies alba* tree-ring sensitivity to summer drought in the Vosges mountains, western Europe. Forest ecology and management, 303, 61-71.

Liang, H., Huang, J.-G., Ma, Q., Li, J., Wang, Z., Guo, X., Zhu, H., Jiang, S., Zhou, P., Yu, B., and Luo, D. (2019). Contributions of competition and climate on radial growth of *Pinus massoniana* in subtropics of China. Agricultural and Forest Meteorology, 274, 7–17.

Liang, J., Crowther, T.W., Picard, N., Zhou, M., Alberti, G., Schulze, E-D., McGuire, A.D., Bozzato, F., Pretzsch, H., de-Miguel, S., Paquette, A., Hérault, B., Scherer-Lorenzen, M., Barrett, C.B., Glick, H.B., Hengeveld, G.M., Nabburs, G-J., Pfautsch, S., Viana, H., Vibrans, A.C., Ammer, C., Schall, P., Verbyla, D., Tchebakova, N., Fischer, M., Watson, J.V., Chen, H.Y.H., Lei, X., Schelhaas, M-J., Lu, H., Gianelle, D., Parfenova, E.I., Salas, C., Lee, E., Lee, B., Kim, H.S., Bruelheide, H., Coomes, D.A., Piotto, D., Sunderland, T., Schmid, B., Gourlet-Fleury, S., Sonké, B., Tavani, R., Zhu, J., Brandl, S., Vayreda, J., Kitahara, F., Searle, E.B., Neldner, V.J., Ngugi, M.R., Baraloto, C., Frizzera, L., Bałazy, R., Oleksyn, J., Zawiła-Niedźwiecki, T., Bouriaud, O., Bussotti, F., Finér, L., Jaroszewicz, B., Jucker, T., Valladares, F., Jagodzinski, A.M., Peri, P.L., Gonmadje, C., Marthy, W., O'Brien, T., Martin, E.H., Marshall, A.R., Rovero, F., Bitariho, R., Niklaus, P.A., Alvarez-Loayza, P., Chamuya, N., Valencia, R., Mortier, F., Wortel, V., Engone-Obiang, N.L., Ferreira, L.V., Odeke, D.E., Vasquez, R.M., Lewis, S.L., and Reich, P.B. (2016). Positive biodiversity-productivity relationship predominant in global forests. Science, 354(6309): aaf8957.

Liang, P., Wang, X., Sun, H., Fan, Y., Wu, Y., Lin, X., and Chang, J. (2019). Forest type and height are important in shaping the altitudinal change of radial growth response to climate change. Scientific reports, 9(1), 1336.

Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J., Seidl, R., Delzon, S., Corona, P., Kolström, M., Lexer, M.J., Marchetti, M. (2010). Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. Forest Ecology and Management, 259, 698-709.

Lu, H., Mohren, G.M., den Ouden, J., Goudiaby, V., and Sterck, F.J. (2016). Overyielding of temperate mixed forests occurs in evergreen–deciduous but not in deciduous–deciduous species mixtures over time in the Netherlands. Forest Ecology and Management, 376: 321-332.

Martín-Benito, D., Del Río, M., Heinrich, I., Helle, G., and Canellas, I. (2010). Response of climate-growth relationships and water use efficiency to thinning in a *Pinus nigra* afforestation. Forest Ecology and Management, 259(5), 967-975.

Martín-Benito, D., Kint, V., Del Río, M., Muys, B., and Cañellas, I. (2011). Growth responses of West-Mediterranean *Pinus nigra* to climate change are modulated by competition and productivity: past trends and future perspectives. Forest Ecology and Management, 262(6), 1030-1040.

Mencuccini, M., Martínez-Vilalta, J., Vanderklein, D., Hamid, H.A., Korakaki, E., Lee, S., and Michiels, B. (2005). Size-mediated ageing reduces vigour in trees. Ecology letters, 8(11), 1183-1190.

Mérian, P., and Lebourgeois, F. (2011). Size-mediated climate–growth relationships in temperate forests: a multi-species analysis. Forest Ecology and Management, 261(8), 1382-1391.

Metz, J., Seidel, D., Schall, P., Scheffer, D., Schulze, E.D., and Ammer, C. (2013). Crown modeling by terrestrial laser scanning as an approach to assess the effect of aboveground intra-and interspecific competition on tree growth. Forest Ecology and Management, 310: 275-288.

Mölder, I., and Leuschner, C. (2014). European beech grows better and is less drought sensitive in mixed than in pure stands: tree neighbourhood effects on radial increment. Trees. 28(3): 777-792.

Moreno-Gutiérrez, C., Battipaglia, G., Cherubini, P., Saurer, M., Nicolas, E., Contreras, S., and Querejeta, J.I. (2012). Stand structure modulates the long-term vulnerability of *Pinus halepensis* to climatic drought in a semiarid Mediterranean ecosystem. Plant, cell and environment, 35(6), 1026-1039.

Mueller, R.C., Scudder, C.M., Porter, M.E., Talbot Trotter III, R., Gehring, C.A., and Whitham, T.G. (2005). Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts. Journal of Ecology, 93(6), 1085-1093.

Mund, M., Kummetz, E., Hein, M., Bauer, G.A., and Schulze, E.D. (2002). Growth and carbon stocks of a spruce forest chronosequence in central Europe. Forest Ecology and Management, 171(3), 275-296.

Nabuurs, G.J., Delacote, P., Ellison, D., Hanewinkel, M., Hetemäki, L., and Lindner, M. (2017). By 2050 the mitigation effects of EU forests could nearly double through climate smart forestry. Forests, 8(12), 484.

Nicoll, B.C., Gardiner, B.A., Rayner, B., Peace, A.J. (2006). Anchorage of coniferous trees in relation to species, soil type, and rooting depth. Canadian Journal of Forest Research, 36, 1871-1883.

Niinemets, Ü. (2010). A review of light interception in plant stands from leaf to canopy in different plant functional types and in species with varying shade tolerance. Ecological Research, 25(4), 693-714.

Pigott, C.D., and Huntley, J.P. (1978). Factors controlling the distribution of *Tilia cordata* at the northern limits of its geographical range: i. distribution in north-west England. New Phytologist, 81(2), 429-441.

Popescu, S.C., Wynne, R.H., Scrivani, J.A. (2004). Fusion of Small-Footprint Lidar and Multispectral Data to Estimate Plot-Level Volume and Biomass in Deciduous and Pine Forests in Virginia, USA. Forest Science, 50, 551–565.

Pretzsch, H., Biber, P., Schütze, G. et al. (2014a). Forest stand growth dynamics in Central Europe have accelerated since 1870. Nature Communications, 5, 4967.

Pretzsch, H., Biber, P., Schütze, G., and Bielak, K. (2014b). Changes of forest stand dynamics in Europe. Facts from long-term observational plots and their relevance for forest ecology and management. Forest Ecology and Management, 316, 65-77.

Pretzsch, H., Block, J., Dieler, J., Dong, P.H., Kohnle, U., Nagel, J., Spellmann, H., and Zingg, A. (2010). Comparison between the productivity of pure and mixed stands of Norway spruce and European beech along an ecological gradient. Annals of Forest Science, 67(7), 712.

Pretzsch, H., del Río, M., Ammer, C., Avdagic, A., Barbeito, I., Bielak, K., Brazaitis, G., Coll, L., Dirnberger, G., Drössler, L., Fabrika, M., Forrester, D.I., Godvod, K., Heym, M., Hurt, V., Kurylyak, V., Löf, M., Lombardi, F., Matović, B., Mohren, F., Motta, R., den Ouden, J., Pach, M., Ponette, Q., Schütze. G., Schweig, j., Skrzyszewski, J., Sramek, V., Sterba, H., Stojanović, D., Svoboda, M., Vanhellemont, M., Verheven, K., Wellhausen, K., Zlatanov, T., Bravo-Oviedo, A. (2015a). Growth and yield of mixed versus pure stands of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) analysed along a productivity gradient through Europe. European Journal of Forest Research, 134(5), 927-947.

Pretzsch, H., Forrester, D.I., and Rötzer, T. (2015b). Representation of species mixing in forest growth models. A review and perspective. Ecological Modelling, 313, 276-292.

Pretzsch, H., and Zenner, E. K. (2017). Toward managing mixed-species stands: from parametrization to prescription. Forest Ecosystems, 4(1), 19.

Pretzsch, H., Schütze, G., and Uhl, E. (2013). Resistance of European tree species to drought stress in mixed versus pure forests: evidence of stress release by inter-specific facilitation. Plant Biology, 15(3), 483-495.

Reyer, C., Lasch, P., Mohren, G.M., and Sterck, F.J. (2010). Inter-specific competition in mixed forests of Douglas-fir (*Pseudotsuga menziesii*) and common beech (*Fagus sylvatica*) under climate change–a model-based analysis. Annals of Forest Science, 67(8), 805.

Reyes-Hernandez, V., Comeau, P. G., and Bokalo, M. (2013). Static and dynamic maximum size–density relationships for mixed trembling aspen and white spruce stands in western Canada. Forest ecology and management, 289, 300-311.

Rossi, S., Deslauriers, A., Anfodillo, T., and Carrer, M. (2008). Age-dependent xylogenesis in timberline conifers. New Phytologist, 177(1), 199-208.

Sangüesa-Barreda, G., Camarero, J.J., Sánchez-Salguero, R., Gutiérrez, E., Linares, J.C., Génova, M., Ribas, M., Tíscar, P.A., and López-Sáez, J.A. (2019). Droughts and climate warming desynchronize Black pine growth across the Mediterranean Basin. Science of the Total Environment, 697, 133989.

Scarascia-Mugnozza G, Oswald H, Piussi P, Radoglou K (2000). Forests of the Mediterranean region: gaps in knowledge and research needs. Forest ecology and management, 132, 97–109.

Seidl, R., Spies, T.A., Peterson, D.L., Stephens, S.L., and Hicke, J.A. (2016). Searching for resilience: addressing the impacts of changing disturbance regimes on forest ecosystem services. Journal of Applied Ecology, 53(1): 120-129.

Simonson, W., Ruiz-Benito, P., Valladares, F., Coomes, D. (2016). Modelling above-ground carbon dynamics using multi-temporal airborne lidar: Insights from a Mediterranean woodland. Biogeosciences, 13, 961–973.

Sun, S., Cao, Q.V., Cao, T. (2019). Evaluation of distance-independent competition indices in predicting tree survival and diameter growth. Canadian Journal of Forest Research, 49, 440–446.

Tomé, M., Burkhart, H. (1989). Distance-Dependent Competition Measures for Predicting Growth of Individual Trees. Forest of Science, 35, 816–831.

Vierling, K. T., Vierling, L. A., Gould, W. A., Martinuzzi, S., and Clawges, R. M. (2008). Lidar: shedding new light on habitat characterization and modeling. Frontiers in Ecology and the Environment, 6(2), 90-98.

Voltas, J., Chambel, M. R., Prada, M. A., and Ferrio, J. P. (2008). Climate-related variability in carbon and oxygen stable isotopes among populations of Aleppo pine grown in common-garden tests. Trees, 22(6), 759-769.

Weber, P., Bugmann, H., Fonti, P., and Rigling, A. (2008). Using a retrospective dynamic competition index to reconstruct forest succession. Forest Ecology and Management, 254(1): 96-106.

Wimberly, M.C., and Bare, B.B. (1996). Distance-dependent and distance-independent models of Douglas-fir and western hemlock basal area growth following silvicultural treatment. Forest Ecology and Management, 89(1-3), 1-11.

Zhang, T., Niinemets, Ü., Sheffield, J., and Lichstein, J.W. (2018). Shifts in tree functional composition amplify the response of forest biomass to climate. Nature, 556(7699), 99.

CHAPTER 1

Interannual radial growth sensitivity to climatic variations and extreme events in mixed-species and pure stands of silver fir and European beech in the Italian Peninsula

1.1. Introduction

Continuous climate change and extreme events have made many forests more vulnerable to drought globally (Allen et al. 2010). The occurrence of disturbance events is altering species distribution and tree growth in many regions of Europe (Way and Oren 2010), as they threat structure and function of forest ecosystems (Castagneri et al. 2014). Studies on global and regional occurrences of extreme events have shown that the decrease in tree growth is linked to drought (Anderegg et al. 2016, 2019) and that these effects may last for several years (Camarero et al. 2015). Combined effects of drought spells and heat waves may undermine the ability of trees to tolerate biotic and abiotic stress, causing diffuse die-off (Anderegg et al. 2016). Drought-induced tree decline has shown spread and irregular patterns, triggering forest disequilibrium (Anderegg et al. 2012), vegetation shifts and successional dynamics (Breshears et al. 2005). Vegetation shifts and successional dynamics after drought-induced mortality may lead to the survival of only the dominant tree species (Suarez and Lloret 2018), or replace less drought-resistant species with more resistant ones (Gazol et al. 2017a).

How forests and trees react to drought is complex and varies across forest stands, sites, regions and continents, depending on type of climate (Zhang et al. 2017), kind of biome (Vicente-Serrano et al. 2013; Mitchell et al. 2016) and tree species traits (Lopez-Iglesias et al. 2014; García-Forner et al. 2016). These impacts on forests and trees may accentuate differences between regions due to long-term climatic differences (Seim et al. 2014). The effect of climate change on regional and local drought variability is expected to be particularly pronounced in forests located in the Mediterranean area (Sangüesa-Barreda et al. 2019). Mediterranean forests represent one of the most vulnerable ecosystems to climate change (Scarascia-Mugnozza et al. 2000). Here, many European tree species reach their southernmost distribution limits (Luterbacher et al. 2012). A significant increase in temperatures is expected in the next few decades in Mediterranean regions (IPCC 2013, IPCC 2017), with dramatic implications for the future of these forest ecosystems. According to Sitch et al. (2008), the intensification of recurrent drought stress may lead to a reduction in the productivity of Mediterranean forests, eventually increasing the risk of tree mortality and forest dieback (Leonelli et al. 2017). The Mediterranean basin has a complex and heterogeneous climate, due to its geographical position and transitional nature (Sangüesa-Barreda et al. 2019). The complexity of Mediterranean climate and the legacy effect of human impact make mountain forests of this region ideal for testing the effects of extreme events on forest resilience and tree growth (Marziliano et al. 2019).

Tree-ring traits provide strong evidence of past disturbance events and growth-related indicators of long-term trajectories of forest development, resulting from silvicultural options. Studying growth responses to warming trends can be useful to envisage species-specific warning signals of tree mortality risk (Cailleret et al. 2016, 2017; Tognetti et al. 2019). Dendrochronological studies have been often conducted on trees that grow close to their environmental limits, since the climate response is more evident (e.g., Carrer et al. 2010). Yet, stem radial growth responses observed under limiting environmental conditions are not always indicative of the influence of climate change (Castagneri et al. 2014). According to Castagneri et al. (2012) and Eilmann and Rigling (2012), species-specific responses to extreme climatic conditions can be altered and modified by site- and stand-specific characteristics. Local site conditions (e.g., elevation and soil depth) (Lebourgeois et al. 2013) and plant functional traits (Lopez-Iglesias et al. 2014; García-Forner et al. 2016) may determine specific-species growth-climate relationships (Gazol et al. 2017b).

In recent decades, adaptive forest management has been proposed as an effective solution to cope with the negative impacts of variation in disturbance regime associated with climate change. For example, thinning may reduce intra-specific competition (Lindner et al. 2010), while favoring species coexistence may facilitate complementarity in resource use (Zalloni et al. 2019). In mixed-species forests, differences in plant functional traits may have positive effects on long-term growth trends (Isbell et al. 2019) and increase forest resilience (Hooper et al. 2005). In these conditions, allometric variation and hydraulic redistribution, together with species-specific shade tolerance, plant phenology, crown structure, and root depth of coexisting species (Lebourgeois et al. 2013; Conte et al. 2018) would provide more efficient uptake and use of resources within mixed-species forests (Pretzsch et al. 2015a). According to Leuschner et al. (2004) and Bréda et al. (2006), a deeper root system would favour water (and nutrients) uptake during the growing season, especially during dry years. Silver fir (*Abies alba* Mill.) has a deeper root system than that of European beech (*Fagus sylvatica* L.) (Konôpka 2001; Schmid and Kazda 2001; Nicoll et al. 2006). Silver fir and European beech are two important late successional forest species, both sensitive to summer drought and spring frost (Carrer et al. 2010; Cailleret and Davi 2011; Mérian and Lebourgeois 2011; Lebourgeois et al. 2013). Silver fir shows a sensitive stomatal closure in relation to drought (i.e., isohydric; Guehl et al. 1991; Magh et al. 2019; Bachofen et al. 2020). European beech, on the other hand, has a low capacity to maintain leaf water potential during drought events (i.e., anisohydric; Klein et al. 2014; Magh et al. 2019; Bachofen et al. 2020).

Castagneri et al. (2014) and Rita et al. (2014) have observed higher sensitivity to warmer and drier conditions in European beech than in silver fir, in mixed-species forests of the Dinaric Alps in Bosnia and Herzegovina (*Fagus-Abies-Picea*) and in southern Italy (*Fagus-Abies*). Mixing silver fir with

European beech has been found to improve the balance of soil greenhouse gases (Rehschuh et al. 2019) and the hydraulic redistribution of soil water under drought conditions (Magh et al. 2018). Mixed-species forests have been found to be more resistant to the impact of disturbance and productive than monocultures (Zhang et al. 2012; Lebourgeois et al. 2013; Pretzsch et al. 2013; Forrester and Bauhus 2016; Russo et al. 2020), and also to improve the provision of ecosystem services (Gamfeld et al. 2013). Nevertheless, there is conflicting evidence of the effect of climate and climate change on the radial growth of trees in forests of mixed species. According to Forrester et al. (2016), a greater species diversity not always leads to a reduced influence of climatic variations. The influence of climatic variations may vary between regions (Forrester et al. 2016), and the positive or negative effects in the mixtures can also derive from water related interactions (Forrester and Bauhus 2016). Therefore, additional insights on the functions of mixed-species forest stands and the causes of their over-yielding is required for implementing efficient management strategies.

The objective of this study was to understand the influence of climate and extreme events on the radial growth of European beech and silver fir, in the Italian Peninsula. We selected nine plots along a latitudinal gradient of the Italian peninsula (Trentino, Molise and Calabria), considering both mixed-species and corresponding pure plots of silver fir and European beech. Extending southeast from the Alps into the Mediterranean Sea, the Italian Peninsula has a variety of climatic conditions. This distinctive feature may make it possible to verify whether any clinal variation in growth-related characteristics occurs under warming trends and drought gradients in mixed-species vs. corresponding pure plots of these species. We hypothesized that: i) the change in the climate-growth relationship has a similar pattern along the latitudinal gradient; and ii) the effect of the mixture is stronger at the southern distribution limit (southern Italy) of these species than in populations closest to the core (Alps) of their range. To better understand the influence of climate on species growth, climate-growth relationships were investigated for European beech and silver fir, using correlation and response functions. In addition, tree growth responses to extreme climatic events were identified through the analysis of pointer years.

1.2 Materials and Methods

1.2.1 Study sites and plots

1.2.1.1 Sites description

This study was conducted in three mountain sites selected along a latitudinal transect in the Italian Peninsula. In particular, the three sampling sites were located in: i) Lavarone and Cembra (Trentino), ii) "Abeti Soprani" (Molise) and iii) Sila National Park ("Sila Piccola"; Calabria) (Fig. 1).

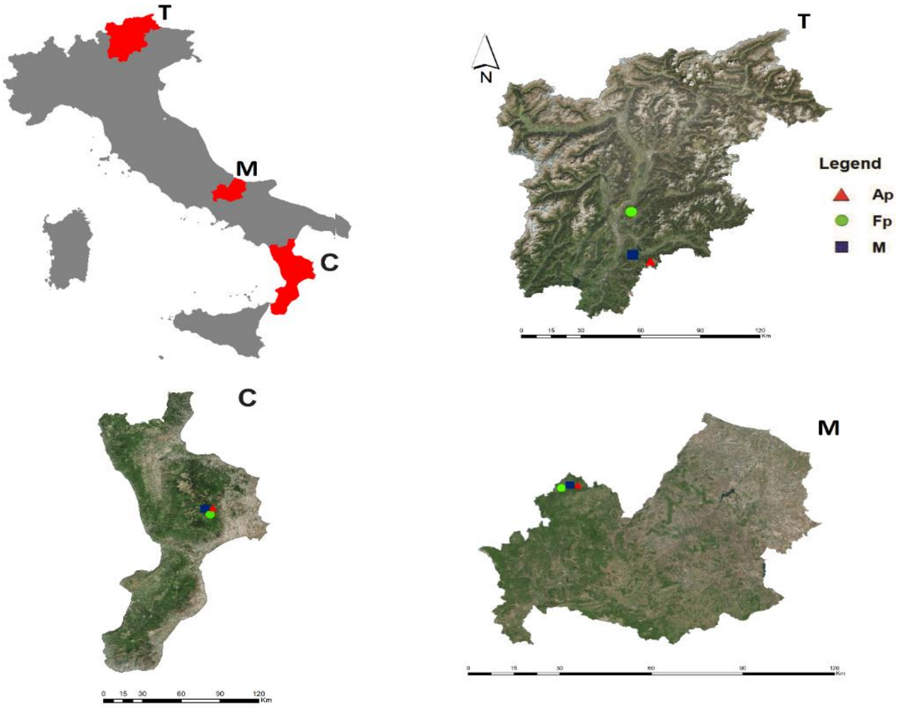


Figure 1. Location of the study sites along the Italian Peninsula. Red triangle indicates silver fir in pure plots (Ap); green circle indicates European beech in pure plots (Fp); blue square indicates the mixed-species plots (m). The sites are indicated as: T for Trentino, M for Molise, and C for Calabria.

The sites differ along the latitudinal transect both in terms of climatic characteristics and soil types. In particular, Trentino has higher mean annuals precipitations and mean temperatures than Molise and Calabria (Table 1). Moreover, Trentino has a mesic soils (Lithosoil) than Molise and Calabria that has moist (Rendzina) and dry (Distrudept) soils, respectively. The sites are indicated as: T for Trentino, M for Molise, and C for Calabria.

Table 1. Characteristics of the study sites. Exposure (°); altitude (m) and slope (°). Mean annuals precipitation (mm) and mean temperatures (°C) (period 1951–2016), derived from interpolation between grids data (European Observations (E-OBS) in combination with WorldClim) and meteorological stations.

Sites	Stands	Latitude (N)	Longitude (E)	Exposure (°)	Altitude (m a.s.l.)	Slope (°)	Precipitation (mm)	Temperature (°C)
Trentino	pure_beech	46°12'6.12"	11°12'37.05"	91	1276	20	682.9	7.0
	pure_fir	45°56'57.18"	11°18'53.14"	123	1446	18	830.7	5.8
	mixed-species	45°57'43.72"	11°16'26.63"	164	1423	19	611.6	6.0
Molise	pure_beech	41°52'13.65"	14°16'37.85"	354	1182	21	664.5	9.7
	pure_fir	41°52'11.02"	14°17'26.03"	317	1230	20	669.1	9.6
	mixed-species	41°52'14.35"	14°16'51.26"	327	1182	27	664.5	9.7
Calabria	pure_beech	39°9'13.49"	16°39'53.05"	343	1289	24	402.1	11
	pure_fir	39°9'19.31"	16°41'2.30"	319	1220	37	649.0	10.7
	mixed-species	39°9'7.96"	16°40'12.33"	307	1332	28	673.4	10.9

1.2.1.2 Plot characteristics

Each site is composed of three plots: i) pure European beech (Fp), ii) pure silver fir (Ap) and iii) mixture of both species (m). Plot sizes ranged from 0.12 ha to 0.19 ha (Table 2). The plots in Trentino are circular, while in Molise and Calabria they are rectangular.

Plot selection was based on the basal area occupied by each species within the plot (Mina et al. 2018), on the minimum number of individuals (≥ 50 trees of investigated species per plot) and on the elevation range (< 250 m between the triplets). Plots were considered pure when the basal area of the one single species was at least 85%. Mixed-species plots, on the other hand, were classified as a mixture of the two species, when both species represented 85% or more of the total basal area and each of the two species had contributed at least 20% of the basal area (Table 2). Plots are uneven aged and have random horizontal structure. In the mixed-species plots, silver fir is the dominant species and European beech is sub-dominant (Table 2). All plots have been unmanaged since 1979–80, with the exception of the mixed-species plot in Trentino, where selective logging was carried out in 2001–2002.

Table 2. Structural parameters obtained for each triplet of pure and mixed-species plots. Stand basal area, BA (m^2 ha^{-1}); percentage of basal area occupied by the main species (%); stand density (n. treesha^{-1}); average diameter at breast height, d_m (cm); average tree height, h_m (m); size of plot (m^2).

Sites	Stands	Basal area (m^2 ha^{-1})	Basal area main species (%)	Basal area minor species (%)	Stand density (n. trees ha^{-1})	d_m (cm)	h_m (m)	Cores /trees (n)	Size stand (m^2)
Trentino	pure_beech	36.8	85%	8% Norway spruce 7% European larch	1019	21	20	80/60	1256
	pure_fir	57.8	86%	15% Norway spruce	740	31	25	100/60	1256
	mixed_beech	40.6	26%	19% Norway spruce	937	15	13	54/36	1963
	mixed_fir		53%			33	21	45/36	
Molise	pure_beech	33.6	92%	5% Hop hornbeam 3%Silver fir	992	21	15	110/60	1200
	pure_fir	59.2	92%	8% European beech	533	37	21	86/44	1200
	mixed_beech	54.6	20%	2% Italian maple	446	28	19	47/31	1435
	mixed_fir		78%			58	27	38/19	
Calabria	pure_beech	59.8	87%	2% Italian maple 9% Lime	650	35	22	60/46	1200
	pure_fir	61.5	85%	9% Italian maple 5% Hop hornbeam	750	32	21	71/43	1200
	mixed_beech	76.5	33%	4% European black pine 1% Italian maple	628	35	22	42/25	1435
	mixed_fir		61%			47	27	42/29	

1.2.2 Tree sampling and ring-width chronologies

At the beginning of summer 2017, the structural attributes and dendrometric parameters were determined for all trees with a diameter ≥ 7 cm. For each tree, the stem diameter at 1.30 m, total height, tree species and spatial position were measured through Field-Map technology and software (http://www.fieldmap.cz/) in Calabria and Molise, and with Laser Technology Criterion 400 (Skovsgaard et al. 1998) in Trentino. Dominant and co-dominant trees were sampled for the dendrochronological analysis. Suppressed trees were excluded from the study due to their high sensitivity to competition. Two cores per tree were collected at breast height (1.3 m) at 120 ° from each other. In order to avoid compression wood (for silver fir) and tension wood (for European beech), cores were taken perpendicular to the slope. A total of 290 European beech and 235 silver fir trees were sampled (Table 2).

Cores were glued to grooved wooden supports and sanded with progressively finer grade abrasive paper up to an optimal surface resolution, thus allowing the reading of the annual rings. Ring-width series were measured with a LINTAB measuring table with an accuracy of 0.01 mm, equipped with a Leica MS5 stereoscope. The analysis was performed with the TSAP software package (Rinn 2003). The individual tree-ring width series were cross-dated visually against each other and statistically versus the respective mean chronology, using the software COFECHA (Holmes et al. 1989; Grissino-Mayer 2001). Only the successfully cross-dated cores, with a significant ($P \leq 0.05$) ‘‘Gleichlaüfigkeit’’, were used for further analyses. In order to remove non-climatic trends due to tree age, size and stand dynamics, each single series was standardized using ARSTAN program (Cook and Holmes 1984) with a cubic spline curve function with a 50% frequency cut-off. For all sites, a 32-years cubic smoothing spline was applied, except for pure silver fir plot; in the latter case, a 20-years cubic smoothing spline was used, due to the younger age of trees.

To compare tree-ring chronologies, several descriptive statistics were calculated: i) the mean chronology, being the average number of years for two cores per tree; ii) the mean sensitivity (MS), which is the average difference between successive ring width values (Fritts 1976); iii) the first order autocorrelation (AC1) to detect the persistence retained before and after the standardization; iv) the expressed population signal (EPS), indicating the reliability of a chronology by comparing the chronology with the theoretical chronology based on an infinite number of trees, with a threshold of 0.85 (Wigley et al. 1984); v) the mean RBAR, which is the average correlation coefficient calculated for a common time interval between the single series in a chronology.

1.2.3 Meteorological data

A downscaled version of European Observations (E-OBS) in combination with WorldClim climate surfaces, to achieve a 0.0083° (about 1×1 km grid) resolution climate data set (Moreno and Hasenauer 2015), was utilized. E-OBS is an interpolated gridded daily climate data set that covers all of Europe (Haylock et al. 2008). WorldClim, on the other hand, has been designed to provide long-term monthly averages of precipitation and minimum and maximum temperatures based on a set of climate surfaces (Hijmans et al. 2005). Extrapolation of maximum and minimum monthly temperatures (Tmax, Tmin) and total monthly precipitation (P), from 1951 to 2012, was obtained through the package *raster* of the R software (Hijmans et al. 2019), considering the grid data and the plot coordinates. Grid data were used due to the short period and spatial fragmentation of data from the nearest meteorological stations: 1998–2016 Faedo and Vezzena (Trentino), 1961–2016 Capracotta (Molise), and 2001–2016 Taverna (Calabria). However, due to the lack of information for the last four years, a general linear model was used between data obtained from extrapolation of grid data and climatic records of the nearest meteorological stations. The linear regression function allowed us to calculate, for each plot, the determination coefficient R^2, (Trentino ($R^2 = 0.98$, $R^2 = 0.97$, $R^2 = 0.63$, respectively, for Tmax, Tmin and P), Molise ($R^2 = 0.94$, $R^2 = 0.95$, $R^2 = 0.57$, respectively, for Tmax, Tmin and P), and Calabria ($R^2 = 0.96$, $R^2 = 0.97$, $R^2 = 0.60$, respectively, for Tmax, Tmin and P)). The exact equation (Table S1) was then used to extrapolate the climatic data (T and P) of each month in the last years, and obtain a complete chronology (1951 to 2016).

1.2.4 Drought indices

The aridity indices are defined as numerical indicators of the degree of dryness of the climate at a given position, classifying the climate in relation to water availability (Tabari et al. 2014). In this study, we used De Martonne aridity index (1926) to determine the water supply in the three sites analyzed. De Martonne (1926) aridity index (AI) was calculated through the following formula:

$$AI = \left(\frac{P_{year}}{T_{year} + 10}\right)$$

where P_{year} is the annual mean precipitation in mm and T_{year} is the annual mean air temperature in °C. A higher value of De Martonne aridity index (AI) indicates a greater water supply for the growth of trees. On the contrary, a lower value of this index indicates a greater probability of drought. To better understand the term "high and low value" we have inserted the climatic classification based on the values of AI (Table 3).

Table 3. Type of climate according to De Martonne aridity index (Croitoru et al. 2013).

Climate type	AI values
Arid	AI < 10
Semi-arid	10 ≤ AI < 20
Mediterranean	20 ≤ AI < 24
Semi-humid	24 ≤ AI < 28
Humid	28 ≤ AI < 35
Very Humid	35 ≤ AI < 55
Extremely humid	AI > 55

1.2.5 Identification of pointer years

Pointer years indicate those years in which conspicuously wide or narrow tree rings are created in response to extreme environmental conditions and/or climatic events (Schweingruber et al. 1990). To determine the pointer years, we used the method proposed by Becker (1989) and used by Lebourgeois et al. (2010) and Lebourgeois et al. (2013). Through the pointer function of the *dplR* package (Bunn 2010) of the R software, the relative variations in radial growth (RGV%) were calculated:

$$RGV\% = 100 \times (\frac{RW_n - RW_{n-1}}{RW_{n-1}})$$

where RW_n is the ring width of the year n, and RW_{n-1} the ring width of the previous year.

Relative radial growth variation (RGV%) expresses to which extent the ring of the current year is narrower (negative value) or wider (positive value) than the previous one. Therefore, a pointer year is a year for which at least 70% of the cross-dated trees present RGV% of at least 15%.

1.2.6 Statistical analysis

1.2.6.1 Climate-growth

Climate-growth relationships were based on a common maximum period in all plots (1958–2016). In detail, trees showing growth series lengths of 58 years (356 trees) were identified, omitting all younger trees (31 trees). The climate-growth relationships were evaluated through the calculation of correlation and response functions, with the *treeclim* package (Zang and Biondi 2015) of the R software. The correlation functions are coefficients obtained from univariate estimates of Pearson’s correlation (e.g., Morrison 1983). The response functions, on the other hand, are multivariate coefficients obtained from a principal component regression model (Morzuch and Ruark 1991). The use of this approach allows an accurate evaluation of statistical significance and may generate appropriate ecophysiological hypotheses (e.g., Biondi et al. 1997). For the correlation and response functions, at $P \leq 0.05$, the growth chronology was considered as the dependent variable, and the monthly climatic variables (Tmax, Tmin e P) were used as regressors. The time period considered was established from April of the previous year to September of the current year.

Temporal changes in climate-growth relationships were analysed by calculating correlation functions from 1951 to 2016 in moving time windows of 20 years, in consecutive shifts of one year.

In order, to determine differences among sites, species (silver fir vs. European beech) and plots (pure vs. mixture), analysis of variance (ANOVA) was performed (Statistica software). Analyses were performed for each site and plot (both species-specific and mixture-pure) to identify significant variability of correlation coefficients. ANOVA and Bonferroni’s test were performed to compare results.

1.2.6.2 Growth and drought indices

Climatic data (precipitation and temperature) representative of each plot were used to calculate the De Martonne aridity index. The aridity index was calculated through the *climclass* package (Eccel et al. 2016) of the R software. Furthermore, to assess the influence of drought on the radial growth of European beech and silver fir in mixed-species and pure plots, Pearson's linear correlation function ($P \leq 0.05$) was carried out through the Statistics software. The correlation functions were performed between standardized mean chronologies and De Martonne aridity index.

1.2.6.3 Growth and extreme climatic events

To detect stem radial growth responses of mixed-species and pure plots to extreme climatic events, principal component analysis (PCA) was performed on pointer years. To construct the matrix, all the pointer years of the period 1958–2016 and 36 climatic variables referred to the pointer years were used. The 36 variables included Tmax, Tmin and P in summer (May, June, July and August) and winter (November, December, January and February) of the previous and current year. PCA was calculated from variance matrix with descriptors of the same order of magnitude. PCA analyses were performed using the library *factoextra* (Kassambara and Mundt 2017) of the R software.

1.3. Results

1.3.1 Tree-ring width chronologies

Table 4 reports the descriptive statistics of the 12 tree-ring chronologies. Tree-ring width ranged from 1.05 to 2.96 mm and had a mean time span that varied significantly among the investigated plots. In Calabria, trees were generally younger than those of the other populations (FpC (109 ± 14), AmC (108 ± 15) and ApC (82 ± 8)). The oldest population, however, was observed in Trentino, ApT (208 ± 35).

Mean sensitivity (MS) ranged from 0.101 to 0.199. European beech showed, especially in pure plots, higher values of MS (FpT (0.199), FpM (0.187)) in comparison with silver fir, except for the pure plot in Calabria (FpC (0.153)). The first order of autocorrelation (AC1), on the other hand, showed high values especially in European beech in mixed-species plots (FmT (0.910), FmC (0.949). Ranges of RBAR (0.228–0.338) and EPS (0.92–0.98) indicated a likely common stem radial growth response to climatic variability and similar variability across all the tree-ring series.

Table 4. The descriptive statistics of mean ring widths (MRW) with the standard deviation (SD) calculated on the series of raw annual ring widths used in the analysis. Maximum and minimum age of a single chronological series; mean tree diameter at breast height (DHB) of sampled trees; mean sensitivity (MS); correlation of mean intersections (RBAR); expressed population signal (EPS) calculated on the accretion series of indexed rings; first-order autocorrelation (AC1).

Sites	Stands	Time span (n. of years)	Maximum Age	Minimum Age	DBH (cm)	MRW ± SD (mm)	MS	RBAR	EPS	AC1
Trentino	pure_beech	1888-2016 (129)	129	55	23	1.43±1.26	0.199	0.287	0.95	0.874
	pure_fir	1809-2016 (208)	208	50	39	1.79±0.60	0.114	0.323	0.94	0.913
	mixed_beech	1922-2016 (95)	95	50	25	1.26±0.43	0.157	0.262	0.94	0.910
	mixed_fir	1849-2016 (168)	168	53	32	1.63±1.46	0.101	0.267	0.95	0.772
Molise	pure_beech	1877-2016 (140)	140	50	24	1.05±0.36	0.187	0.311	0.98	0.393
	pure_fir	1846-2016 (171)	171	57	42	1.31±0.44	0.122	0.303	0.96	0.837
	mixed_beech	1898-2016 (119)	119	50	39	1.82±0.77	0.184	0.25	0.96	0.611
	mixed_fir	1856-2016 (161)	161	76	40	1.92±0.54	0.132	0.338	0.92	0.755
Calabria	pure_beech	1908-2016 (109)	109	50	34	2,19±0.81	0.152	0.25	0.95	0.843
	pure_fir	1935-2016 (82)	82	39	36	2.80±0.94	0.159	0.228	0.94	0.790
	mixed_beech	1889-2016 (128)	128	53	43	2.00±0.73	0.149	0.235	0.98	0.949
	mixed_fir	1909-2016 (108)	108	51	45	2.96±0.90	0.114	0.284	0.97	0.896

1.3.2 Plot structure

The plots showed differences in stem diameter distribution (Fig. 2). Diameter distribution showed the typical pattern of uneven aged forests in almost all sites (Fig. 2). The DBH had a continuous distribution, within a range of 7 to 100 cm except for pure silver fir, with a maximum diameter of 60 cm (Fig. 2D), and pure European beech, within a range from 7 to 40 cm (Fig. 2B and 2E) in Molise. Moreover, European beech in mixture (Fig. 2C and 2F) showed stem diameter (from 7 to 40 cm) lower than silver fir (from 7 to 80 cm), except for Calabria, where European beech had maximum diameter of 60 cm in the mixed-species plot (Fig. 2I).

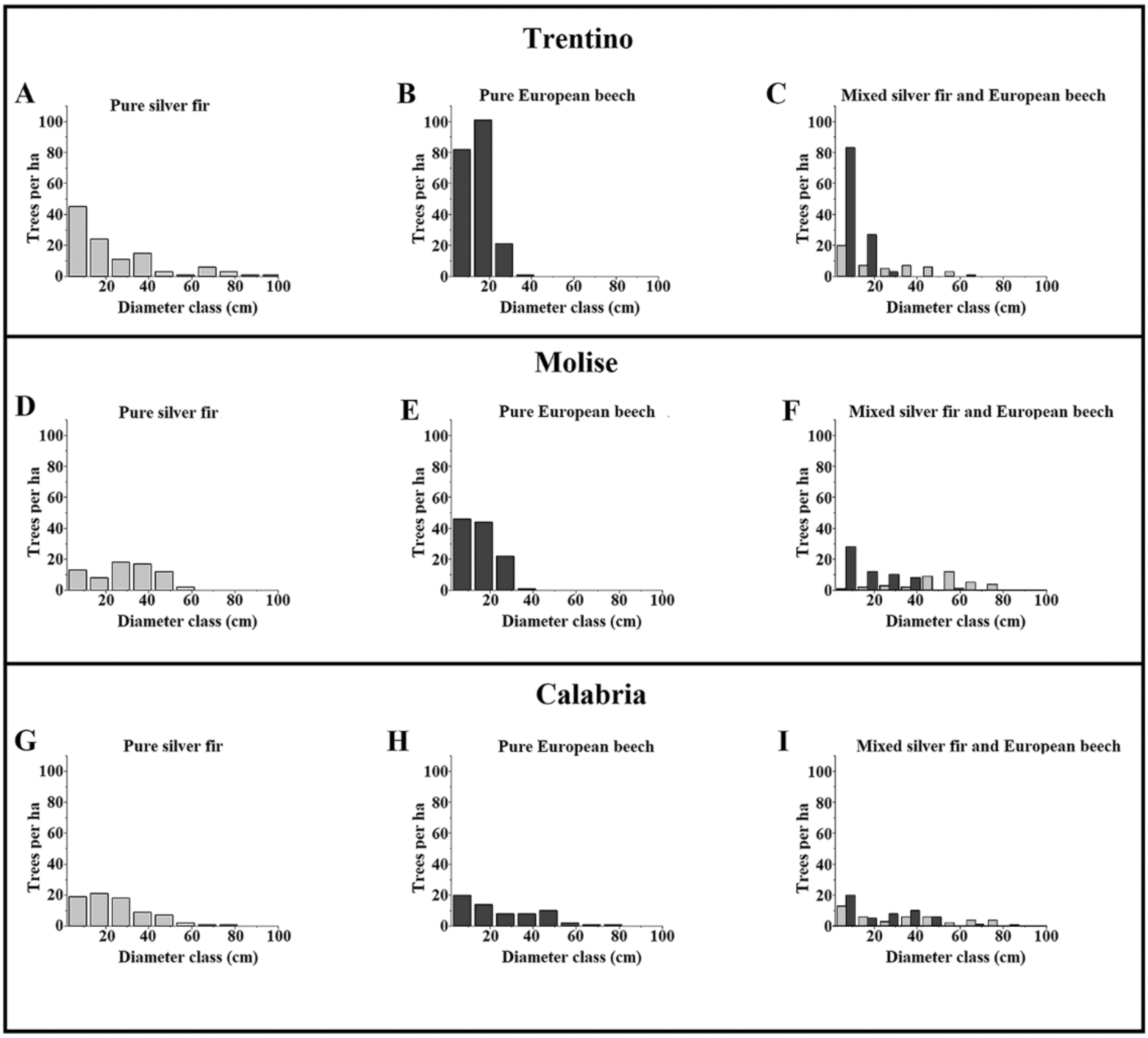


Figure 2. DBH distribution classes of silver fir and European beech within the plots, in Trentino, Molise and Calabria. Grey bars indicate silver fir and black bars indicates European beech.

1.3.3 Climate-growth relationships, and site- and stand-level differences

Correlations and response functions highlighted the main climatic variables that influenced growth of European beech and silver fir (Table 5). In particular, temperatures (Tmax) seemed to influence both species the most.

In Trentino, growth of silver fir had positive correlations with winter temperatures of current years (in AmT with January, February and March and in ApT with February). Moreover, in Trentino, growth of silver fir showed also positive response functions with February temperatures (in AmT and in ApT). In Molise, growth of silver fir mixed plot (AmM) had positive correlations with February temperatures of current years. The growth of silver fir pure plots in Molise (ApM) and Calabria (ApC) had negative correlation with November temperatures. In Trentino, both in mixed (AmT) and pure (ApT) plots growth of silver fir had positive correlations and response functions with precipitation in August of the previous year. In Molise, on the other hand, correlations with winter precipitation (in AmM with January and in ApM with January and February) were negative. In Calabria growth of silver fir, both mixed (AmC) and pure (ApC) plot, did not have any significant correlations with precipitation.

Growth of European beech was influenced mainly by spring and summer temperatures and precipitations of the previous and current year. In Trentino, both in mixed (FmT) and pure plots (FpT), positive correlations with temperatures in May of the current year were observed. Moreover, in Trentino, growth of European beech mixed plot (FmT) had also positive correlation with temperatures in July of the current year. Growth of European beech mixed plot in Molise (FmM) had negative correlations with spring temperatures of the previous year (April and May) with equally negative response functions. In Calabria, growth of European beech pure plot (FpC) had negative correlations with April of the previous year. In Trentino, growth of European beech mixed plot (FmT) had negative correlations and response functions with August temperatures of the previous year. In Molise, growth of European beech mixed plot (FmM) had positive correlations and response functions with May temperatures of the current year, and positive correlations with July temperatures of the previous year. In Calabria, growth of European beech mixed plot (FmC) had positive correlations with July and August of the previous year. In Molise, negative correlations with September temperatures of the previous year (FpM) and with June of the current year (FmM) were observed. In Calabria, mixed plots (FmC) negative correlations with September temperatures of current year.

In Trentino, growth of European beech pure plot (FpT) had negative correlations and response functions with April precipitation of the previous year, in comparison with Calabria (positive in FpC). Growth of European beech mixed plot (FmT) had positive correlations with August precipitation of the previous year, in Trentino. In mixed plot of Molise, correlations and response functions with July precipitation were negative. Moreover, growth of European beech mixed plot of Molise had positive correlations with June precipitation of the current year. In Calabria, growth of European beech mixed plot had positive correlations with July precipitation of the current year.

Table 5. Significant correlation coefficient (cc) and response function (r) ($P \leq 0.05$) between the standardized chronologies of tree rings and monthly climatic variables (T_{max} and P).

		FpT		ApT		FmT		AmT		FpM		ApM		FmM		AmM		FpC		ApC		FmC		AmC	
		cc	r	cc	r	cc	r	cc	r	cc	r	cc	r	cc	r	cc	r	cc	r	cc	r	cc	r	cc	r
Precipitation	Apr. prev.	-0.23	-0.26															0.37	0.29						
	Jun. prev.									0.25															
	Jul. prev.													-0.24	-0.26										
	Aug. prev.			0.37	0.33	0.27		0.28																	
	Nov. prev.																					-0.29	-0.23		
	Jan. curr.											-0.25				-0.20									
	Feb. curr.											-0.23													
	Apr. curr.																	-0.20							
	Jun. curr.													0.22											
	Jul. curr.																					0.19			
	Aug. curr.																	0.27							
Temerature max	Apr. prev.					0.30								-0.33	-0.28			-0.20							
	May prev.							0.22						-0.30	-0.26										
	Jul. prev.													0.23								0.21			
	Aug. prev.					-0.26	-0.23											-0.19				0.15			
	Sep. prev.									-0.22															
	Nov. prev.											-0.28								-0.21					
	Dec. prev.	0.34																							
	Jan. curr.					0.29		0.35																	
	Feb. curr.			0.31	0.23			0.49	0.32							0.28									
	Mar. curr.							0.27						0.26	0.25										
	May. curr.	0.40	0.23			0.29																			
	Jun. curr.													-0.24											
	Jul. curr.						0.35																		
	Sep. curr.																	-0.22	0.23					-0.24	

In Trentino, maximum temperature differed significantly ($p < 0.05$) from the other two sites (Fig. 3A and 3C). On the contrary, precipitation showed no difference among sites (Fig. 3B and 3D). Between plots (mixture and pure) and between species (beech and silver fir), no significant differences were observed, either for maximum temperatures or for precipitation.

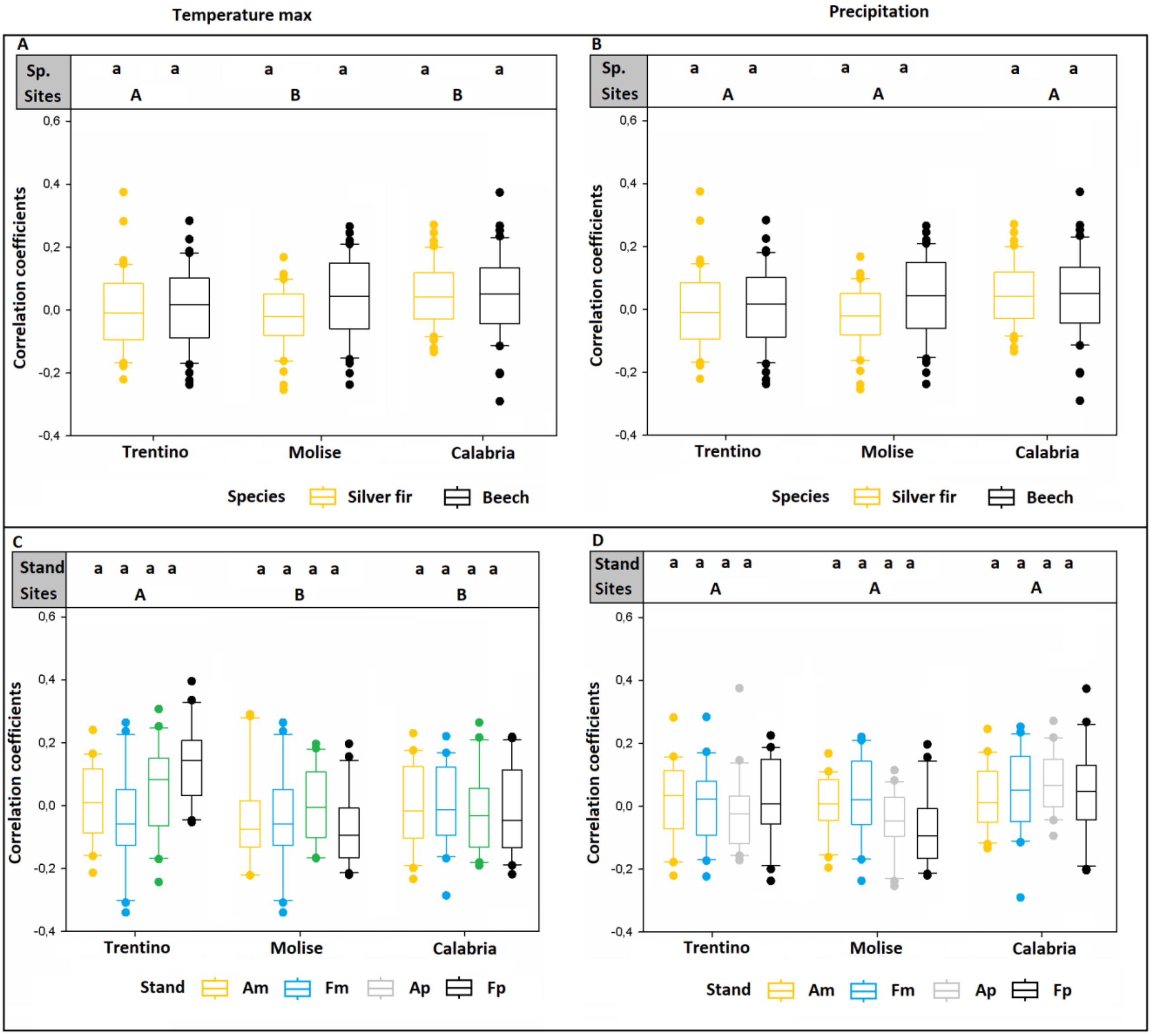


Figure 3. Correlation coefficients of maximum temperatures and precipitation. Panels A and B indicate species-specific (silver fir vs. European beech) differences, while C and D differences plot-specific (mixed-species vs. pure plots). Capital letters indicate the differences among the three sites, and small letters indicate the differences between species or plots (ANOVA with $P \leq 0.05$). Stand indicated with: Ap = silver fir in pure plots; Fp = European beech in pure plots; Am = silver fir in mixed-species plots; Fm = European beech in mixed-species plots.

1.3.4 Temporal variability in climate-growth relationships

Winter temperatures and precipitation of the previous summer influenced growth of silver fir positively, particularly in Trentino (Fig. 4). In Trentino, positive correlations were observed in 1958–1986 (August precipitation) and in 1987–2016 (maximum and minimum December, January and February temperatures). In Molise and Calabria, correlations with temperature maximum (Tmax) were positive in current and previous years. In the period 1958–1986 positive correlations were observed with maximum temperatures in March of current year, both in Molise and Calabria. In Molise, correlations were positive with precipitation in June and July of previous year, in the period 1977–2010, and precipitation in August of current year (1958–1986). In Calabria, positive correlations were observed with precipitation in June of current year, in the period 1969–1999.

Growth of European beech was influenced by summer precipitation of previous and current years positively (Fig. 5). Correlations with summer precipitation of the previous year were positive in Trentino (July in 1967–2006 and August in 1958-1980) and in Molise (July in 1970–20064), in current year. In Calabria, instead, positive correlations with June and July precipitation of the current years were observed in 1958–1986. However, in Trentino positive and negative correlations were found with temperatures of the current spring (mainly in May month,1958–1996) and of the previous summer (mainly in August month, 1958–1990), respectively. In Molise negative correlations were observed both with temperatures of the previous spring (in April (1967–1996) and May (1977–2014) month) and current summer (mainly in June month, 1970–2006).

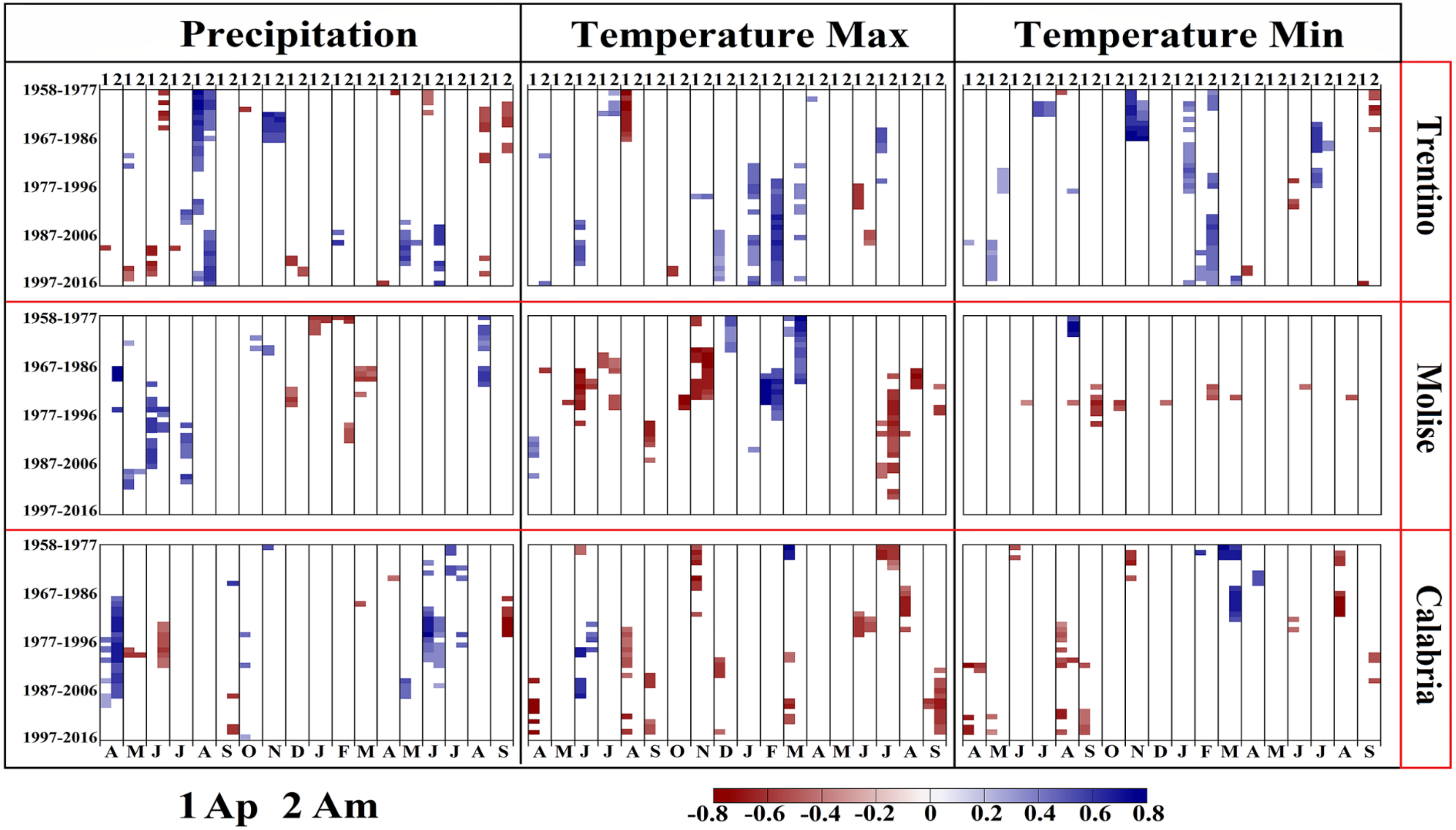


Figure 4. Temporal variability in climate-growth relationships of silver fir mixed-species and pure plots. Climate-growth relationships between standardized tree-ring chronologies and monthly climatic variables (Tmax, Tmin and P), calculated using moving windows. Coefficients are represented, for each time window, in five periods on the y axis. White cells indicate non-significant correlations, while cells with red (negative) and blue (positive) marks are significant (P ≤ 0.05). Numbers above indicate the plots in the three regions of Italy: 1 indicate the pure plot of silver fir and 2 indicate silver fir in the mixed-species plot.

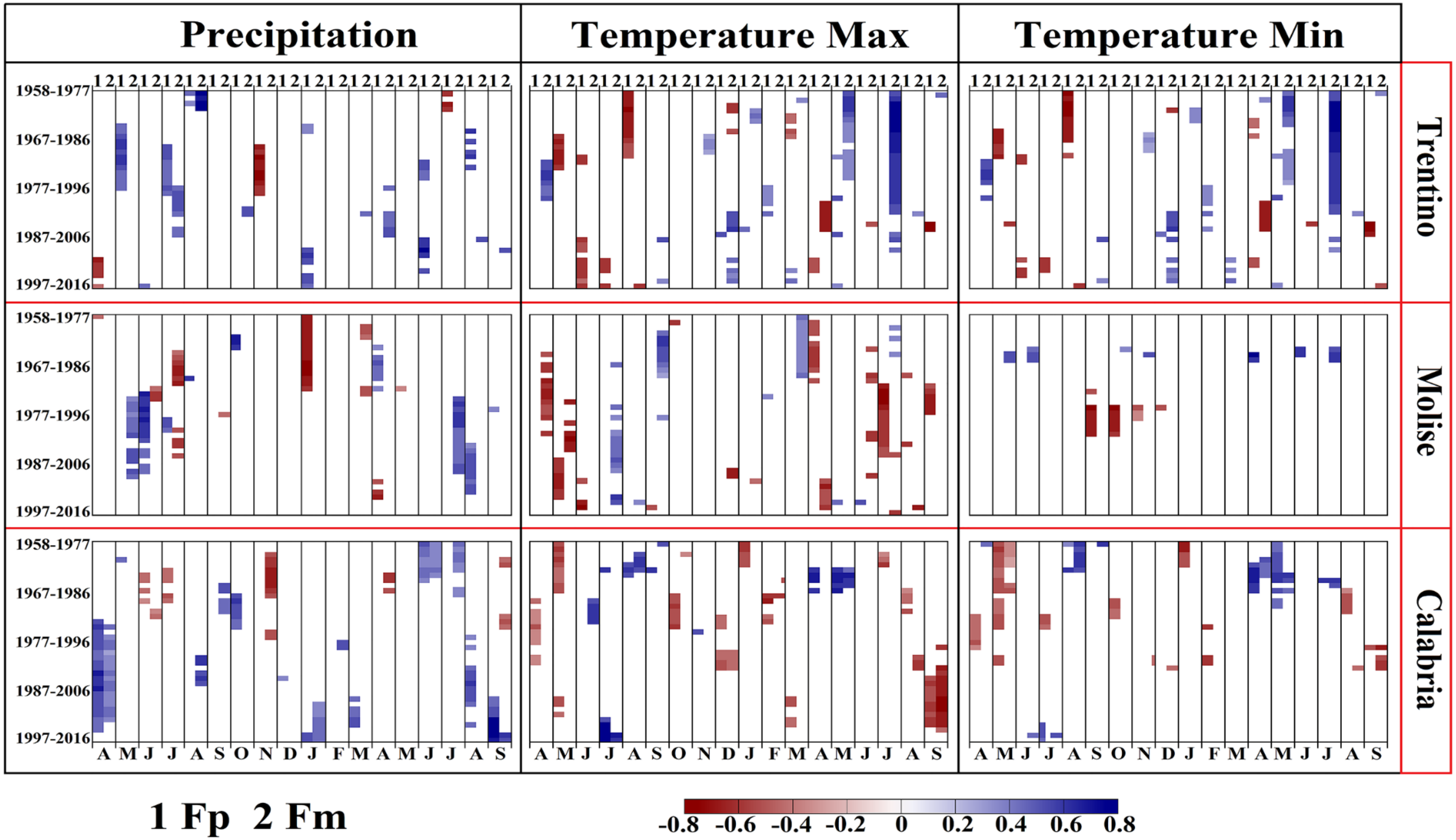


Figure 5. Temporal variability in climate-growth relationships of European beech mixed-species and pure plots. Climate-growth relationships between standardized tree-ring chronologies and monthly climatic variables (Tmax, Tmin and P), calculated using moving windows. Coefficients are represented, for each time window, in five periods on the y axis. White cells indicate non-significant correlations, while cells with red (negative) and blue (positive) marks are significant (P ≤ 0.05). Numbers above indicate the plots in the three regions of Italy: 1 indicate the pure plot of European beech and 2 indicate European beech in the mixed-species plot.

1.3.5 Growth-drought index relationship

The values of De Martonne aridity index are shown in Table 6. All the plots, except for the pure European beech plot in Calabria, showed relatively good water supply and rather humid climate (higher values). In particular, Trentino showed very high values of De Martonne aridity index (AI = 38 for the mixed-species plot, AI = 41 for European beech in the pure plot and AI > 50 for silver fir in the pure plot). In Molise, AI values were relatively lower (AI = 34, for all plots), as well as in Calabria (AI = 30, for the pure silver fir and AI = 33 for the mixed-species plot). Only the pure European beech plot in Calabria showed a typically Mediterranean climate, with AI = 20.

The relationships between the radial growth of European beech and silver fir and the aridity index did not show significant correlations in any plot (not shown).

Table 6. Values of the de Martone aridity indices in all the plots analyzed.

Sites	Stands	De Martonne aridity index
Trentino	pure_beech	41
	pure_fir	53
	mixed	38
Molise	pure_beech	34
	pure_fir	34
	mixed	34
Calabria	pure_beech	20
	pure_fir	30
	mixed	33

1.3.6 Pointer years

The individual ring-width series showed an average of 8 pointer years (from 5 to 15, in the 9 plots). Positive pointer years were more frequent than the negative ones (Table 7). The number of pointer years differed between mixed-species and pure plots of the two species. European beech showed more numerous pointer years in pure plots than in mixture with silver fir. Silver fir, instead, showed a lower frequency of pointer years in pure plots. Radial growth variation (RGV%), both for positive and negative pointer years, showed higher values in European beech pure plots of Trentino and Molise than silver fir pure plots. The RGV% for positive pointer years showed higher values in European beech mixed plots of Trentino and Calabria than silver fir mixed plots. By contrast, the values of

RGV% for negative pointer years were higher in European beech mixed plots of Molise and Calabria than silver fir mixed plots (Table 7 and Table S2).

Table 7. Summary pointer years for European beech and silver fir in the nine stands over the period 1958-2016.

Sites	Plot	Total n. of pointer years	Negative pointer years		Positive pointer years	
			N.	RGV%	N.	RGV%
Trentino	pure-beech	8	3	-38	5	77
	pure-fir	5	1	-28	4	35
	mixed-beech	5	1	-16	4	53
	mixed-fir	6	2	-28	4	40
	mean	7	2	-27	4	51
Molise	pure-beech	11	3	-41	8	96
	pure-fir	9	4	-32	5	36
	mixed-beech	7	2	-29	5	44
	mixed-fir	15	6	-31	9	44
	mean	10	4	-33	7	55
Calabria	pure-beech	12	4	-26	8	34
	pure-fir	5	2	-28	3	27
	mixed-beech	10	4	-26	6	60
	mixed-fir	6	2	-24	4	33
	mean	8	3	-26	5	38

Note: RGV% = radial growth variation (%); Total n. = total number of pointer years; N = number of negative and positive pointer years.

The ordination diagram, resulting from PCA applied to all pointer years, is reported in Figure 6. The first two components explained 52.2% of the variance. The first component (axis 1) explained the greatest variance (42.9%), discriminating temperatures (positive coordinates) from precipitation (negative coordinates). Stem radial growth of both species in mixed-species and pure plots was influenced (greater number of positive pointer years) by summer precipitation of the previous and current years in Trentino, and summer and winter temperatures of the previous year positively in Calabria. In Molise, on the other hand, several climatic variables influenced the response of stem radial growth in both species. European beech in both pure and mixed-species plots, and silver fir in the pure plot showed a positive response to summer precipitation of the previous year and to current summer temperatures. Silver fir in mixture showed negative response (more frequent negative pointer years) to winter and summer temperatures (Tmax and Tmin) of the previous year. At the same time, silver fir in mixture also showed positive response to winter and summer temperatures (Tmax) of the current year and summer precipitation of the previous year (Fig. 7).

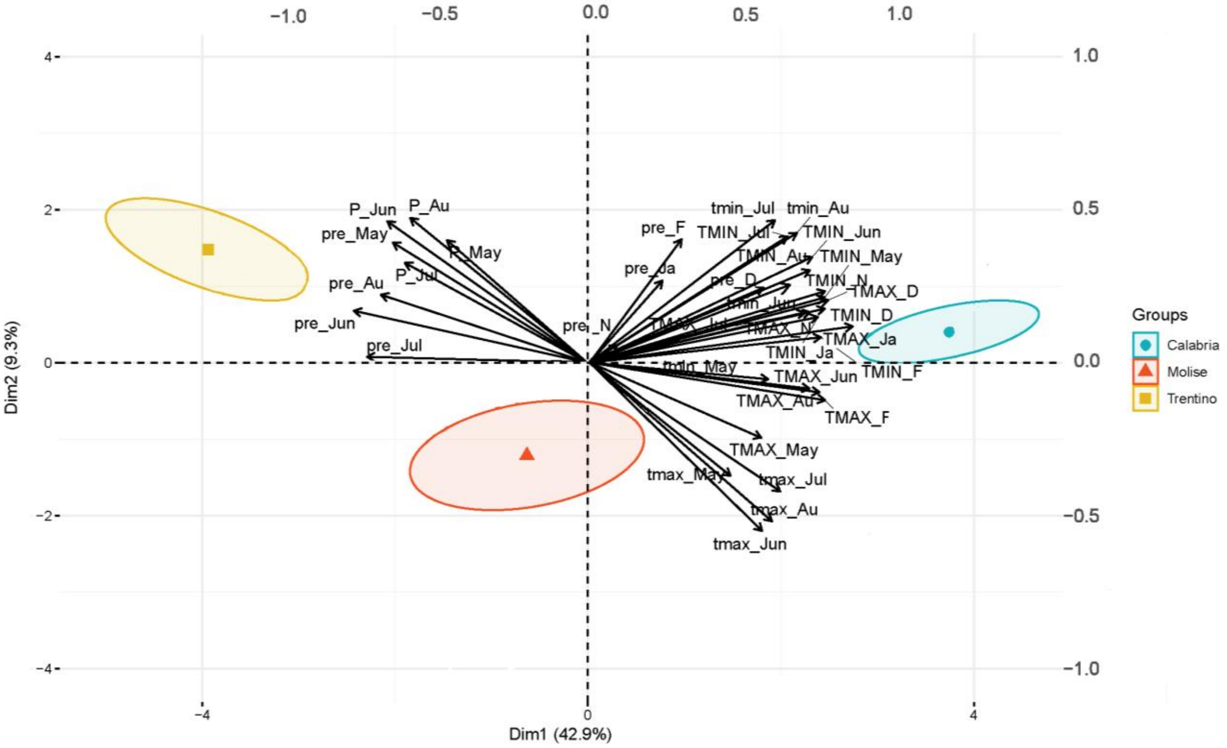


Figure 6. Ordination diagram of PCA (axes 1 and 2) applied to the winter and summer climatic variables of the previous (pre_, TMAX_ and TMIN_) and current (P_, tmax_and tmin_) years and to all pointer years, grouped at the site level. Sites are indicated to by yellow square for Trentino, red triangle for Molise, and blue circle for Calabria.

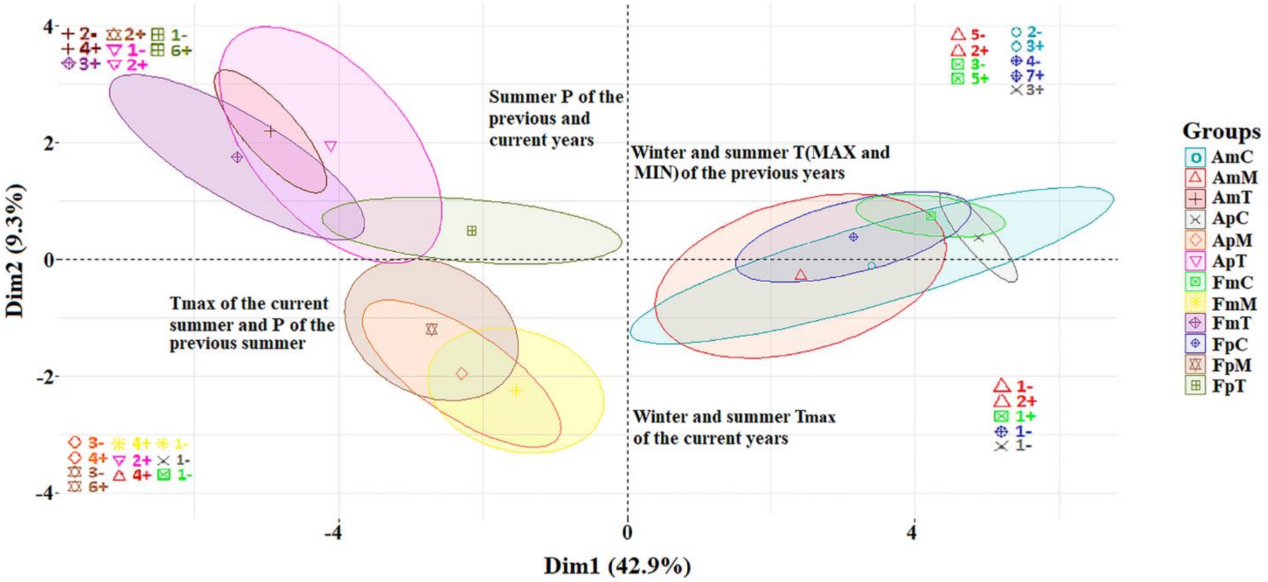


Figure 7. Ordination diagram of PCA (axes 1 and 2) applied to all the pointer years, grouped at the plot level. Pointer years were symbolized with the plus sign (positive pointer years) or with the minus sign (negative pointer years). Each quadrant indicates the climatic variables that affected stem radial growth and the number of positive (+) and negative (-) pointer years in each plot. Plots are indicated to by colors in the legend.

1.4. Discussion

1.4.1 Species-specific response to climate factors

Results showed that the response to climate was site-specific, with clinal variation in stem radial growth. Maximum temperatures influenced stem radial growth differently along the latitudinal gradient. The proximity to the distribution limit of both European beech and silver fir, and the geographic and biogeo-climatic complexity of the Italian Peninsula may explain the differences between plots in Trentino and those in Molise and Calabria. The effect of climate on the relationships between tree species diversity and forest stand productivity is still under debate, and needs to be tested both in the central area of species distribution and peripheral populations (e.g. Jactel et al. 2018). Assisted migration has been proposed as a potential management option to maintain optimal health and productivity of European's forests. However, a better understanding of species-specific productivity shifts in response to climate change is needed to inform forest managers on adaptive silviculture for co-occurring tree species.

Carrer et al. (2010) showed varying stem radial growth to climate responses of silver fir along a latitudinal gradient in Italy. Their findings are consistent with the climate-growth relationships observed for this species in the present study. In particular, the radial growth of silver fir was influenced by winter maximum temperatures. Silver fir showed positive response functions and higher correlations between stem radial growth and winter maximum temperatures in Trentino, in comparison with Molise. In Calabria, instead, correlations were mainly negative. In addition, the positive impact of winter maximum temperatures on stem radial growth of silver fir decreased from Alpine to Mediterranean mountain conditions. This suggests that winter maximum temperatures represent an important driver for stem radial growth of this species, especially in Alpine environments. Indeed, high winter temperatures have been already found to play a fundamental and advantageous role in the primary growth of silver fir (Pinto et al. 2008). Lebourgeois et al. (2013), in French mountains, and Castagneri et al. (2014), in Balkan Mountains, found significant positive responses of stem radial growth to high winter temperatures for silver fir, mainly in humid conditions. Warmer winter temperatures would probably favor an earlier start of cambial activity (Rossi et al. 2007), extending the growth period of silver fir along the Italian Peninsula (Antonucci et al. 2019). Consequently, silver fir might benefit from the increase in winter photosynthesis (Guehl 1985) and the decrease in frost-induced embolism (Cruiziat et al. 2002). Although high winter temperatures promote growth, extreme frosts might still cause substantial growth reductions (Lebourgeois et al. 2010). The principal component analysis (PCA) highlighted a negative effect of extreme events (winter maximum temperatures) only on the radial growth of silver fir, in Molise. This negative effect of winter temperatures could be linked to the sensitivity of silver fir to extreme frosts (Desplanque et al. 1999). Lebourgeois et al. (2010) found that silver fir was more sensitive to winter conditions than Norway spruce, confirming a greater sensitivity of this species to extreme cold years. The radial growth of silver fir along the Italian Peninsula was also affected by summer maximum temperatures and precipitation. Summer precipitation influenced the growth of silver fir positively, showing no difference between sites. Summer maximum temperatures, on the other hand, had a greater negative impact mainly in the southernmost sites (Molise and Calabria). In other studies, silver fir was found to be very sensitive to summer drought (e.g., Cailleret and Davi 2011; Rita et al. 2014). This high sensitivity of silver fir to summer drought has been linked to its low water-use efficiency and its drought-avoidance strategy (Aussenac 2002). However, positive response to extreme events and the absence of significant correlations (silver fir radial growth-De Martonne aridity index) indicated that this species was not affected by summer droughts. This suggests that in the analyzed sites, silver fir was not sensitive to summer drought.

Similarly, European beech showed negative correlations between the stem radial growth and summer maximum temperatures (mainly in southernmost sites), though no significant correlation was observed with the aridity index. The absence of sensitivity to summer drought, observed in both species, was probably related to the presence of sufficient water supply. Generally, trees are able to cope with high ambient temperatures for short periods, provided they have a sufficient water source to limit stress conditions (Teskey et al. 2015). Availability of soil water may prevent the occurrence of detrimental effects of high temperature on stem radial growth (e.g., cambium) (Kolb and Robberecht 1996). The absence of marked drought stress circumstances was confirmed by responses to summer maximum temperatures and precipitation, which had a positive impact on stem radial growth of European beech. According to Tegel et al. (2014), European beech in some Mediterranean forests has shown a recent increase in stem radial growth. By contrast, Tognetti et al. (2019) and Bosela et al. (2018) found that the growth of beech in southern locations has declined, starting from the mid-20th century to the present day. These studies suggest that the stem radial growth of European beech may depend on local site conditions, probably related to regional climate and/or stand productivity (Aertsen et al. 2014; Bosela et al. 2016).

1.4.2 Comparison of mixed-species vs. pure stands

Contrary to our initial hypothesis, the analysis of variance did not reveal any significant difference in the responses to climate between pure and mixed-species plots in three sites. This result was confirmed by the principal component analysis (PCA). PCA showed that mixed-species and pure plots of both species were influenced by the same climatic variables, and that responses to extreme events were similar. The absence of different responses to climate and extreme events between mixed-species and pure plots is in contrast with several studies (e.g., Pretzsch and Schütze 2016; Forrester 2019). According to Pretzsch and Schütze (2016), stronger size inequality (small and tall individuals of both species) in mixed-species forest stands leads to a better use of resources (e.g., light, water and nutrients) in comparison with pure stands. In our case the absence of significant differences between the responses to climate of both mixed-species and pure plots can be related to the structural position of European beech within mixed-species plots, which was sub-dominant. Smaller tree size of European beech than silver fir would probably limit the benefits of niche separation and complementarity.

1.4.3 Methodological considerations

Univariate approach has been used, with correlation or response functions, to identify the climatic variables that mostly influence the stem radial growth of trees (e.g., Lebourgeois et al. 2013; Battipaglia et al. 2009). In our case, a multivariate approach was used to evaluate relationships between tree-ring traits and climatic variables, considering both response and correlation functions (see Rita et al. 2014). The use of a multivariate approach made it possible to obtain an accurate evaluation of the statistical significance and to formulate more accurate ecophysiological hypotheses (e.g., Biondi et al. 1997). Correlation functions are coefficients obtained from linear estimates of Pearson's correlation (Morrison 1983). Response functions are obtained from a principal component regression model (Morzuch and Ruark 1991). However, the significance of the coefficients in the response functions can be misleading due to the underestimation of errors (Morzukh and Ruark 1991). Correlation functions can also be incorrectly tested, and bootstrapping confidence intervals for both response and correlation functions is required (Biondi 1997). Here we used the treeclim package, which allows to calculate the response and correlation functions correctly, eliminating the incorrect identification of climatic variables that influence tree growth (Zang and Biondi 2015).

Although the majority of tree-ring studies are based on sampling dominant trees, the increase in size and age may affect stomatal conductance and photosynthetic efficiency (i.e., water-use efficiency) (Hubbard et al. 1999). In this study, however, we sampled both dominant and co-dominant trees, the latter representing a significant proportion of the composition of these forest stands and contributing ecologically to forest functions and services. Sampling co-dominant trees may have, in part, smoothed the response to climate (poor correlations between tree-ring traits and climatic variables). The lower sensitivity to summer drought in European beech and silver fir trees of smaller size could be associated with higher moisture of the sub-dominant canopy layer, especially under warm and dry climate (Mérian and Lebourgeois 2011), affecting the vertical profile of water relations.

1.5. Conclusion

Results showed that the proximity to the distribution limits of these peripheral populations and the bio-geoclimatic complexity of the Mediterranean environment influence the responses of European beech and silver fir differently along the latitudinal gradient in the Italian Peninsula. In particular, Trentino differed from Molise and Calabria, in terms of response to maximum temperatures. Although both species showed lower negative impacts of climatic variables in Trentino than in Molise and Calabria, correlations between stem radial growth and De Martonne aridity index were not significant. The absence of sensitivity to summer drought was also observed through principal component analysis (PCA). Precipitation and summer temperatures influenced the stem radial growth of both species positively (high number of positive pointer years). Consequently, the low sensitivity of sensitivity to summer drought in European beech and silver fir can be linked to the presence of a sufficient water supply at these sites. A comparison between the correlation coefficients of mixed-species and pure plots did not reveal significant differences in the responses of stem radial growth to the climate. Smaller tree size of European beech than silver fir in mixed-species plots may have limited the benefits of niche separation and complementarity. Minor complementarity between the two species and, therefore, reduced exploitation of resources may explain the absence of significant differences between mixed-species and pure plots in the response of stem radial growth to climate. Further studies are needed to determine whether these diversity-productivity relationships and the stand-specific responsiveness in radial stem growth hold in different forest types and harsher climatic conditions.

1. Acknowledgements

This study generated from the COST (European Cooperation in Science and Technology) Action CLIMO (Climate-Smart Forestry in Mountain Regions - CA15226) financially supported by the EU Framework Programme for Research and Innovation HORIZON 2020. The authors thank: Alberto Garofalo and Agostino Venturino (Carabinieri Forestali), and Lorenzo Frizzera for their suggestion in selecting the study sites; Damiano Zanocco for providing information on past forest management; Chiara Calderaro, Tommaso Tagliafierro, Stefania Di Lella, Marco di Cristofaro, Francesco Parisi, Serena Antonucci, Giovanni Santopuoli and Maaz Hashmi for helping in field activities; Michele Dalponte for his support in data processing.

1. Supplementary material

Table S1. Equations used to obtain the meteorological data of each plot.

	Precipitation	R^2	Temperature MAX		Temperature MIN	R^2
FpT	13.812x+11.216	0.71	1.1049x+0.1459	0.97	1.0767x+1.0522	0.96
ApT	13.975x+16	0.54	1.0454x+0.8025	0.98	1.0637x-1.0554	0.98
MT	13.754x+15.843	0.54	1.0456x+0.8752	0.98	1.0655x-0.8025	0.98
FpM	0.386776x+1.327469	0.51	0.982071x+0.973201	0.98	0.971142x+0.9683	0.94
ApM	0.396899x+1.345453	0.53	0.980700x+0.973428	0.95	0.978078x+0.966910	0.94
MM	0.386776x+1.327469	0.51	0.982071x+0.973201	0.98	0.971142x+0.9683	0.94
FpC	1.010578x+0.523114	0.53	1.016602x+0.953778	0.97	0.899813x+1.065747	0.96
ApC	1.006569x+0.499733	0.50	1.014663x+0.955389	0.97	0.900412x+1.065217	0.96
MC	1.017152x+0.523054	0.53	1.010421x+0.959490	0.97	0.896719x+1.069379	0.96

Table S2. Pointer years for total ring (period: 1958–2016). For each plot, pointer years were defined as those years when at least 75% of the cross-dated trees presented the same sign of change (at least 10% of relative growth variation between two consecutive years). The numbers indicate the relative growth variations (RGV%) (-: negative pointer year).

Years	AmC	ApC	FmC	FpC	AmM	ApM	FmM	FpM	AmT	ApT	FmT	FpT
2016	32.39			35.05	56.25	43.1						-44.21
2015		-33.02			-34.15							43.28
2014								108.79		40.06		
2013								-33.79				
2008			27.04									
2007												65.06
2005								80.37				
2004					44.77							
2002			58.91	43.81	-35.76	-32.23		206				
2001	34.76				61.03	39.28	20.64					
2000			-23.19	-29.27								
1999				27.67		30.99	46.28					
1998	30.07	30.17			-25.66	-27.69				-27.6		
1997	-23.74			-25.16					42.99	43.01		
1996		21.71				34.1						
1995			122.6		45.27			172.85				

1994			-37.88		-28.03			-46.58			47.65	
1992					65.28			39.96				
1991					-35.71	-37.43	63.54					
1989	35.47	31.42	37.79		36.97							
1988		-26.18									83.33	126.82
1987							-34.96		37.25	27.76		
1986									-25.2			
1985				30.03								
1984			-4.3	28.51					-31.18			
1983				38.04					34.6	27.38		
1982											35.20	57.71
1981				35.54								
1980				-25.24	-25.02							-39.75
1979			93.1		35.32	32.39						
1976								44.12				
1975			20.1	37.02								
1974							50.35					
1973	-24.17											
1972					31.08							
1971							37.66					
1970							-22.8				-15.96	
1969											45.33	
1968						-31.84						
1967								66.78				
1966								-44.1				
1965			-38.51	-23.74								
1964									43.93			
1963					22.72			47.34				
1959												-30.74
1958												91.92

1. References

Aertsen W, Janssen E, Kint V, Bontemps JD, Van Orshoven J, Muys B (2014) Long-term growth changes of common beech (Fagus sylvatica L.) are less pronounced on highly productive sites. For Ecol Manag 312, 252-259.

Allen CD et al (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For Ecol Manag 259, 660–684.

Anderegg WRL, Anderegg LDL, Kerr KL, Trugman AT (2019) Widespread drought-induced tree mortality at dry range edges indicates climate stress exceeds species' compensating mechanisms. Glob Change Biol 15, 3793–3802.

Anderegg WRL, Kane JM, Anderegg LDL (2012) Consequences of widespread tree mortality triggered by drought and temperature stress. Nat Clim Change 3, 30–36.

Anderegg WRL et al (2016) When a tree dies in the forest: scaling climate-driven tree mortality to ecosystem water and carbon fluxes. Ecosystems 19, 1133–1147.

Antonucci S, Rossi S, Lombardi F, Marchetti M, Tognetti R (2019) Influence of climatic factors on silver fir xylogenesis along the Italian Peninsula. IAWA 40, 259–275.

Aussenac G (2002) Ecology and ecophysiology of circum-Mediterranean firs in the context of climate change. Ann For Sci 59, 823–832.

Bachofen C, D’Odorico P, Buchmann N (2020) Light and VPD gradients drive foliar nitrogen partitioning and photosynthesis in the canopy of European beech and silver fir. Oecologia 1-17.

Battipaglia G, Saurer M, Cherubini P, Siegwolf RT, Cotrufo MF (2009) Tree rings indicate different drought resistance of a native (*Abies alba* Mill.) and a nonnative (*Picea abies* (L.) Karst.) species co-occurring at a dry site in Southern Italy. For Ecol Manag 257, 820–828.

Becker M (1989) The role of climate on present and past vitality of silver fir forests in the Vosges mountains of northeastern France. Can J For Res 19, 1110–1117.

Biondi F (1997) Evolutionary and moving response functions in dendroclimatology. Dendrochronologia 15, 139–150.

Biondi F, Cayan DR, Berger WH (1997) Dendroclimatology of Torrey pine (*Pinus torreyana* Parry ex Carr.). Am Midl Nat 237–251.

Bosela M et al (2018) Contrasting effects of environmental change on the radial growth of co-occurring beech and fir trees across Europe. Sci Total Environ 615, 1460–1469.

Bosela M, Štefančík I, Petráš R, Vacek S (2016) The effects of climate warming on the growth of European beech forests depend critically on thinning strategy and site productivity. Agr Forest Meteorol 222, 21-31.

Bréda N, Huc R, Granier A, Dreyer E (2006) Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. Ann For Sci 63, 625–644.

Breshears DD et al (2005) Regional vegetation die-off in response to global-change-type drought. Proc Natl Acad Sci U.S.A. 102, 15144–15148.

Bunn AG (2010) Statistical and visual crossdating in R using the dplR library. Dendrochronologia 28, 251–258.

Cailleret M et al (2016) Towards a common methodology for developing logistic tree mortality models based on ring-width data. Ecol Appl 26, 1827–1841.

Cailleret M, Davi H (2011) Effects of climate on diameter growth of co-occurring *Fagus sylvatica* and *Abies alba* along an altitudinal gradient. Trees 25, 265–276.

Cailleret M et al (2017) A synthesis of radial growth patterns preceding tree mortality. Glob Change Biol 23, 1675–1690.

Camarero JJ, Gazol A, Sangüesa-Barreda G, Oliva J, Vicente-Serrano SM (2015) To die or not to die: early warnings of tree dieback in response to a severe drought. J Ecol 103, 44–57.

Carrer M, Nola P, Motta R, Urbinati C (2010) Contrasting tree-ring growth to climate responses of *Abies alba* toward the southern limit of its distribution area. Oikos 119, 1515–1525.

Castagneri D, Nola P, Cherubini P, Motta R (2012) Temporal variability of size–growth relationships in a Norway spruce forest: the influences of stand structure, logging, and climate. Can J For Res 42, 550–560.

Castagneri D, Nola P, Motta R, Carrer M (2014) Summer climate variability over the last 250 years differently affected tree species radial growth in a mesic *Fagus–Abies–Picea* old-growth forest. For Ecol Manag 320, 21–29.

Conte E, Lombardi F, Battipaglia G, Palombo C, Altieri S, La Porta N, Marchetti M, Tognetti R (2018) Growth dynamics, climate sensitivity and water use efficiency in pure vs. mixed pine and beech stands in Trentino (Italy). For Ecol Manag 409, 707–718.

Cook ER, Holmes RL (1984) Program ARSTAN users manual. Laboratory of Tree-Ring Research, University of Arizona, Tucson, 15.

Croitoru AE, Piticar A, Imbroane AM, Burada DC. (2013) Spatiotemporal distribution of aridity indices based on temperature and precipitation in the extra-Carpathian regions of Romania. Theor Appl Climatol 112(3-4), 597-607.

Cruiziat P, Cochard H, Améglio T (2002) Hydraulic architecture of trees: main concepts and results Ann For Sci 59, 723–752.

de Martonne E (1926) Une nouvelle function climatologique: L'indice d'aridité. Meteorologie 2 449–459.

Desplanque C, Rolland C, Schweingruber FH (1999) Influence of species and abiotic factors on extreme tree ring modulation. Trees 13, 218–227.

Eccel E, Zollo AL, Mercogliano P, Zorer R (2016) Simulations of quantitative shift in bio-climatic indices in the viticultural areas of Trentino (Italian Alps) by an open source R package. Comp Electron Agr 127, 92–100.

Eilmann B, Rigling A (2012) Tree-growth analyses to estimate tree species' drought tolerance. Tree Physiol 32, 178–187.

Forrester DI, Bauhus J (2016) A review of processes behind diversity - productivity relationships in forests. Curr For Rep 2, 45–61.

Forrester DI, Bonal D, Dawud S, Gessler A, Granier A, Pollastrini M, Grossiord C (2016) Drought responses by individual tree species are not often correlated with tree species diversity in European forests. J Appl Ecol 53, 1725–1734.

Forrester DI (2019) Linking forest growth with stand structure: Tree size inequality, tree growth or resource partitioning and the asymmetry of competition. For Ecol Manag 447, 139–157.

Fritts HC (1976) Tree Rings and Climate. Academic Press, New York.

Fritts HC (2001) Tree Rings and Climate. The Blackburn Press, London.

Gamfeldt L et al (2013) Higher levels of multiple ecosystem services are found in forests with more tree species. Nat Commun 4, 1340.

Garcia-Forner N et al. (2016) Responses of two semiarid conifer tree species to reduced precipitation and warming reveal new perspectives for stomatal regulation. Plant Cell Environ 39, 38–49.

Gazol A, Sangüesa-Barreda G, Granda E, Camarero JJ (2017a) Tracking the impact of drought on functionally different woody plants in a Mediterranean scrubland ecosystem. Plant Ecol 218, 1009–1020.

Gazol A, Camarero JJ, Anderegg WRL, Vicente-Serrano SM (2017b) Impacts of droughts on the growth resilience of Northern Hemisphere forests. Glob Ecol Biogeogr 26, 166–176.

Grissino-Mayer HD (2001) Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA.

Guehl JM 1985 Etude comparée des potentialités hivernales d'assimilation carbonée de trois coniféres de la zone tempérée (*Pseudotsuga menziesii* Mirb, *Abies alba* Mill et *Picea excelsa* Link). Ann For Sci 42, 23–38.

Guehl JM, Aussenac G, Bouachrine J, Zimmermann R, Pennes JM, Ferhi A, Grieu P (1991) Sensitivity of leaf gas exchange to atmospheric drought, soil drought, and water-use efficiency in some Mediterranean Abies species. Can J For Res 21(10), 1507–1515.

Haylock M, Hofstra N, Tank AK (2008) A European daily high-resolution gridded data set of surface temperature and precipitation for 1950–2006. J Geophys Res 113: D20119,

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25: 1965–1978.

Hijmans RJ et al (2019) Raster: geographic data analysis and modelling (The R Foundation). https ://CRAN.R-proje ct.org/packa ge=raste r.

Holmes RL, Adams RK, Fritts HC (1986) Tree-ring chronologies of western North America: California, eastern Oregon and northern Great Basin with procedures used in the chronology development work including users manuals for computer programs COFECHA and ARSTAN.

Hooper DU et al (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol Monogr 75, 3–35.

Hubbard RM, Bond BJ, Ryan MG (1999) Evidence that hydraulic conductance limits photosynthesis in old *Pinus ponderosa* trees. Tree Physiol 19, 165–172.

IPCC (2017) “Meeting report of the intergovernmental panel on climate change expert meeting on mitigation, sustainability and climate stabilization scenarios,” in IPCC Working Group III Technical Support Unit, eds PRJ Shukla, R Skea, K van Diemen, Ø Calvin, F Christophersen, J Creutzig, et al (London: Imperial College London).

Isbell F, Tilman D, Reich PB, Clark AT (2019) Deficits of biodiversity and productivity linger a century after agricultural abandonment. Nat Ecol Evol 3, 1533–1538.

Jactel H, Gritti ES, Drössler L, Forrester DI, Mason WL, Morin X, Pretzsch H, Castagneyrol B (2018) Positive biodiversity–productivity relationships in forests: climate matters. Biol Lett 14, 20170747.

Klein T (2014) The variability of stomatal sensitivity to leaf water potential across tree species indicates a continuum between isohydric and anisohydric behaviours. Funct. Ecol. 28, 1313–1320.

Kolb PF, Robberecht R (1996) High temperature and drought stress effects on survival of *Pinus ponderosa* seedlings. Tree Physiol 16, 665–672.

Konopka B (2001) Analysis of interspecific differences in tree root system cardinality. J For Sci 47, 366–372.

Lebourgeois F, Gomez N, Pinto P, Mérian P (2013) Mixed stands reduce *Abies alba* tree-ring sensitivity to summer drought in the Vosges mountains, western Europe. For Ecol Manag 303, 61–71.

Lebourgeois F, Rathgeber CB, Ulrich E (2010) Sensitivity of French temperate coniferous forests to climate variability and extreme events (*Abies alba*, *Picea abies* and *Pinus sylvestris*). J Veg Sci 21, 364–376.

Leonelli G, Coppola A, Salvatore MC et al (2017) Climate signals in a multispecies tree-ring network from central and southern Italy and reconstruction of the late summer temperatures since the early 1700s. Clim Past 13, 1451–1471.

Leuschner C, Coners H, Icke R (2004) In situ measurement of water absorption by fine roots of three temperate trees: species differences and differential activity of superficial and deep roots. Tree Physiol 24, 1359–1367.

Lindner M, Maroschek M, Netherer S, Kremer A, Barbati A, Garcia-Gonzalo J, Seidl R, Delzon S, Corona P, Kolström M, Lexer MJ, Marchetti M (2010) Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. For Ecol Manag 259, 698–709.

Lopez-Iglesias B, Villar R, Poorter L (2014) Functional traits predict drought performance and distribution of Mediterranean woody species. Acta Oecol 56, 10–18.

Luterbacher J et al (2012) A review of 2000 years of paleoclimatic evidence in the Mediterranean. In: Lionello, P. (Ed.), The Climate of the Mediterranean Region: Fromthe Past to the Future. Elsevier Amsterdam pp. 87–185.

Magh R-K, Grün M, Knothe, VE, Stubenazy T, Tejedor J, Dannenmann M, Rennenberg H (2018) Silver-fir (*Abies alba* Mill.) neighbors improve water relations of European beech (*Fagus sylvatica* L.), but do not affect N nutrition. Trees 32, 337–348.

Magh RK, Bonn B, Grote R, Burzlaff T, Pfautsch S, Rennenberg H (2019) Drought Superimposes the Positive Effect of Silver Fir on Water Relations of European Beech in Mature Forest Stands. Forests 10(10), 897.Marziliano PA, Tognetti R, Lombardi F (2019) Is tree age or tree size reducing height increment in *Abies alba* Mill. at its southernmost distribution limit? Ann For Sci 76, 17.

Marziliano PA, Tognetti R, Lombardi F. (2019) Is tree age or tree size reducing height increment in Abies alba Mill. at its southernmost distribution limit?. Ann. For. Sci. 76(1), 17.

Mérian P, Lebourgeois F (2011) Size-mediated climate–growth relationships in temperate forests: a multi-species analysis. For Ecol Manag 261, 1382–1391.

Mina M, Huber MO, Forrester DI, Thürig E, Rohner B (2018) Multiple factors modulate tree growth complementarity in central European mixed forests. J. Ecol. 106(3): 1106-1119.

Mitchell PJ et al (2016) An ecoclimatic frame-work for evaluating the resilience of vegetation to water deficit. Glob Change Biol 22, 1677–1689.

Moreno A, Hasenauer H (2015) Spatial downscaling of European climate data. Int J Climatol 36, 1444–1458.

Morrison DF (1983) Applied Linear Statistical Methods.Prentice-Hall, Englewood Cliffs, NJ, 562pp

Morzuch BJ, Ruark GA (1991) Principal components regression to mitigate the effects of multicollinearity. For Sci 37, 191–199.

Nicoll BC, Gardiner BA, Rayner B, Peace AJ (2006) Anchorage of coniferous trees in relation to species, soil type, and rooting depth. Can J For Res 36, 1871–1883.

Pinto PE, Gegout JC, Herve JC, Dhote JF (2008) Respective importance of ecological conditions and stand composition on *Abies alba* Mill. dominant height growth. For Ecol Manag 255, 619–629.

Pretzsch H et al (2015) Growth and yield of mixed versus pure stands of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) analysed along a productivity gradient through Europe. Eur J For Res 134, 927–947.

Pretzsch H, Schütze G, Uhl E (2013) Resistance of European tree species to drought stress in mixed versus pure forests: evidence of stress release by inter-specific facilitation. Plant Biol 15, 483–495.

Pretzsch H, Schütze G (2016) Effect of tree species mixing on the size structure, density, and yield of forest stands. Eur J For Res 135, 1–22.

Rehschuh S, Fuchs M, Tejedor J, Schäfler-Schmid A, Magh R-K, Burzlaff T, Rennenberg H, Dannenmann M (2019) Admixing fir to European beech forests improves the soil greenhouse gas balance. Forests 10, 213.

Rinn F (2003) TSAP-win. Time Series Analysis and Presentation for Dendrochronology and Related Applications. User Reference, Heidelberg.

Rita A, Gentilesca T, Ripullone F, Todaro L, Borghetti M (2014) Differential climate–growth relationships in *Abies alba* Mill. and *Fagus sylvatica* L. in Mediterranean mountain forests. Dendrochronologia 32, 220–229.

Rossi S, Deslauriers A, Anfodillo T, Carraro V (2007) Evidence of threshold temperatures for xylogenesis in conifers at high altitudes. Oecologia 152, 1–12.

Russo D, Marziliano PA, Macrì G, Zimbalatti G, Tognetti R, Lombardi F (2020) Tree Growth and Wood Quality in Pure Vs. Mixed-Species Stands of European Beech and Calabrian Pine in Mediterranean Mountain Forests. Forests 11(1), 6.

Sangüesa-Barreda G, Camarero JJ, Sánchez-Salguero R, Gutiérrez E, Linares JC, Génova M, Ribas M, Tíscar PA, López-Sáez JA (2019) Droughts and climate warming desynchronize Black pine growth across the Mediterranean Basin. Sci Total Environ 697, 133989.

Scarascia-Mugnozza G, Oswald H, Piussi P, Radoglou K (2000) Forests of the Mediterranean region: gaps in knowledge and research needs. For Ecol Manag 132, 97–109.

Schmid I, Kazda M, (2001) Vertical distribution and radial growth of coarse roots in pure and mixed stands of *Fagus sylvatica* and *Picea abies*. Can J For Res 31, 539–548.

Schweingruber FH, Eckstein D, Serre-Bachet F, Bräker OU (1990) Identification, presentation and interpretation of event years and pointer years in dendrochronology. Dendrochronologia 8, 9–38.

Seim A, Treydte K, Trouet V, Frank D, Fonti P, Tegel W, Panayotov M, Fernández-Donado L, Krusic P, Büntgen U (2014) Climate sensitivity of Mediterranean pine growth reveals distinct east-west dipole. Int J Climatol 35, 2503–2513.

Sitch S et al (2008) Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five Dynamic Global Vegetation Models (DGVMs). Glob Change Biol 14, 2015–2039.

Skovsgaard JP, Johannsen VK, Vanclay JK (1998) Accuracy and precision of two laser dendrometers. Forestry 71, 131–139.

Suarez ML, Lloret F (2018) Self-replacement after small-scale partial crown dieback in austral Nothofagus dombeyi forests affected by an extreme drought. Can J For Res 48, 412–420.

Tabari H, Talaee PH, Nadoushani SM, Willems P, Marchetto A (2014) A survey of temperature and precipitation based aridity indices in Iran. Quat Int 345, 158–166.

Tegel W, Seim A, Hakelberg D, Hoffmann S, Panev M, Westphal T, Büntgen U (2014) A recent growth increase of European beech (*Fagus sylvatica* L.) at its Mediterranean distribution limit contradicts drought stress. Eur J For Res 133(1), 61–71.

Teskey R, Wertin T, Bauweraerts I, Ameye M, McGuire MA, Steppe K (2015) Responses of tree species to heat waves and extreme heat events. Plant Cell Environ 38, 1699–1712.

Tognetti R, Lasserre B, Di Febbraro M, Marchetti M (2019) Modeling regional drought-stress indices for beech forests in Mediterranean mountains based on tree-ring data. Agric For Meteorol 265, 110–120.

Vicente-Serrano SM, Gouveia C, Camarero JJ et al (2013) Response of vegetation to drought time-scales across global land biomes. PNAS 110, 52–57.

Way DA, Oren RAM (2010) Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data. Tree Physiol 30, 669–688.

Wigley TM, Briffa KR, Jones PD (1984) On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. J Climate Appl Meteorol 23, 201–213.

Zalloni E, Battipaglia G, Cherubini P, Saurer M, De Micco V (2019) Wood growth in pure and mixed *Quercus ilex* L. forests: drought influence depends on site conditions. Front Plant Sci 10, 397.

Zang C, Biondi F (2015) treeclim: an R package for the numerical calibration of proxy-climate relationships. Ecography 38, 431–436.

Zhang Q, Shao MA, Jia X, Wei X (2017) Relationship of climatic and forest factors to drought-and heat-induced tree mortality. PloS one 12, e0169770.

Zhang Y, Chen HYH, Reich PB (2012) Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis. J Ecol 100, 742–749.

CHAPTER 2

Competition interaction in pure and mixed-species stands of silver fir and European beech in southern Italy

2.1. Introduction

Spatial and temporal changes in resource availability influence interactions between trees in forest stands, leading to dynamic relationships between species (Forrester 2014). However, changes in species composition and different spatial patterning of trees (clustered or uniform), may also increase competitive interactions between species (Lorimer et al. 2001), strongly influencing tree growth. Therefore, interactions between tree species are considered the main mechanisms responsible for the effects of niche complementarity and the most important drivers for the dynamics of forest communities. Several studies have shown that higher tree species richness may lead to greater forest stand productivity (e.g., Liang et al. 2016).

Mixed-species stands may have higher degree of resistance and resilience to biotic and abiotic disturbances (e.g., Seidl et al. 2016), and provide wider range of ecosystem services in comparison to monocultures (Gamfeldt et al. 2013). Nevertheless, additional insights on the functions of mixed-species stands and the causes of their over-yielding is required for implementing resource-efficient management strategies (Forrester 2014), particularly, in drought-prone environments (Grossiord et al. 2014; Conte et al. 2018). Indeed, under limited resource availability, as the number of individuals in a tree population fills the available growing space and the density continues to increase, competition for water (besides nutrients and light) increases as well.

Interactions between individual trees in a forest stand can be studied and identified through the use of competition indices (Bosela et al. 2015). Several studies (e.g. Coates et al. 2013; Mölder and Leuschner 2014) have shown that interactions in mixed-species stands are often less severe than in corresponding monocultures. However, the positive effects of neighborhood complementarity on tree growth in mixed-species stands may depend on several factors, such as stand density (Condés et al. 2013), site quality (Pretzsch et al. 2010) and changes in growth conditions (del Río et al. 2014).

Competitive interactions between tree species may occur above- and/or below-ground. In forests with tree species that differ in the architecture and phenology of the canopy (e.g., deciduous vs. evergreen species, conifers vs. broadleaved trees), species-specific occupation of the growing space and partition of the intercepted radiation may play a major role in the use of complementary resources (Forrester and Albrecht 2014). Moreover, in mixed-species stands, with shade-tolerant species and a heterogeneous spatial structure, the use of limiting resources (e.g., light) can be more efficient, since the trees in the dominated plane may take advantage of irradiance transmitted through the crown of the dominant trees, so as to survive and grow (Lu et al. 2016). However, also co-occurrence of species that differ in their root architecture may improve the uptake of nutrients and water (Brassard et al. 2013). Below-ground competitions do not only consider the interactions between dominant or/and subdominant trees with the subject tree, but also those trees whose roots occupy the root distribution area of the subject tree (Bosela et al. 2015). For example, silver fir presents a deeper root system than European beech and adopts a strategy that allows the absorption of water during the growing season, namely in periods of high drought stress (Toigo et al. 2015). Silver fir promptly close the stomata to maintain leaf water potential during drought events (i.e., isohydric behavior), while European beech continues to transpire even when soil water content diminishes (i.e., anisohydric behavior). Differences in stomatal adjustment capacity between these species may affect the hydraulic redistribution of soil water, particularly at these drought-prone Mediterranean latitudes.

European beech is one of the most studied species, especially when mixed with the comparatively drought-intolerant Norway spruce (*Picea abies* (L.) H. Karst.) (e.g., Pretzsch and Schütze 2009). However, mixed-species forests of silver fir (*Abies alba* Mill.) and European beech have recently earned attention and praise amongst forest researchers (del Río et al. 2014; Bosela et al. 2015; Pretzsch and Biber 2016). Probably the increased interest for silver fir is linked to recent findings about the enhanced productivity of silver fir in central Europe (Bosela et al. 2014) and to the relatively high drought tolerance of this species, particularly in southern Italy (Antonucci et al. 2019).

This study aimed to analyze the interactions between European beech and silver fir and the influence these interactions have on the growth of trees in mixed-species and corresponding pure stands. In order to better understand the interactions between these two species, we used competition indices at the individual level. Individual competition indices reflect the local density of the competitors, who interact with the reference tree (Tomé and Burkhart 1989), giving the possibility to quantify the influence of neighboring individuals on the growth of the reference tree. In this study we hypothesized that species mixing can mitigate the negative effects of competition for resources among trees.

2.2. Materials and methods

2.2.1 Study site

The study includes two triplets located in southern Italy (Molise and Calabria). In particular, the following forest sites were sampled: i) "Abeti Soprani" (Molise) and ii) Sila National Park ("Sila Piccola"; Calabria) (Fig.1).

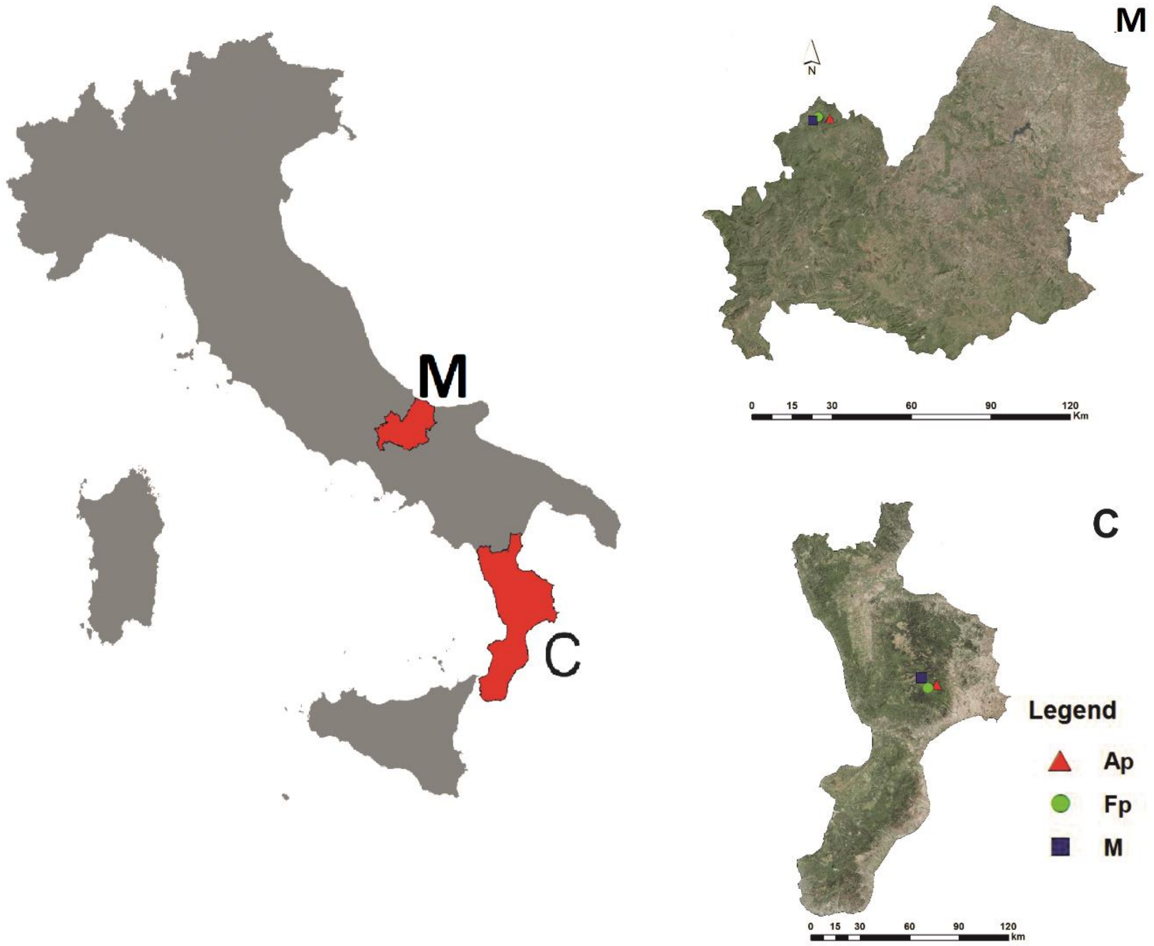


Figure 1. Location of the study sites in southern Italy. Red triangle indicates silver fir in pure stands (Ap); green circle indicates beech in pure stands (Fp); blue square indicates the mixed stands (M).

Each triplet is composed of three rectangular stands including two pure stands of silver fir and European beech and one mixed stand of these species. Stand sizes varies between 0.12 and 0.28 ha. Stands selection was based on the basal area occupied by the species within the stand (Mina et al. 2018), on the minimum number of individuals (≥ 50 trees of investigated species per stand) and on the elevation range (<250 m between the triplets). Stands were considered pure when the basal area of the studied species was at least 85%. Mixed stands, on the other hand, were classified as a mixture of the two species when both species represented 85% or more of the total basal area and each of the two species had contributed at least 20% of the basal area (Table 1). The horizontal structure was different in the two regions. Stands of Molise showed a random spatial arrangement of the trees, while in Calabria the structure was mainly clustered (Fig.2).

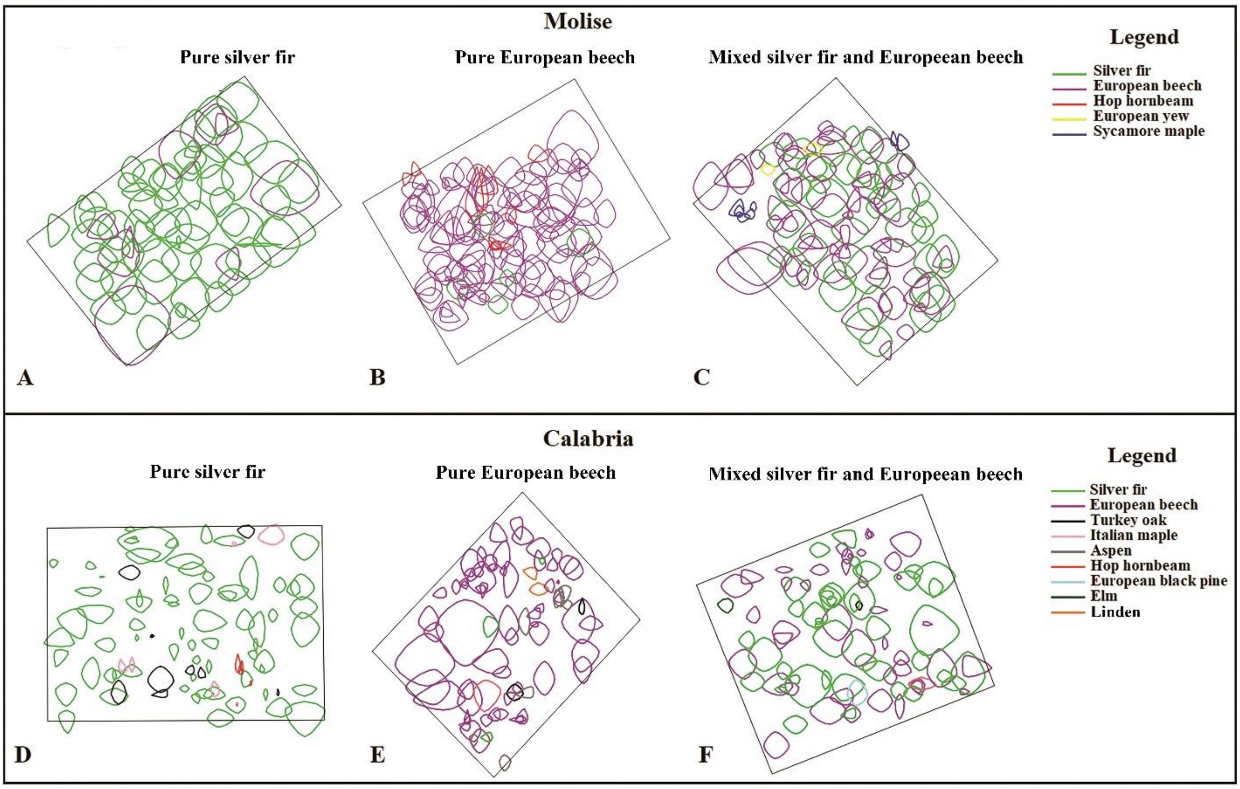


Figure 2. Spatial arrangement of trees inside the stands: A, B and C indicate trees arrangement in pure (green for silver fir and violet for European beech) and mixed-species stands in Molise, respectively; D, E and F indicate the arrangement in pure and mixed-species stands in Calabria, respectively. A different color is assigned to each species.

Stands show similar slope, between 19° and 28°, except for the pure silver fir stand in Calabria (37°), but differ for soil type and depth. Stands in Molise have humid soils (Rendzina), whereas soils of those in Calabria are dry (Distrudept). Soils differ in depth mainly in the pure European beech stands, where they are relatively shallow and rocky in comparison with mixed-species and pure silver fir stands (Table 1). All triplets have not been thinned since 1979-80.

Table 1. Location of the study sites and structural parameters obtained in pure and mixed-species stands of European beech and silver fir.

Site	Stand	Latitude (N)	Longitude (E)	Exposure (°)	Altitude (m)	Slope (°)	BA (m^2 ha^{-1})	BAs (%)	n. trees ha^{-1}	d_g (cm)	h_g (m)	Soil depth (cm)
Molise	$beech_{pure}$	41°52'13.65"	14°16'37.85"	354	1182	21	33.6	92%	989	21	15	20
	fir_{pure}	41°52'11.02"	14°17'26.03"	317	1230	20	54.4	92%	486	37	21	50
	$beech_{mixed}$	41°52'14.35"	14°16'51.26"	327	1182	27	45.2	20%	372	28	19	40
	fir_{mixed}							78%		58	27	
Calabria	$beech_{pure}$	39°9'13.49"	16°39'53.05"	343	1289	24	59.7	86%	641	35	22	50
	fir_{pure}	39°9'19.31"	16°41'2.30"	319	1220	37	61.5	85%	750	32	21	70
	$beech_{mixed}$	39°9'7.96"	16°40'12.33"	307	1332	28	74.6	33%	613	35	22	90
	fir_{mixed}							61%		47	27	

Note: BA (m^2 ha^{-1}) referred to stand basal area; BAs (%) basal area percentage of the main species; n. trees ha^{-1} number of trees per hectare; d_g (cm) quadratic mean diameter, h_g quadratic mean height.

2.2.2 Field measurements

At the beginning of summer 2017, the structural attributes and dendrometric parameters were determined for all living trees with a diameter ≥ 7 cm, through Field-Map technology and software (http://www.fieldmap.cz/) in Calabria and Molise. For each tree, the stem diameter at 1.30 m, the tree height, the crown radius in the four cardinal directions, the tree species and the spatial position were recorded. Only dominant-codominant trees were sampled in each stand.

Two cores per tree were collected at breast height (1.3 m) in opposite directions and perpendicular to the slope, in order to avoid compression wood (for silver fir) and tension wood (for European beech). Ring-width series were measured with a LINTAB measuring table with an accuracy of 0.01 mm, equipped with a Leica MS5 stereoscope (Frank Rinn, Heidelberg, Germany). The analysis was performed with the TSAP software package (Frank Rinn, Heidelberg, Germany) and subsequently were cross-dated using COFECHA (Grissino-Mayer, 2001) to assess measurement and dating accuracy. We successfully cross-dated 526 total cores (Table 2).

The raw chronologies were converted into tree basal area increment (BAI) according to the following standard equation:

$$BAI = \pi(r_t^2 - r_{t-1}^2) \quad (1)$$

where BAI in year *t* is equivalent to the width of the ring, r_t is the stem radius at the end of the annual growth and r_{t-1} is the stem radius at the beginning of the annual growth.

Table 2. Tree age (maximum and minimum), average diameter at breast height (DBH) of sampled trees, average total basal area increment (BAI_TOT) with the standard deviation (SD), and number of trees and cores used in the study.

Site	Stand	Tree age	DBH (cm)	BAI_TOT ± SD (cm^2 yr^{-1})	Cores/trees
Molise	beech$_{pure}$	140-50	24	4.86±2.61	110/60
	fir$_{pure}$	171-57	42	9.86±5.28	86/44
	beech$_{mixed}$	119-50	39	7.90±7.44	46/31
	fir$_{mixed}$	161-76	40	19.10±13.98	38/19
Calabria	beech$_{pure}$	109-50	34	14.53±9.12	78/46
	fir$_{pure}$	82-39	36	20.72±10.69	82/43
	beech$_{mixed}$	128-53	43	11.66±10.41	38/25
	fir$_{mixed}$	108-51	45	25.92±16.65	48/29

2.2.3 Individual-based competition indices

To analyze the competitive dynamics in the stands, we used distance-dependent competition indices. Generally, although not for stands with stationary structures (Weiskittel et al. 2011), these indices are considered more useful for explaining competitive interactions between trees (Stadt et al. 2007). Distance-dependent indices, in addition to the individual tree sizes, may also provide spatial information on the competitive status of an individual tree (Whang et al. 2012).

To calculate the distance-dependent indices several methods can be applied (e.g., Hegyi 1974; Daniels et al. 1986; Tomé and Burkhart 1989). In our case, to determine the competitive status of the trees, we used the index proposed by Hegyi (1974) based on the relationship between the stem radial diameters and the distances between the subject tree and the competitors. Although some criticism emerged in the last years around this index (e.g., Bosela et al. 2015), the Hegyi index is still the most used index in competitive studies (e.g. Weber et al. 2008).

The competition indices, both total and intra- and inter-specific, were calculated using the following formula:

$$CI_{i=} \sum_{j=1}^{n} \frac{DBH_j/DBH_i}{dist_{ij}+1} \qquad (2)$$

where CI_i is the competition index for the subject tree i, DBH_i the diameter at breast height of the subject tree i, DBH_j the diameter at breast height of the competitor tree j, $dist_{ij}$ the distance between the subject tree i and the competitor tree j, and n is the number of competitors in the neighborhood zone.

The first step to calculate individual-based competition indices is to identify the trees competing with the subject tree. There are several methods for selecting competitors (e.g. Staebler 1951; Lorimer 1983). In our case, we have used the method proposed by Lorimer (Lorimer 1983), i.e., a search radius obtained by multiplying the average radius of the tree crown in each stand by the constant 3.5. Since larger trees may compete at greater distances than smaller trees (Martin and Ek, 1984), we deemed that a search radius of 3.5 times the mean crown radius of overstory trees (Lorimer 1983) was more appropriate for our sites. The search radius was different for each stand due to the different mean radius of the tree crowns (Table 3). This difference in search radius allowed us to identify, for each stand, the competing trees that have a significant influence on the subject tree (Bosela et al. 2015). Moreover, the search radius was used to create a subplot within each stand, in order to avoid the buffer effect. Only trees with a DBH ≥ 20 cm inside the stand were used as subject trees for the analysis of the competition. We used this DBH threshold as the response of trees, in terms of radial growth, the variability of environmental conditions and intra- and inter-specific competition depend on the social status of trees (Zang et a. 2012; del Río et al. 2014).

In order to calculate the competition indices prior to the sampling date, only European beech and silver fir were considered, being the only species considered in this study. All basal area increments of European beech and silver fir trees in mixed-species and pure stands were reconstructed. Basal area increments in the last 5 years (2011-2016) and the thickness of the bark (in some cores also the beginning of growth in 2017) of all sampled trees were considered. The 5-year basal area increment and bark thickness were adapted to DBH measured in 2017, using linear models for each site and each species. Based on the correct equation, we estimated the 5-year basal area increment and the bark thickness of unsampled trees, which were sequentially subtracted from their DBH measured in 2017 to reconstruct DBH of all other European beech and silver fir trees.

Table 3. Average radius of tree crowns and search radius identified for each stand.

Site	Stand	Mean crown radius (m)	Search radius (m)
Molise	$\text{beech}_{\text{pure}}$	2.36	8.28
	fir_{pure}	3.12	10.95
	$\text{beech-fir}_{\text{mixed}}$	3.46	12.12
Calabria	$\text{beech}_{\text{pure}}$	1.52	5.35
	fir_{pure}	1.03	3.63
	$\text{beech-fir}_{\text{mixed}}$	1.62	5.68

2.2.4 Modelling approach

To investigate the effects of competitive interactions between mixed-species and pure stands, we used the model structure suggested by Sterba et al. (2002) and Condés and Sterba (2008). Specifically, we selected the basal area increment of individual trees ($\text{cm}^2 \text{ year}^{-1}$) as the dependent variable, because it is less influenced by the age of trees than the basal area increment (Biondi 1999); only those subject trees with a DBH $\geq$ 20 cm were used. A natural logarithmic transformation of the original dependent variable was executed, usually being one of the best variables reflecting the non-linear tree growth curve (Wykoff 1990).

The models, we considered the hypothesis that the basal area increment of the subject tree is a function of the size of the tree (SIZE), of the competition (COMP), of site characteristics (SITE), and of species in admixture (MIXTURE):

$$\ln(BAI_5) = a + bSIZE + cCOMP + dSITE + eMIXTURE \qquad (3)$$

where the dependent variable is the 5-year basal area increment (BAI5) (cm^2 for 5-year basal radial increment);

$$SIZE = b_1 \ln(DBH) + b_2 DBH^2 + b_3 (\frac{1}{Age}) \quad (4)$$

size of the tree is the DBH (cm), measured at the beginning of the growth period, and tree total age (years);

$$COMP = c_1 ln(BA) + c_2 ln(N) + c_3 CI\_DBH + c_4 N^{\circ}\_COMP + c_5 (\frac{N}{DIST}) \quad (5)$$

competition variables are the basal areas of trees per hectare (*BA*), the number of trees per hectare (*N*), the competition index (*CI_DBH*) (calculated at the beginning of the growth period only of European beech and silver fir trees), the number of competitors (*N°_COMP*) and the relationship number/distance between the competitors and the subject tree (*N/DIST*);

$$SITE = d_1 ALT + d_2 SLOPE + d_3 DEPTH \quad (6)$$

site variables used are some topographic features of the stand such as elevation (ALT), slope and depth of the soil;

$$MIXTURE = e_1 ln(BA_{beech}) + e_2 ln(BA_{fir}) \quad (7)$$

finally, mixture variables consider the logarithm of the basal area, measured at the beginning of the growth period, of European beech (BA_{beech}) and silver fir (BA_{fir}).

The model (mixed - pure stands) was developed with competition variables referring only to European beech and silver fir and not to all species present in the plots.

To test whether there was variability in the basal area increment between plots, we fitted a linear mixed model, including the stand (intercept) as a random effect.

Prior to fit the models through the lmer function of the *lme4* package (Bates et al. 2013), the presence of multicollinearity between the independent variables was evaluated, with the VIF function of the car package (Fox et al. 2012). The threshold used to assess multicollinearity was 10 variables. After sub-setting the independent variables according to multicollinearity, models were fitted through the likelihood criterion (ML) (Pinheiro e Bates 2000). Moreover, we drop redundant explanatory variables through the chisq.test function of the standard *statistics* package in R (R Core Team) and the limited maximum likelihood method (REML), with a significance test of $p < 0.05$. Normality and homogeneity of the residuals of the final models have been visually inspected by the diagnostic plots of residuals against fitted values (Zuur et al. 2009) (Fig. S2). R^2 (conditional) was obtained through the r.squared GLMM function of the *MuMIn* package (Barton 2013).

2.2.5 Statistical analyses

The differences of mixed - pure stands, in terms of competition and basal area increment, were assessed through analysis of variance (ANOVA). Analyses were performed for each stand to identify significant correlations between the competition indices calculated at the beginning of the growing period (silver fir - beech) and basal area increment. For multiple comparisons of subgroups of variables, Tukey's post hoc test was performed. The analyses were performed using the R software.

2.3. Results

2.3.1 Stand structure

The stands showed differences both in tree age (Table 2) and stem diameter distribution (Fig. 3). Age differences were observed between Molise and Calabria, as generally younger trees were found in Calabria (Table 2).

Diameter distribution showed the typical pattern of uneven aged forests in almost all sites (Fig. 3). The DBH had a continuous distribution, within a range of 7 to 80 cm except for pure silver fir, with a maximum diameter of 60 cm (Fig. 3A), and pure European beech, within a range from 7 to 30 cm (Fig. 3B) in Molise. Even the height variation showed differences between the stands of Molise and Calabria (Fig. S1). In particular, trees of silver fir in Molise were taller than those of European beech. In Calabria, instead, only in the mixed-species stand, trees of silver fir grew taller than those of European beech, the first species occupying the dominant layer while the second the sub-dominated layer.

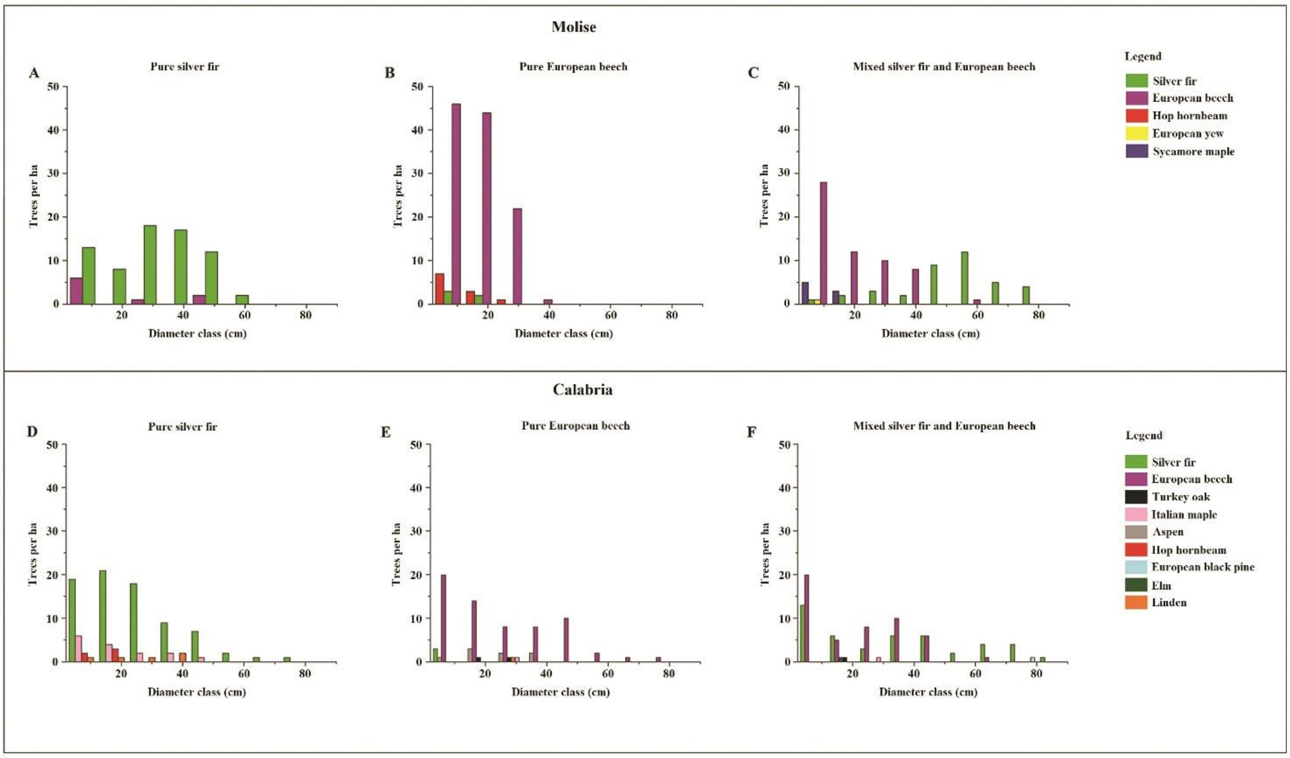


Figure 3. DBH distribution classes of all species within the stands: A, B and C indicate the DBH distribution in pure (green for silver fir and violet for European beech) and mixed-species stands in Molise, respectively; D, E and F indicate the distribution in pure (green for ilver fir and violet for European beech) and mixed-species stands in Calabria, respectively. Other tree species are represented by colours in the legend.

2.3.2 Individual-level competition of mixed-species versus pure stands

Tables 4 show the competition indices calculated for trees with DBH ≥ 20cm. CI_{2011}_befi indicates the competition indices calculated at the beginning of the growing period considering only European beech and silver fir as competing trees. The indices calculated at the beginning of the growing period showed higher levels of competition in Molise than in Calabria. In particular, in Molise, the pure stands of both species showed higher values of CI than the mixed stand (1.51). In contrast, in Calabria, the pure stands showed lower competition index than the mixed stand (0.85).

Table 4. Competition indices referring to European beech and Silver fir at the beginning of the growing period (CI2011_befi) and basal area increment of the last 5 years (BAI5years) of the analyzed species.

Site	Stand	CI_{2011}_befi	$\mathrm{BAI}_{5\mathrm{years}}$ ($\mathrm{cm}^2\ \mathrm{yr}^{-1}$)
Molise	beech$_{\mathrm{pure}}$	2.47	45.94
	fir$_{\mathrm{pure}}$	2.20	54.33
	beech-fir$_{\mathrm{mixed}}$	1.51	127.18
Calabria	beech$_{\mathrm{pure}}$	0.63	116.93
	fir$_{\mathrm{pure}}$	0.63	105.82
	beech-fir$_{\mathrm{mixed}}$	0.85	150.90

2.3.3 Growth models

The final models of mixed-species and pure stands are shown in Table 6. In the mixed-pure model eight independent variables were used (Table 5). Only four variables were significant for the basal area increment (Table 6). CI_{2011}_befi and slope are the variables that mostly influenced the basal area increment. Basal area increment decreased, with increasing CI_{2011}_befi and slope. Age and DBH^2, on the other hand, showed direct responses to basal area increment. Furthermore, the model showed differences between stands, with an R^2 of 0.49, when all effects were included, and R^2 of 0.43, when only fixed effects were considered.

Table 5. Growth models for all the independent variables selected through autocorrelation, differentiating variables at stand level from those specific for the two species (N°comp. and N/DIST). Parameter estimates are shown for the model.

	Mixed - pure stands		
Fixed effects	Est.	SE	p
Age	0.4594	0.1691	0.0079
DBH2	0.3157	0.1108	0.0055
Slope	-0.7187	0.2955	0.0171
N/DIST	0.0883	0.1438	
Ln_fir	0.0394	0.1723	
Ln_beech	0.2427	0.2741	
Altitude	-0.3722	0.1455	0.0122
CI2011_befi	-0.9702	0.1783	<10-3
Random effects			
Name	Variance	Std. Dev.	
Plot (intercept)	0.00	0.00	
Residual	0.7636	0.8738	

Table 6. Parameter estimations and fitting statistics for the best growth models.

	Mixed - pure stands		
Fixed effects	Est.	SE	p
Age	0.5545	0.1725	0.0019
DBH2	0.2819	0.1136	0.015
Slope	-1.0107	0.2448	0.0027
Altitude	-0.3159	0.1756	
CI2011_befi	-0.9859	0.1727	<10-3
Random effects			
Name	Variance	Std. Dev.	
Plot (intercept)	0.0873	0.2955	
Residual	0.8011	0.8961	

The box plots (Fig. 4B) showed that the competition indices (CI_{2011}_befi) differed significantly between the two regions ($p< 0.05$), with higher levels of competition in Molise than in Calabria. In addition, in Molise, European beech in the pure stand showed higher competition than in the mixed-species stand ($p< 0.05$). Basal area increment, on the other hand, did not reveal significant differences between the two regions, except for European beech in the pure stand, in Molise, and in the mixed stand, in Calabria (Fig. 4A).

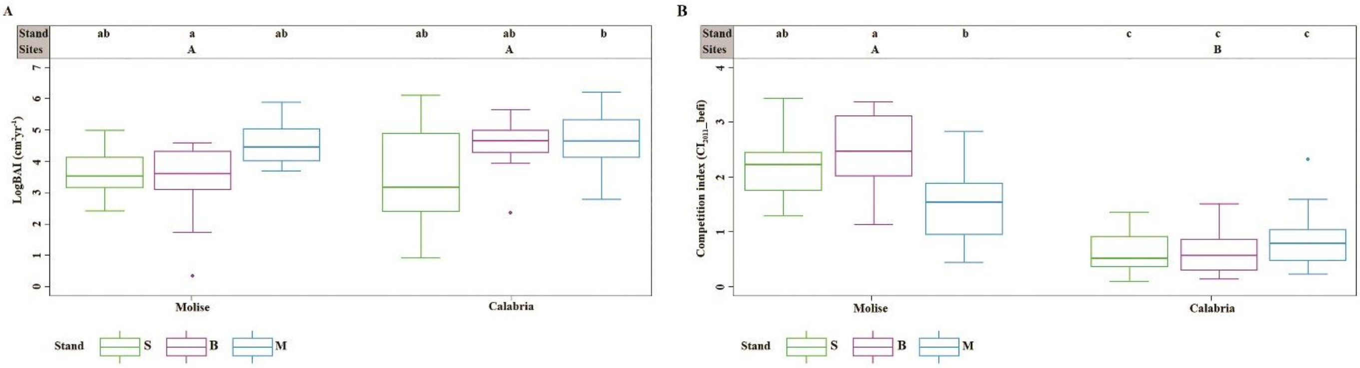


Figure 4. Basal area increment (logBAI) and competition indices (CI_{2011}_befi) in the stands, considering the last 5 years and the beginning of the growing period. Stands refer to M for mixed-species stands (Calabria and Molise) and to B (European beech) and S (Silver fir) for pure stands (Calabria and Molise). Capital letters indicate differences between the sites for each basal area increment and competition indices, and small letters indicate the differences between species (ANOVA and post hoc tests, $p < 0.05$). The vertical lines represent the “whiskers” for the 5 and 95 percentiles of data distribution.

2.4. Discussion

We analyzed the influence of interactions between tree species on the basal area increment of uneven-aged mixed-species and pure stands of European beech and silver fir, implementing growth models and competition indices at the individual tree level. Results of the growth models (mixed-pure) showed that high levels of competition between species and high terrain slopes had a negative impact on the basal area increment (Table 6). In particular, the negative influence of competition was observed mainly in Molise (Fig. 4B). Although competition should decline with stand age due to spatial resource partitioning, in our case high levels of competition were observed in Molise, where trees grew relatively older than in Calabria. A different spatial arrangement of trees in the two regions (random in Molise and clustered in Calabria) could explain these peculiarities (Fig. 2). Clustered offspring may arise when competitive thinning of large trees leads to gaps. Gap recruitment of small competing trees leading to clustered regeneration may occur more frequently in drier sites (Spies et al. 1990). Edaphic heterogeneity and local aridity may also cause clumped spatial distribution of trees.

Several studies found that the stand-level spatial arrangement of trees may influence the competitive intensity between species (Fraver et al. 2014), especially in uneven-aged and uneven-structured stands (Weber et al. 2008) and in those stands with trees differing in crown morphology, crown efficiency and space occupation (Metz et al. 2013). This would suggest that the forest structure (e.g., spatial arrangement, crown morphology, etc.) may regulate the competition between trees and their growth in structurally diverse forests (Fraver et al. 2014). However, according to Coomes and Allen (2007), the strength and result of competitive interactions can also be influenced by the intrinsic conditions of the site.

In sub-boreal multi-species conifer forests, tree size, competition, soil fertility and crowding were found to influence tree growth (Coates et al. 2013). Complementary crown and growth characteristics may reduce the severity of interactions in mixed-species forests (Kelty 2006). Consistent with the theory of resource partitioning, Boyden et al. (2008) observed that competition in mixed-species forests was stronger on genetically more similar trees than genetically dissimilar trees. Mölder and Leuschner (2014) found that mixed-species stands evidenced less impact of competition on basal area increment. In our case, a lower impact of competition on mixed-species stands was observed only in Molise (lower values of competition in comparison with the pure European beech stand), partially supporting our first hypothesis (Fig. 4B). This lower level of competition found in the mixed stand in Molise could be linked to the low stand density. The high difference in stand density between mixed and pure stands of European beech could explain the lack of significance found among other mixed and pure stands (Table 1). Stand density can influence the resource that is more limiting for tree growth (Forrester et al. 2013). For example, if light interception was the most limiting factor in tree growth in Molise, an increase in stand density might imply a greater competition among trees. Indeed, Richards et al. (2010) showed that over-yielding or under-yielding of mixed-species vs. pure stands were linked to capture, or use efficiency of resources.

It is worth noting that the data sets used in this model considered only European beech and silver fir as competitors within the six stands. Although the presence of the other species in each stand was of minor importance, in terms of basal area, consider all species would be required to make more general conclusions about the effect of interactions between species on tree basal area increment.

2.5. Conclusion

The growth modeling approach was useful for exploring interactions that occurred in mixed-species and pure stands of European beech and silver fir. Results showed that the basal area increment was negatively affected by both high competition levels and slope terrains. Competition for resources was higher in Molise than in Calabria. Such a difference was probably linked to the spatial arrangement of trees, which might regulate and modify the strength of interactions between these late-successional shade-tolerant species. Lower values of competition on the basal area increment of European beech in mixed-species than in pure stands were probably due to differences in tree density between these stands. These results partially support our first hypothesis.

Understanding the interactions that occur between forest species provides information on ecological stability and stand resistance to environmental disturbance that may become useful in core areas, under a climate change perspective.

2. Acknowledgements

The authors are grateful to Carabinieri Forestali of Petilia Policastro (KR) for their help in selecting the study sites. This study generated from the COST (European Cooperation in Science and Technology) Action CLIMO (Climate-Smart Forestry in Mountain Regions - CA15226) financially supported by the EU Framework Programme for Research and Innovation HORIZON 2020.

2. Supplementary material

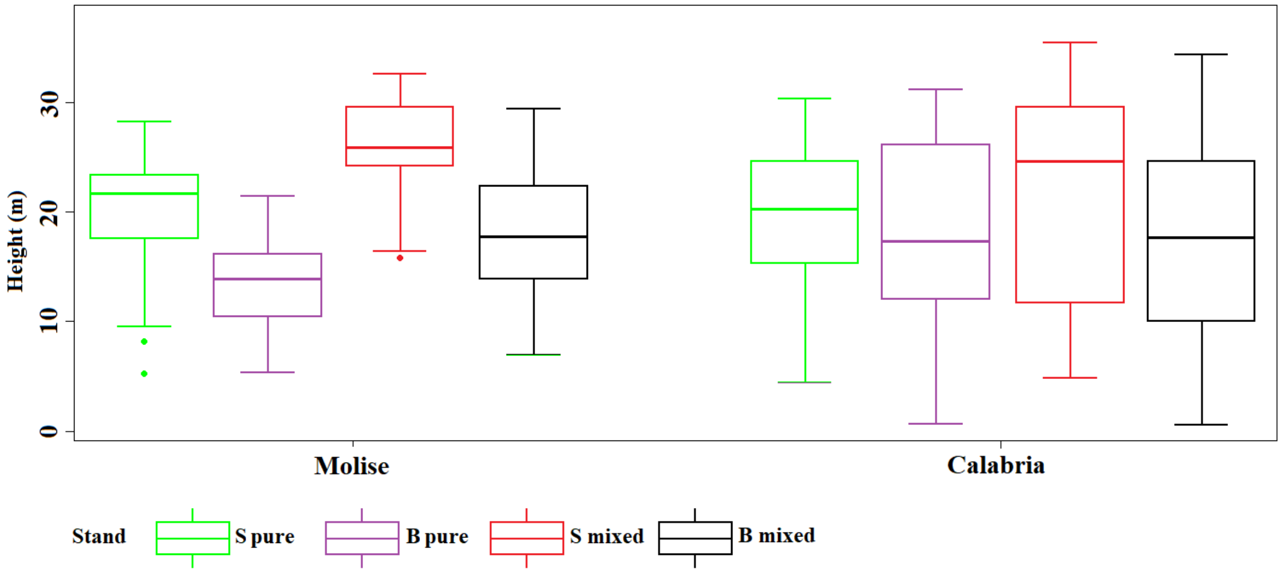


Figure S1: Height of all European beech and silver fir trees inside the stands. Stands refer to S mixed and B mixed for mixed-species stands (Calabria and Molise) and to B pure (European beech) and S pure (silver fir) for pure stands (Calabria and Molise).

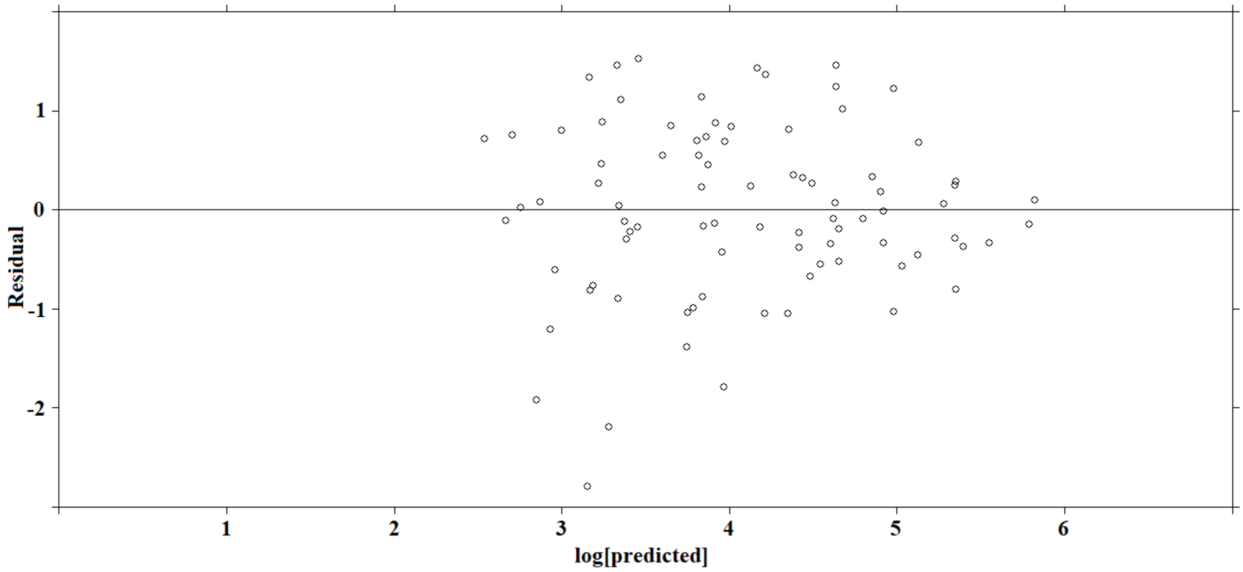


Figure S2: Residuals vs. predicted log-transformed BAI of growth models in Table 6. Silver fir, European beech monocultures and silver fir – European beech mixtures in Molise and Calabria.

2. References

Antonucci, S., Rossi, S., Lombardi, F., Marchetti, M., and Tognetti, R. 2019. Influence of climatic factors on silver fir xylogenesis along the Italian Peninsula. IAWA J. 40(2): 259-275.

Barton, K. 2013. MuMln: Multi-Model Inference. R Package Version 1.9. 5. r-project. org/web/packages/Mu-MIn/index. html.

Bates, D., Maechler, M., Bolker, B., and Walker, S. 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version, 1, 1-23.

Biondi, F. 1999. Comparing tree-ring chronologies and repeated timber inventories as forest monitoring tools. Ecol. Appl. 9(1): 216-227.

Bolte, A., and Villanueva, I. 2006. Interspecific competition impacts on the morphology and distribution of fine roots in European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) Karst.). Eur. J. For. Res. 125(1): 15-26.

Bošeľa, M., Petráš, R., Sitková, Z., Priwitzer, T., Pajtík, J., Hlavatá, H., Sedmák, R., and Tobin, B. 2014. Possible causes of the recent rapid increase in the radial increment of silver fir in the Western Carpathians. Environ. Pollut. 184: 211-221.

Bošeľa, M., Tobin, B., Šebeň, V., Petráš, R., and Larocque, G.R. 2015. Different mixtures of Norway spruce, silver fir, and European beech modify competitive interactions in central European mature mixed forests. Can. J. For. Res. 45(11): 1577-1586.

Boyden, S., Binkley, D., and Stape, J.L. 2008. Competition among Eucalyptus trees depends on genetic variation and resource supply. Ecology. 89(10): 2850-2859.

Brassard, B.W., Chen, H.Y., Cavard, X., Laganière, J., Reich, P.B., Bergeron, Y., Paré, D., and Yuan, Z. 2013. Tree species diversity increases fine root productivity through increased soil volume filling. J. Ecol. 101(1): 210-219.

Coates, K.D., Lilles, E.B., and Astrup, R. 2013. Competitive interactions across a soil fertility gradient in a multispecies forest. J. Ecol. 101(3): 806-818.

Condés, S., and Sterba, H. 2008. Comparing an individual tree growth model for *Pinus halepensis* Mill. in the Spanish region of Murcia with yield tables gained from the same area. Eur. J. For. Res. 127(3): 253-261.

Conte, E., Lombardi, F., Battipaglia, G., Palombo, C., Altieri, S., La Porta, N., Marchetti, M., and Tognetti, R. 2018. Growth dynamics, climate sensitivity and water use efficiency in pure vs. mixed pine and beech stands in Trentino (Italy). For. Ecol. Manag. 409: 707-718.

Coomes, D.A., and Allen, R.B. 2007. Effects of size, competition and altitude on tree growth. J. Ecol. 95(5): 1084-1097.

Daniels, R.F., Burkhart, H.E., and Clason, T.R. 1986. A comparison of competition measures for predicting growth of loblolly pine trees. Can. J. For. Res. 16(6): 1230-1237.

Del Río, M., Condés, S., and Pretzsch, H. 2014. Analyzing size-symmetric vs. size-asymmetric and intra-vs. inter-specific competition in beech (*Fagus sylvatica* L.) mixed stands. For. Ecol. Manag. 325: 90-98.

Forrester, D.I., Kohnle, U., Albrecht, A.T., and Bauhus, J. 2013. Complementarity in mixed-species stands of *Abies alba* and *Picea abies* varies with climate, site quality and stand density. For. Ecol. Manag. 304: 233-242.

Forrester, D.I. 2014. The spatial and temporal dynamics of species interactions in mixed-species forests: from pattern to process. For. Ecol. Manag. 312: 282-292.

Forrester, D.I., and Albrecht, A.T. 2014. Light absorption and light-use efficiency in mixtures of *Abies alba* and *Picea abies* along a productivity gradient. For. Ecol. Manag. 328: 94-102.

Fox, J. et al. 2012. Package 'car'. *Vienna: R Foundation for Statistical Computing*.

Fraver, S., D'Amato, A.W., Bradford, J.B., Jonsson, B.G., Jönsson, M., and Esseen, P.A. 2014. Tree growth and competition in an old-growth *Picea abies* forest of boreal Sweden: influence of tree spatial patterning. J. Veg. Sci. 25(2): 374-385.

Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., Riuz-Jaen, M.C., Fröberg, M., Stendahl, J., Philipson, C.D., Mikusiński, G., Andersson, E., Westerlund, B., Andrén, H., Moen, J., and Bengtsson, J. 2013. Higher levels of multiple ecosystem services are found in forests with more tree species. Nat. Commun. 4: 1340.

Grissino-Mayer, H.D. 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. Tree Ring Res. 57: 205–221.

Grossiord, C., Granier, A., Ratcliffe, S., Bouriaud, O., Bruelheide, H., Chećko, E., Forrester, D.I., Dawud, S.M., Finér, L., Pollastrini, M., Scherer-Lorenzen, M., Valladares, F., Bonal, D., and Gessler, A. 2014. Tree diversity does not always improve resistance of forest ecosystems to drought. Proc. Natl. Acad. Sci. U.S.A. 111(41): 14812-14815.

Hegyi, F. 1974. A simulation model for managing jack-pine stands simulation. Fries, J. (ed.). Royal College of Forestry, Stockholm, Sweden. pp. 74–90.

Kelty, M.J. 2006. The role of species mixtures in plantation forestry. For. Ecol. Manag. 233(2-3): 195-204.

Liang, J., Crowther, T.W., Picard, N., Zhou, M., Alberti, G., Schulze, E-D., McGuire, A.D., Bozzato, F., Pretzsch, H., de-Miguel, S., Paquette, A., Hérault, B., Scherer-Lorenzen, M., Barrett, C.B., Glick, H.B., Hengeveld, G.M., Nabburs, G-J., Pfautsch, S., Viana, H., Vibrans, A.C., Ammer, C., Schall, P., Verbyla, D., Tchebakova, N., Fischer, M., Watson, J.V., Chen, H.Y.H., Lei, X., Schelhaas, M-J., Lu, H., Gianelle, D., Parfenova, E.I., Salas, C., Lee, E., Lee, B., Kim, H.S., Bruelheide, H., Coomes, D.A., Piotto, D., Sunderland, T., Schmid, B., Gourlet-Fleury, S., Sonké, B., Tavani, R., Zhu, J., Brandl, S., Vayreda, J., Kitahara, F., Searle, E.B., Neldner, V.J., Ngugi, M.R., Baraloto, C., Frizzera, L., Bałazy, R., Oleksyn, J., Zawiła-Niedźwiecki, T., Bouriaud, O., Bussotti, F., Finér, L., Jaroszewicz, B., Jucker, T., Valladares, F., Jagodzinski, A.M., Peri, P.L., Gonmadje, C., Marthy, W., O̓Brien, T., Martin, E.H., Marshall, A.R., Rovero, F., Bitariho, R., Niklaus, P.A., Alvarez-Loayza, P., Chamuya, N., Valencia, R., Mortier, F., Wortel, V., Engone-Obiang, N.L., Ferreira, L.V., Odeke, D.E., Vasquez, R.M., Lewis, S.L., and Reich, P.B. 2016. Positive biodiversity-productivity relationship predominant in global forests. Science. 354(6309): aaf8957.

Lorimer, C.G., Dahir, S.E., and Nordheim, E.V. 2001. Tree mortality rates and longevity in mature and old-growth hemlock-hardwood forests. J. Ecol. 89(6): 960-971.

Lorimer, C.G. (1983). Tests of age-independent competition indices for individual trees in natural hardwood stands. For. Ecol. Manag. 6(4): 343-360.

Lu, H., Mohren, G.M., den Ouden, J., Goudiaby, V., and Sterck, F.J. 2016. Overyielding of temperate mixed forests occurs in evergreen–deciduous but not in deciduous–deciduous species mixtures over time in the Netherlands. For. Ecol. Manag. 376: 321-332.

Martin, G.L., and Ek, A.R. 1984. A comparison of competition measures and growth models for predicting plantation red pine diameter and height growth. For. Sci. 30(3), 731-743.

Metz, J., Seidel, D., Schall, P., Scheffer, D., Schulze, E.D., and Ammer, C. 2013. Crown modeling by terrestrial laser scanning as an approach to assess the effect of aboveground intra-and interspecific competition on tree growth. For. Ecol. Manag. 310: 275-288.

Mina, M., Huber, M.O., Forrester, D.I., Thürig, E., and Rohner, B. 2018. Multiple factors modulate tree growth complementarity in central European mixed forests. J. Ecol. 106(3): 1106-1119.

Mölder, I., and Leuschner, C. 2014. European beech grows better and is less drought sensitive in mixed than in pure stands: tree neighbourhood effects on radial increment. Trees. 28(3): 777-792.

Pinheiro, J.C., and Bates, D.M. 2000. Statistics and computing. Mixed-effects models in S and S-PLUS. 3-56.

Pretzsch, H., and Schütze, G. 2009. Transgressive overyielding in mixed compared with pure stands of Norway spruce and European beech in Central Europe: evidence on stand level and explanation on individual tree level. Eur. J. For. Res. 128(2): 183-204.

Pretzsch, H., and Biber, P. 2016. Tree species mixing can increase maximum stand density. Can. J. For. Res. 46(10): 1179-1193.

Pretzsch, H., Block, J., Dieler, J., Dong, P.H., Kohnle, U., Nagel, J., Spellmann, H., and Zingg, A. 2010. Comparison between the productivity of pure and mixed stands of Norway spruce and European beech along an ecological gradient. Ann. For. Sci. 67(7): 712.

Richards, A.E., Forrester, D.I., Bauhus, J., and Scherer-Lorenzen, M. 2010. The influence of mixed tree plantations on the nutrition of individual species: a review. Tree Physiol. 30(9): 1192-1208.

Seidl, R., Spies, T.A., Peterson, D.L., Stephens, S.L., and Hicke, J.A. 2016. Searching for resilience: addressing the impacts of changing disturbance regimes on forest ecosystem services. J. Appl. Ecol. 53(1): 120-129.

Spies, T.A., Franklin, J.F., and Klopsch, M. 1990. Canopy gaps in Douglas-fir forests of the Cascade Mountains. Can. J. For. Res. 20(5): 649-658.

Stadt, K.J., Huston, C., Coates, K.D., Feng, Z., Dale, M.R., and Lieffers, V.J. 2007. Evaluation of competition and light estimation indices for predicting diameter growth in mature boreal mixed forests. Ann. For. Sci. 64(5): 477-490.

Staebler, G.R. 1951. Growth and spacing in an even-aged stand of Douglas-fir (Doctoral dissertation).

Sterba, H., Blab, A., and Katzensteiner, K. 2002. Adapting an individual tree growth model for Norway spruce (*Picea abies* L. Karst.) in pure and mixed species stands. For. Ecol. Manag. 159(1-2): 101-110.

Toïgo, M., Vallet, P., Perot, T., Bontemps, J.D., Piedallu, C., and Courbaud, B. 2015. Overyielding in mixed forests decreases with site productivity. J. Ecol. 103(2): 502-512.

Tomé, M., and Burkhart, H.E. 1989. Distance-dependent competition measures for predicting growth of individual trees. Forest Sci. 35(3): 816-831.

Wang, D.H., Tang, S.C., Hsieh, H.C., Chung, C.H., and Lin, C.Y. 2012. Distance-dependent competition measures for individual tree growth on a Taiwania plantation in the Liuguei area. 臺灣林業科學. 27(3): 215-227.

Weber, P., Bugmann, H., Fonti, P., and Rigling, A. 2008. Using a retrospective dynamic competition index to reconstruct forest succession. For. Ecol. Manag. 254(1): 96-106.

Weiskittel, A.R., Hann, D.W., Kershaw Jr, J.A., and Vanclay, J.K. 2011. Forest growth and yield modeling. John Wiley and Sons.

Wykoff, W.R. 1990. A basal area increment model for individual conifers in the northern Rocky Mountains. Forest Sci. 36(4): 1077-1104.

Zang, C., Pretzsch, H., and Rothe, A. 2012. Size-dependent responses to summer drought in Scots pine, Norway spruce and common oak. Trees. 26(2): 557-569.

Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A., and Smith, G.M. 2009. Mixed effects models and extensions in ecology with R. Springer Science & Business Media.

CHAPTER 3

remote sensing

Article

Prediction of Competition Indices in a Norway Spruce and Silver Fir-Dominated Forest Using Lidar Data

Soraya Versace [1,2], Damiano Gianelle [1,3], Lorenzo Frizzera [1], Roberto Tognetti [3,4], Vittorio Garfì [2] and Michele Dalponte [1,*]

[1] Department of Sustainable Agro-ecosystems and Bioresources, Research and Innovation Centre, Fondazione E. Mach, Via E. Mach 1, 38010 San Michele all'Adige (TN), Italy; s.versace@studenti.unimol.it (S.V.); damiano.gianelle@fmach.it (D.G.); lorenzo.frizzera@fmach.it (L.F.)

[2] Department of Biosciences and Territory, University of Molise, Contrada Fonte Lappone, 86090 Pesche, Italy; vittorio.garfi@unimol.it

[3] The EFI Project Centre on Mountain Forests (MOUNTFOR), via Edmund Mach 1, 38010 San Michele all'Adige, Italy; tognetti@unimol.it

[4] Department of Agricultural, Environmental and Food Sciences, University of Molise, Via Francesco De Sanctis, 86100 Campobasso, Italy

* Correspondence: michele.dalponte@fmach.it

Received: 24 September 2019; Accepted: 20 November 2019; Published: 21 November 2019

Abstract: Competitive interactions are important predictors of tree growth. Spatial and temporal changes in resource availability, and variation in species and spatial patterning of trees alter competitive interactions, thus affecting tree growth and, hence, biomass. Competition indices are used to quantify the level of competition among trees. As these indices are normally computed only over small areas, where field measurements are done, it would be useful to have a tool to predict them over large areas. On this regard, remote sensing, and in particular light detection and ranging (lidar) data, could be the perfect tool. The objective of this study was to use lidar metrics to predict competition (on the basis of distance-dependent competition indices) of individual trees and to relate them with tree aboveground biomass (AGB). The selected study area was a mountain forest area located in the Italian Alps. The analyses focused on the two dominant species of the area: Silver fir (*Abies alba* Mill.) and Norway spruce (*Picea abies* (L.) H. Karst). The results showed that lidar metrics could be used to predict competition indices of individual trees (R^2 above 0.66). Moreover, AGB decreased as competition increased, suggesting that variations in the availability of resources in the soil, and the ability of plants to withstand competition for light may influence the partitioning of biomass.

Keywords: airborne lidar; remote sensing; modelling; individual-based competition indices; competition–biomass relationship

---

1. Introduction

Tree growth is influenced by several factors, including climate patterns, site conditions, and competition processes [1–4] Among them, tree competition measures are the main predictors of individual trees' growth [5]. Competition among trees is defined as the negative effects that neighboring trees have on a subject tree. These negative effects depend on the interactions between trees in acquiring limited resources, such as light, water, and nutrients [6,7]. Quantifying the competitive effect of neighboring trees is difficult due to the co-occurring effects of various environmental factors on trees.

Many indices have been developed in numerous studies in order to quantify the level of competition that individual trees experience, and to assess how competition affects growth rates (e.g., [8–12]). Competition models, based on competition indices of single trees, can be classified into two main groups: distance-independent and distance-dependent models [13–16]. Distance-independent models use only non-spatial competition indices. These indices are based on the size distribution of competitor trees within a given area, without considering their spatial distribution. Differently, distance-dependent models are based on spatial competition indices that incorporate both the size and the spatial distribution of competitors [17]. Distance-dependent indices may offer more reliable forecasts of the growth of single trees [18,19], as tree size, species composition, and stand structure vary within a stand and, consequently, the availability of resources [20]. In forests with a spatially inhomogeneous distribution of trees, and in particular in unmanaged mountainous areas, there is usually stronger growth competition between neighboring trees and thus biomass growth can be more easily influenced by the available light intensity and site quality.

Several studies (e.g., [16,21]) found that the canopy neighborhood plays a key role in understanding tree competition. Therefore, the availability of light is probably a determining factor for the growth of individual trees [22–25]. However, species-specific differences in crown characteristics may influence light capture differently in different canopy classes [26]. Yet, the co-occurrence of species that differ in their root architecture may improve the uptake of nutrients and water [27,28]. Below-ground competition does not only consider the interactions between dominant and/or subdominant trees with the subject tree but also those trees whose roots occupy the root distribution area of the subject tree [29]. These differences in functional traits for the capture and assimilation of resources (such as light, water, and nutrients) may lead to changes in biomass partitioning and, therefore, change the productivity of forests. According to Fox et al. [30], the productive potential of forest stands can be greatly increased by competition. Competition is linked to the acquisition of environmental resources by species in close spatial proximity, so changes in biomass partitioning may affect the productivity of forests [31,32]. Many studies (e.g., [33,34]) have investigated the relationship between biomass partitioning and plant competition. For example, Lin et al. [34] showed that the allocation of biomass can vary due to different types of competition, above and below ground. Increased competition among trees due to the limitation of underground resources can lead to changes in roots' biomass [35]. Furthermore, according to Petersen et al. [36], removal of the effects of competition in a controlled environment led to an increase in the above ground biomass of Douglas fir. These studies suggest that competition is closely related to biomass partitioning, and biomass distribution directly affects forest productivity. Furthermore, according to Zhou et al. [33], biomass distribution directly affects forest productivity, and productivity is closely related to forest competition.

Obtaining information regarding the spatial distribution of individual trees, and their height, diameter, crown projection, and biomass requires methods based on field measurements. Although these conventional techniques provide reasonably accurate estimates, they often require labor-intensive and time-consuming measurements and inspections. Moreover, the measurements are always limited to small areas while in many cases, it is necessary to have measurements over large areas. Therefore, the use of remote sensing, in particular of light detection and ranging (lidar) remote sensing technology, partially overcomes these limitations. Several methods have been developed using airborne lidar metrics (e.g., [37–39]) for the estimation of forest biomass and volume (e.g., [40]), and other forest characteristics (e.g., [41]). The majority of the studies in the literature have focused on the prediction of volume and biomass, many on forest structure, and few on competition. As an example, Lo et al. [42] predicted volume, DBH, and a height-based competition index using lidar metrics at the individual tree level. Relating volume and DBH to the competition index, they showed that they are negatively related. Similarly, Lin et al. [43] showed that by using a lidar-based height competition index it is possible to predict the aboveground carbon density of individual trees. Ma et al. [44] predicted tree growth in terms of an increase in height crown area and crown volume using bi-temporal airborne lidar data and they related this to some competition indices.

The objective of this study was to use lidar metrics to predict competition indices and to show how they relate with tree aboveground biomass (AGB). In particular, we focused on two competition indices, one related to height and one to the diameter at breast height (DBH). To the best of our knowledge, no study has explored the possibility of predicting DBH and height competition indices for individual trees detected on lidar data, using lidar metrics extracted both at the plot and ITC level.

2. Materials and Methods

The workflow in Figure 1 shows the analyses carried out in this work. In the following subsections, we present the dataset analyzed in this study and each step of the workflow.

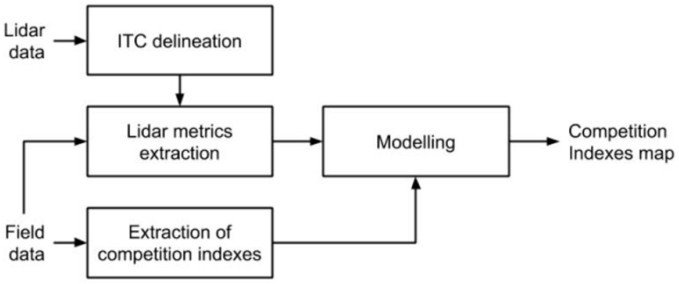


Figure 1. Workflow of the processing steps adopted in this study.

2.1. Data Set Description

2.1.1. Study Area

This study was conducted in the Autonomous Province of Trento (Italy), in the municipality of Lavarone (45°57′30.09″N, 11°16′25.17″E). The study area of approximately 4 km^2 (Figure 2) presents an altitude between 1200 and 1600 m above sea level, and it is composed of an uneven-aged forest with patches of mixed-species and pure-forest stands. The average number of trees per hectare is 839.4. In particular, dominant tree species are Norway spruce (*Picea abies* (L.) H. Karst.), about 47% of the total stem volume, and silver fir (*Abies alba* Mill.), about 36% of the total stem volume. Other tree species are present in the study area, although with a low percentage of the total stem volume: European beech (*Fagus sylvatica* L.) with about 13%, and European larch (*Larix decidua* Mill.) and Scots pine (*Pinus sylvestris* L.) with an overall percentage of about 4%.

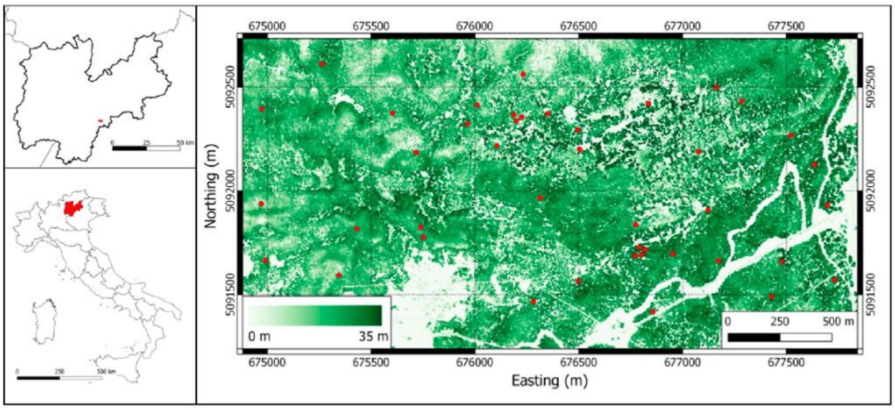


Figure 2. Canopy height model of the study area with plot locations (in red). The coordinate system of the CHM is UTM WGS 84 zone 32N. In the insets on the left, on the bottom, a map of Italy with the location of the Autonomous Province of Trento (in red), and, on the top, the location of the study site (in red) inside the Autonomous Province of Trento.

2.1.2. Lidar Data

Lidar data were acquired in 2015 by an Optech ALTM 3100EA sensor with a maximum scan angle of 21 degrees. The mean point density was 21.5 points per square meter for the first return. Up to four returns per pulse were measured. A digital terrain model (DTM) was generated from the lidar points by the vendor using the TerraScan software with a grid size of 0.5 m. The lidar point cloud was normalized to create a canopy height model (CHM) by subtracting the DTM from the z values of the lidar pulses. This operation was carried out using the software *lasground* of the package LAStools (https://rapidlasso.com/). The intensity value of each lidar point was range calibrated using the following equation:

$$I_C = I * \left(\frac{R}{Rs}\right)^{\alpha}, \quad (1)$$

where I_C is the calibrated intensity, I is the raw intensity, R is the sensor-to-target range, and Rs is the reference range or average flying height. An exponential factor, α, of 2.5 was considered since the environmental factors can be considered stable and the same acquisition parameters and instruments were maintained during the survey [45].

2.1.3. Field Data

Inside the study area, 49 circular plots of a 15-m radius were placed (see Figure 2). In summer 2016, within each plot, diameter at breast height (DBH), species, and positions were measured for all the trees with DBH $\geq$ 7 cm. Height was measured only for certain trees while for the others, it was predicted using height–DBH models defined on the basis of the measured trees. Above-ground biomass was obtained for all trees using local stem volume equations [46,47] multiplied by a conversion factor [48]. In Table 1, a summary of the collected field data and plot characteristics is presented.

Table 1. Summary of the field data collected in the 49 field plots. Data refer to the mean, maximum, and minimum values.

	All Trees	**Norway Spruce**	**Silver Fir**
Height (m)	16.9 (40.1, 2.1)	20.5 (40.1, 3.1)	18.1 (40.0, 3.2)
DBH (cm)	22.3 (81.0, 7.0)	28.6 (79.5, 7.0)	25.4 (81.0, 7.0)
AGB (kg)	284.7 (3468.5, 1.2)	453.5 (3215.0, 1.6)	353.6 (2917.7, 1.6)
CI_H	5.1 (19.3, 0.04)	5.0 (18.3, 0.7)	4.2 (19.3, 0.04)
CI_{DBH}	5.7 (22.8, 0.02)	5.1 (17.5, 0.5)	4.3 (15.8, 0.02)

2.2. *Extraction of Competition Indices*

Competition dynamics were analyzed using distance-dependent individual competition indices (CIs). These indices provide spatial information of the competitive status of an individual tree [49]. In this study, we used the indices proposed by Hegyi [50] in order to represent different combinations of tree characteristics (i.e., DBH and height).

The first step to calculate individual-based competition indices for a tree (called the subject tree) is the identification of the trees actively competing with it. A search radius around the subject tree needs to be defined: The radius influences the number of competitors to consider and thus the indices. A too small or too large radius may lead to underestimates or overestimates of the competitive effects between the subject tree and its real competitors [49]. In the literature, different methods to define the neighborhood area are presented. In our case, to evaluate the level of competition for each tree, we considered only the competitors located within a certain radius from the subject tree. Previous studies showed that a search radius of 10 m is sufficiently wide to capture all the competitive effects of neighboring trees [51,52]. In particular Szwagrzyk et al. [53] used a radius of 10 m in an area with similar structural parameters to the area in this study. Thus, we decided to use such a value. Moreover, to avoid edge effects, the competition indices were calculated only for trees positioned less than 10 m from any of the plot borders.

Two competition indices were considered in this study, one related to stem DBH and one to tree height. The two indices were calculated using the following formulas [50]:

$$CI^{i}_{DBH} = \sum\nolimits_{j=1}^{n}\left(\frac{\frac{DBH_j}{DBH_i}}{dist_{ij}+1}\right), \tag{2}$$

$$CI^{i}_{H} = \sum\nolimits_{j=1}^{n}\left(\frac{\frac{H_j}{H_i}}{dist_{ij}+1}\right), \tag{3}$$

where CI^{i}_{DBH} and CI^{i}_{H} are the DBH and height competition indices for the subject tree, i; DBH_i is the diameter at breast height of the subject tree, i; DBH_j is the diameter at breast height of the competitor tree, j; H_i is the height of the subject tree, i; H_j is the height of the competitor tree, j; $dist_{ij}$ is the distance between the subject tree, *i*, and the competitor tree, *j*; and *n* is the number of competitors in the neighborhood zone.

Because the most abundant species in our study area are silver fir and Norway spruce, we considered only these species as subject trees, while all trees were competitors.

2.3. ITCs Delineation

The delineation of the ITCs was carried out on the lidar data using the delineation algorithm of the R package *itcSegment* [54]. In particular, we used the function *itcLiDAR*. A detailed description of the method adopted can be found in [55]. This approach takes as input the canopy height model (CHM) on which local maxima (i.e., treetops) are located, and around them the crowns of the trees are delineated. The approach included three phases: (1) Smoothing of the canopy height model for which a Gaussian low-pass filter is applied to the rasterized CHM to smooth the surface and to reduce the number of potential local maxima; (2) local maxima extraction: A circular moving window of variable size is applied to the smoothed CHM to find a set of potential treetops (local maxima). A pixel of the CHM is identified as a local maximum when its value is greater than the other values contained in the moving window. The window size is defined according to the height of its central pixel and it spans in a range of odd values defined by the user (e.g., 3,5,7,9). If the height of the central pixel is low, a small value of the window size is used and vice versa; and 3) crown region growing: The crown of a tree is identified by the algorithm through the proximity of the pixels to that particular local maximum. A pixel is considered to belong to a specific region when its vertical distance is less than a percentage of a default difference given by the height of the local maximum. This process is repeated until no pixel is added to a region. Once the region is fully grown, a 2D convex hull is applied, resulting in polygons that represent individual trees (ITCs). The algorithm assigns to each delineated ITC a value of height (i.e., the value of the maximum elevation value of the lidar points inside the ITC) and a value of the crown area derived from the convex hull. The input parameters of the function *itcLiDAR* used in this study were: Resolution 0.5, MinSearchFilSize 3, MaxSearchFilSize 9, TRESHSeed 0.55, TRESHCrown 0.6, minDIST 5, maxDIST 40, HeightThreshold 2, and cw 1. For each ITC, DBH and AGB were predicted using the equations of Jucker et al. [56] implemented in the R package *itcSegment* considering the temperate coniferous forest as the biome.

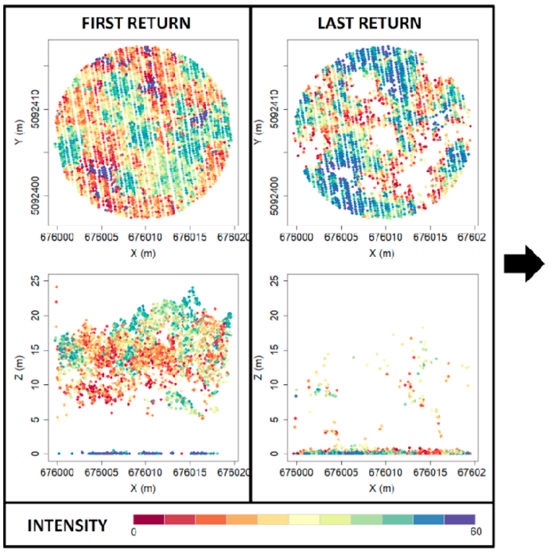
To generate the ITCs dataset to use in the modelling part, a matching process between delineated ITCs and reference ground observations was done. The matching procedure followed two steps: (1) Candidate search: all ground reference trees falling inside an ITC were considered as matching candidates; (2) candidate vote: selected candidates were ranked by their difference in height with the delineated ITCs and their Euclidean distance to the treetop. A distance metric, *D*, was estimated by considering both parameters to select the best candidate as follows:

$$D = \sqrt{(x_{\text{CAN}} - x_{\text{ITC}})^2 + (y_{\text{CAN}} - y_{\text{ITC}})^2 + w * (h_{\text{CAN}} - h_{\text{ITC}})^2}, \tag{4}$$

where x and y denote the locations and h the heights of the field-measured trees and the delineated ITCs, respectively; w is a user-defined weight (set to 0.5 in this study) [57].

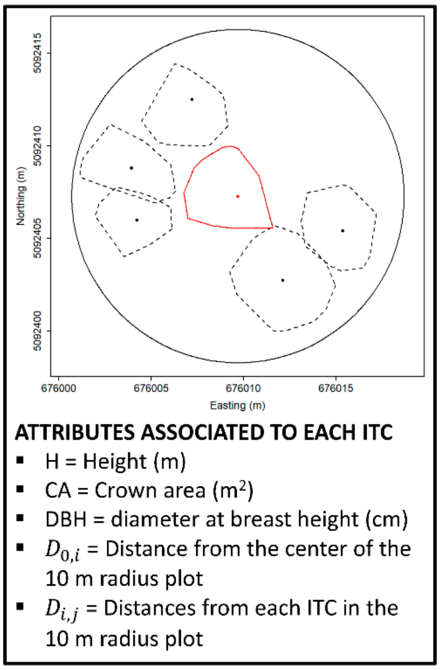
2.4. Lidar Metrics Extraction

Lidar metrics were extracted for each delineated ITC. As explained before, the competition indices computed on the field tree data refer to the competing trees in a radius of 10 m from the subject tree. Thus, for each ITC, two sets of metrics were defined: (i) plot metrics: 93 elevation and intensity metrics (see Figure 3) extracted from the first and last return of the lidar point cloud data. For each ITC, we considered lidar points located in an area of radius of 10 m from the ITC location. These metrics were extracted from the entire set of points in the 10-m radius from the ITC location, and they did not depend on the ITCs characteristics. Each metric was extracted from the first return points only (*_F*), and last return points only (*_L*); and (ii) ITC metrics: 23 metrics computed on the basis of the ITCs located in a radius of 10 m around the considered ITC (see Figure 4). These metrics were computed combining the characteristics (height, crown area, location, DBH) of the ITCs located in a radius of 10 m from the reference ITC.



Metric	Description
Zmax	Maximum Z
Zmean	Mean Z
Zsd	Standard deviation of Z distribution
Zskew	Skewness of Z distribution
Zkurt	Kurtosis of Z distribution
Zentropy	Entropy of Z distribution
ZqP	Ph percentile of height distribution, with P from 5 to 95 at steps of 5
ZpcumP	Cumulative percentage of points in the Pth layer, with P from 5 to 95 at steps of 5
Itot	Sum of intensities for each return
Imax	Maximum intensity
Imean	Mean intensity
Isd	Standard deviation of intensity
Iskew	Skewness of intensity distribution
Ikurt	Kurtosis of intensity distribution
IpcumzqP	Percentage of intensity returned below the Pth percentile of Z, with P from 5 to 95

Figure 3. Example of a point cloud in a radius of 10 m from an ITC. The points are colored according to their intensity value. On the right, a table of the metrics extracted from the first and last returns of the lidar points is shown.



ATTRIBUTES ASSOCIATED TO EACH ITC
- H = Height (m)
- CA = Crown area (m^2)
- DBH = diameter at breast height (cm)
- $D_{0,i}$ = Distance from the center of the 10 m radius plot
- $D_{i,j}$ = Distances from each ITC in the 10 m radius plot

Metric	Description
HminITC	Minimum ITCs height
HmeanITC	Mean ITCs height
HmaxITC	Maximum ITCs height
HsdITC	Standard deviation of the ITCs height
CAminITC	Minimum ITCs crown area
CAmeanITC	Mean ITCs crown area
CAmaxITC	Maximum ITCs crown area
CAsdITC	Standard deviation of the ITCs crown area
DBHminITC	Minimum ITCs DBH
DBHmeanITC	Mean ITCs DBH
DBHmaxITC	Maximum ITCs DBH
DBHsdITC	Standard deviation of the ITCs DBH
DBHsumITC	Sum of the ITCs DBH
DminITC	Minimum distance among the ITCs
DmeanITC	Mean distance among the ITCs
DmaxITC	Maximum distance among the ITCs
DsdITC	Standard deviation of the distances among the ITCs
DsumITC	Sum of the distances among the ITCs
DitcFrmC	Mean distance of the ITCs from the reference ITC
DitcFrmCdbh	Mean distance of the ITCs from the reference ITC, divided by *DBHmeanITC*
DitcFrmCh	Mean distance of the ITCs from the reference ITC, divided by *HmeanITC*
CI_DBH_ITC	DBHs competition index computed on the ITCs
CI_H_ITC	Height competition index computed on the ITCs

Figure 4. Example of competitors' ITCs (dashed ITCs) in a radius of 10 m from a subject ITC (red ITC), and list of attributes associated with each ITC from which the ITCs' metrics were extracted. On the right, a table of the metrics extracted is presented.

2.5. *Prediction*

To evaluate the efficiency of lidar metrics in modelling the competition indices, ordinary least square (OLS) models were built, in which the dependent variables were the competition indices estimated in the field and the independent variables were the lidar metrics. We developed three models for each competition index: One model using all the ITCs matched with the field data, one using only the ones of silver fir, and one using only the ones of Norway spruce. Before building the regression models, the presence of multicollinearity between the independent variables (the lidar metrics) was evaluated with the function *findCorrelation* of the R package *caret* [58]. In order to reduce the number of lidar metrics and to remove the ones most correlated among each other, we set the correlation threshold to 0.9. After this, the OLS models were built using the *stepAIC* function of the R package *MASS*. A natural logarithmic transformation of the original independent variables (the competition indices) was performed in order to avoid non-normality. The *stepAIC* function was restricted in order to reduce/avoid overfitting of the models. In particular, the selection was restricted in order to have at least 10 field samples for each metric selected and to have a value of the accuracy indices, *R2R* (Equation (13)) and *SSR* (Equation (14)), close to one.

The models were validated using a leave-one-out cross-validation and the accuracy statistics used in [59]. In particular, we considered:

(1) The mean difference (MD) between the predicted and the observed values:

$$\mathrm{MD} = \sum\nolimits_{i=1}^{n} \left(pre_i^{CV} - obs_i\right)/n, \tag{5}$$

where n is the total number of samples, pre_i^{CV} is the predicted value of the sample, i, obtained by cross-validation, and obs_i is the observed value of the sample, i.

(2) The mean absolute difference (MAD):

$$\mathrm{MAD} = \sum_{i=1}^{n} \left| pre_i^{CV} - obs_i \right| / n. \tag{6}$$

(3) The root mean squared differences (RMSDs) of the predicted values:

$$\mathrm{RMSD} = \sqrt{SS^{CV}/n}, \tag{7}$$

where the SS^{CV} is the sum of the squared differences between the observed values and the predicted values obtained by cross-validation:

$$SS^{CV} = \sum_{i=1}^{n} \left(pre_i^{CV} - obs_i \right)^2. \tag{8}$$

(4) The coefficient of determination obtained from the models' residuals:

$$R_{fit}^2 = 1 - SS^{fit}/SS_{tot}, \tag{9}$$

where the SS^{fit} is the sum of squares of the model residuals:

$$SS^{fit} = \sum_{i=1}^{n} \left(pre_i^{fit} - obs_i \right)^2, \tag{10}$$

and SS_{tot} is the sum of squared differences of each observation from the overall mean:

$$SS_{tot} = \sum_{i=1}^{n} \left(obs_i - \overline{obs} \right)^2. \tag{11}$$

(5) The coefficient of determination obtained from the cross-validation:

$$R_{CV}^2 = 1 - SS^{CV}/SS_{tot}. \tag{12}$$

(6) The R^2 ratio:

$$R2R = R_{fit}^2 / R_{CV}^2, \tag{13}$$

and (7) the sum of squares ratio:

$$SSR = \sqrt{SS^{CV}} / \sqrt{SS^{fit}}. \tag{14}$$

Each one of these statistics measures a different aspect of the prediction accuracy: MD measures the prediction bias, MAD and RMSD the prediction precision, R_{CV}^2 the agreement, and $R2R$ and SSR the overfitting. Regarding these last statistics, a desirable value for $R2R$ and SSR in order to avoid overfitting is below 1.1 [59].

2.6. Relationship between AGB and Competition Indices

The relationship between competition and AGB was evaluated by developing two linear models between the AGB of the subject trees and the corresponding competition indices. In particular, we built: (i) an OLS model linking the logarithm of the individual trees AGB estimated in the field with the competition indices estimated in the field, and (ii) an OLS model linking the logarithm of the individual trees AGB predicted using lidar with the competition indices predicted using lidar. The logarithm was used in order to avoid non-linearity. The coefficient of determination was used to evaluate the relationships.

3. Results

3.1. ITC Crown Delineation

Out of 464 trees used as subject trees to calculate the competition indices, only 115 matched with a delineated ITC. The detection rate was not very high at only 24.7%, but it is worth noting that, as we wanted to use these data to build up a reliable model, we excluded all the matched trees for which the field height and lidar height differed by more than 2 m. Among the 115 matched trees, 100 belonged to Norway spruce (34 ITCs) and silver fir (66 ITCs), and in the following analyses, only these ones were considered. In Figure 5, a scatterplot of the field-measured/estimated versus lidar-predicted values of DBH and AGB is reported along with the R^2.

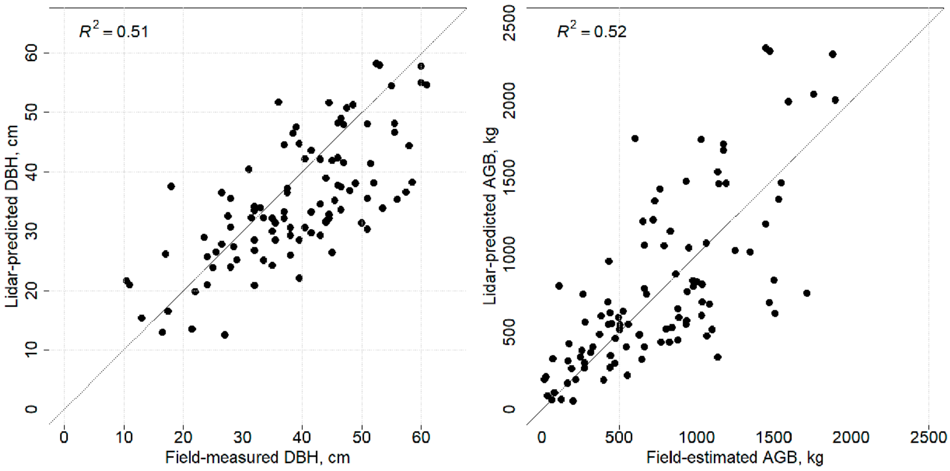


Figure 5. Field-measured DBH and field-estimated AGB versus lidar-predicted DBH and AGB for the 100 detected trees used to build the competition models.

3.2. Prediction of Competition Indices

Regarding the models comprising both species, the CI_{DBH} model (Table 2) was made up of two plot metrics and four ITC metrics. Among the plot metrics, one was an elevation metric (*Zpcum1_F*) and one was an intensity metric (*Iskew_L*). The CI_H model (Table 3) was made up of four plot metrics and one ITC metric. Among the plot metrics, two were elevation metrics (*Z*) and two were intensity metrics (*I*). Regarding the species specific models, for the silver fir (Table 4), the CI_{DBH} model was made up of two elevation plot metrics and one ITC metric, while the CI_H model was made up of one elevation plot metric and two ITC metrics. Contrastingly, the models for Norway spruce (Table 5) were made up by plot metrics only: three intensity metrics for the CI_{DBH} model and one elevation metric and two intensity metrics for the CI_H model.

Among the ITC metrics, five of them were used in the models: *CI_H_ITC, CI_DBH_ITC, DBHsumITC, CAmeanITC,* and *DsdITC*. *CI_H_ITC* is the height competition index (Equation (3)) computed using only the detected ITCs in the 10-m radius from the subject tree and the lidar-predicted heights; *CI_DBH_ITC* is the DBH competition index (Equation (2)) computed using only the detected ITCs in the 10-m radius from the subject tree and the lidar-predicted DBH; *DBHsumITC* is the sum of the predicted DBH values of the delineated ITCs in the 10-m radius around the subject tree; *CAmeanITC* is the mean value of the crown areas of the delineated ITCs in the 10-m radius around the subject tree; and *DsdITC* is the standard deviation of the distances among the delineated ITCs in the 10-m radius around the subject tree. Among the elevation plot metrics, two percentile metrics were used (*Zq20_F,* and *Zq95_L*) and three cumulative percentage of points metrics (*Zpcum1_F, Zpcum2_F*, and *Zpcum2_L*). Six intensity plot metrics were used: *Iskew_L, Iskew_F, Isd_L, Imean_F, Ipcumzq50_L*, and *Ipcumzq90_F*.

Table 2. OLS model for the prediction of CI_{DBH}.

Lidar Metric	Estimate	Std. Error	p	Significance
(Intercept)	−2.77	0.52	0.00	***
CI_H_ITC	1.82	0.21	0.00	***
Zpcum1_F	−0.02	0.00	0.00	***
Iskew_L	−0.28	0.11	0.01	*
DBHsumITC	−0.01	0.00	0.00	***
DsdITC	0.30	0.08	0.00	***
CAmeanITC	0.03	0.01	0.00	***

Significance levels: *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$.

Table 3. OLS model for the prediction of CI_H.

Lidar Metric	Estimate	Std. Error	p	Significance
(Intercept)	2.13	0.58	0.00	***
CI_H_ITC	0.59	0.11	0.00	***
Iskew_F	0.37	0.11	0.00	**
Zpcum2_F	−0.02	0.00	0.00	***
Isd_L	−0.15	0.04	0.00	***
Zq95_L	−0.03	0.01	0.00	**

Significance levels: *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$.

Table 4. OLS models for the prediction of the competition indices for silver fir.

	CI_{DBH}			CI_H	
Lidar metric	**Estimate**	**Significance**	**Lidar metric**	**Estimate**	**Significance**
(Intercept)	−1.07	***	*(Intercept)*	−1.25	**
CI_H_ITC	1.42	***	*CI_DBH_ITC*	0.59	***
Zpcum2_F	−0.03	***	*DsdITC*	0.43	***
Zq20_F	−0.05	***	*Zq95_L*	−0.05	***

Significance levels: *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$.

Table 5. OLS models for the prediction of the competition indices for Norway spruce.

	CI_{DBH}			CI_H	
Lidar metric	**Estimate**	**Significance**	**Lidar metric**	**Estimate**	**Significance**
(Intercept)	17.39	**	*(Intercept)*	3.71	***
Ipcumzq90_F	−0.13	*	*Imean_F*	−0.10	***
Imean_F	−0.09	**	*Isd_L*	−0.19	***
Ipcumzq50_L	−0.05	**	*Zpcum2_L*	0.02	*

Significance levels: *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$.

The accuracy statistics of the models obtained with the leave-one-out cross-validation are shown in Table 6. As can be seen, the behaviors are quite different for each model. Regarding the generic models, the model for the prediction of CI_H obtained slightly better results compared to the one for the prediction of CI_{DBH}: All the statistics except for the R^2_{fit} and R^2_{CV} obtained better values. Among the species-specific models, the ones for the silver fir competition indices had better performances compared to the ones of Norway spruce. All models experienced quite high values of MAD% (over 25%) and RMSD% (over 36%), and all had a negative bias (negative value of MD). Regarding the overfitting statistics (*R2R* and *SSR*), it can be seen that only the generic models have values below

1.1 while for the other models, these values can be higher even if (except for the one for CI_{DBH} of Norway spruce) the values are just slightly above 1.1. Figures 6–8 show the scatterplots between the competition indices predicted by the lidar models and those calculated from the data in the field.

Table 6. Summary of models' accuracy statistics. MD: mean difference (Equation (5)). MD: relative MD. MAD: mean absolute difference (Equation (6)). MAD%: relative MAD. RMSD: root mean squared differences (Equation (7)). RMSD%: relative RMSD. R^2_{fit}: coefficient of determination obtained from the models' residuals (Equation (9)). R^2_{CV}: coefficient of determination obtained from the cross validation (Equation (12)). $R2R$: the R^2 ratio (Equation (13)). SSR: sum of squares ratio (Equation (14)).

	All Trees		**Silver Fir**		**Norway Spruce**	
	CI_{DBH}	CI_H	CI_{DBH}	CI_H	CI_{DBH}	CI_H
Number of samples	100	100	66	66	34	34
Metrics selected	6	5	3	3	3	3
MD	−0.11	−0.09	−0.09	−0.11	−0.30	−0.20
MD%	−4.8	−3.4	−4.1	−4.5	−11.4	−7.2
MAD	0.75	0.67	0.70	0.83	0.89	0.71
MAD%	31.9	26.7	32.0	34.3	33.9	25.7
RMSD	1.03	0.92	0.98	0.99	1.37	1.00
RMSD%	43.9	36.3	44.7	41.2	52.0	36.3
R^2_{fit}	0.68	0.66	0.60	0.53	0.72	0.73
R^2_{CV}	0.64	0.62	0.54	0.44	0.57	0.66
$R2R$	1.08	1.07	1.11	1.19	1.27	1.10
SSR	1.07	1.07	1.07	1.08	1.25	1.11

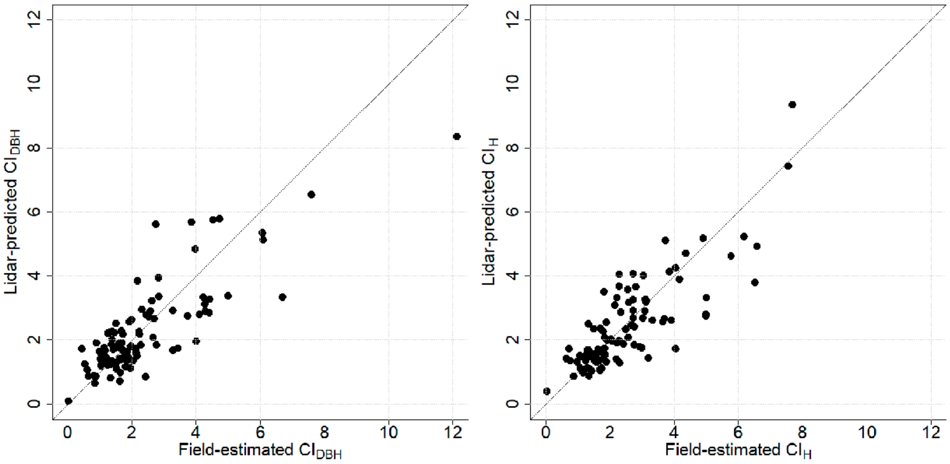


Figure 6. Field-estimated competition indices versus lidar-predicted competition indices. On the right, the CI_{DBH} competition index, and on the left, the CI_H competition index.

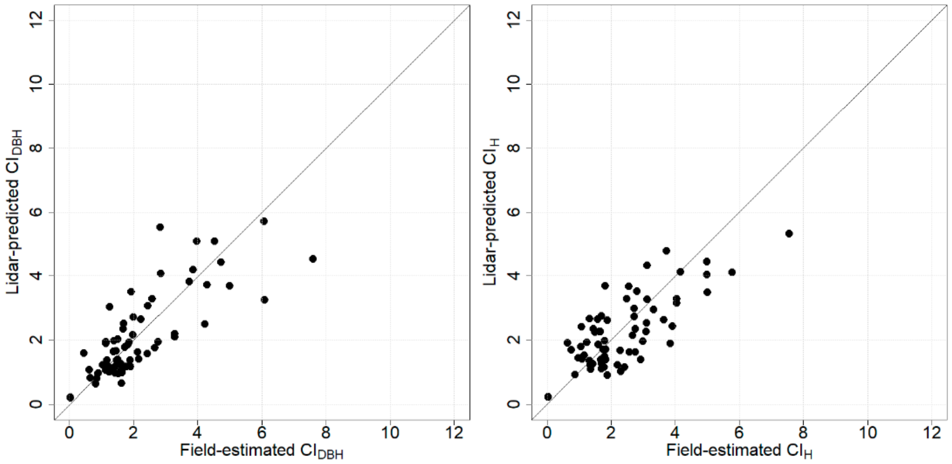


Figure 7. Field-estimated competition indices versus lidar-predicted competition indices for silver fir ITCs. On the right, the CI_{DBH} competition index, and on the left, the CI_H competition index.

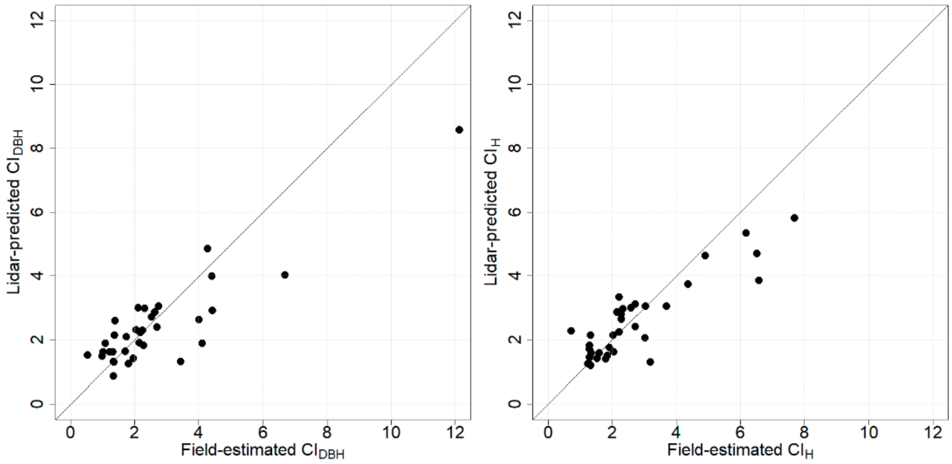


Figure 8. Field-estimated competition indices versus lidar-predicted competition indices for Norway spruce ITCs. On the right, the CI_{DBH} competition index, and on the left, the CI_H competition index.

3.3. *Relationship between Competition Indices and AGB*

In Figure 9 scatterplots of the field-estimated AGB and field-estimated competition indices are shown. This figure shows that high levels of competition resulted in low biomass values while when the competition was below a certain value, it did not influence the biomass. In the figures, the linear models relating the AGB and competition indices are also shown. The model relating log(AGB) to CI_{DBH} showed an R^2 of 0.65 while the one relating log(AGB) to CI_H was 0.44. The same trend was found using the lidar-predicted AGB and competition indices (Figure 10), but with lower values of correlation (R^2 of 0.43 and 0.16, respectively).

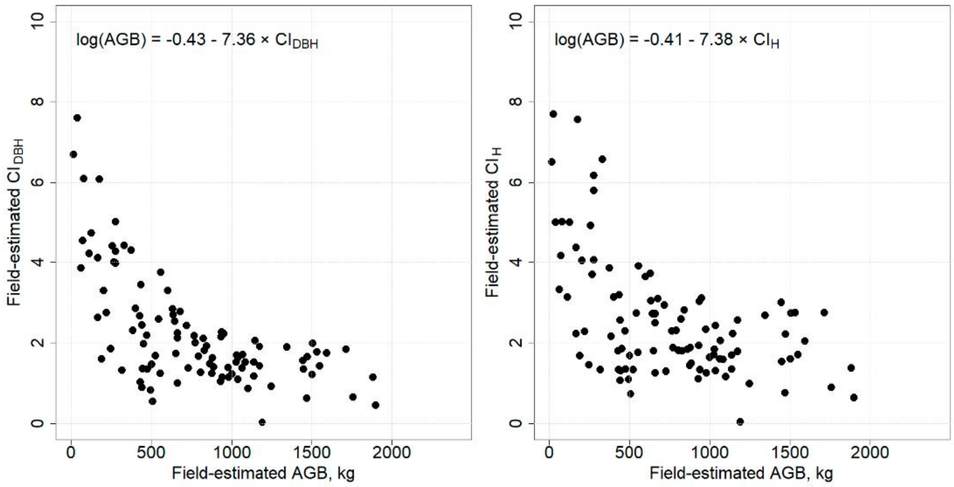


Figure 9. Field-estimated AGB versus field-estimated competition indices for the 100 ITCs matched with the field data.

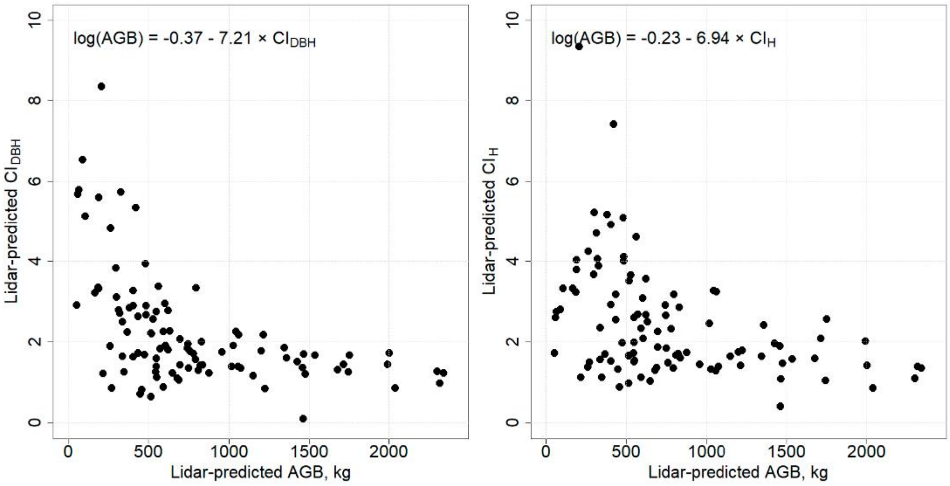


Figure 10. Lidar-predicted AGB versus lidar-predicted competition indices for the 100 ITCs matched with the field data.

4. Discussion

In this study, we demonstrated that it is possible to predict DBH and height competition indices using lidar metrics. We also showed how competition affects the AGB of individual trees. The results showed that no real improvement is gained in using a species-specific model with respect to a general model. It is worth noting that for the species-specific models, we had quite a low number of samples (especially for Norway spruce) and this could have influenced the results. In terms of overfitting, all models showed reasonable values of $R2R$ and SSR; in particular, only the model for CI_{DBH} of Norway spruce showed values much above 1.1, which was suggested by Lipovetsky [60] as a desirable limit in order to not have overfitting.

Analysis of the five ITC metrics selected indicated that they are all related to the competition indices. Some of them are clearly related, like the CI_{DBH} and CI_H indices computed using the ITCs (*CI_DBH_ITC*, and *CI_H_ITC*), while the others are representative of a part of the competition index equations (*DBHsumITC*, and *CAmeanITC*) and of the density of the forest (*DsdITC*), which is related to competition. Regarding the plot metrics, it was slightly harder to find a direct relation to the competition indices. Metrics based on the distribution of Z are likely related to competition even if not directly. The *Zq20_F, Zq95_L*, *Zpcum1_F*, *Zpcum2_F*, and *Zpcum2_L* metrics describe the vertical distribution of the lidar points, and the vertical distribution of the points is related to the forest structure and density, which are related to competition. In contrast, the intensity metrics could be related to the species. As an example, *Imean_F* has a quite different distribution of values for the two species: It has a mean value of 23.47 (standard deviation of 3.63) for silver fir compared to 20.15 (standard deviation of 3.82) for Norway spruce.

The effectiveness of lidar metrics in predicting both AGB and competition indices was also found in the study conducted by Lin et al. [43]. In particular, Lin et al. [43] showed that the height competition index estimated by lidar, especially when combined with other lidar metrics (crown radius and height) of the trees, is capable of effectively estimating above-ground carbon (AGC) at both the stand and tree level. In our case, the competition indices were used to assess the influence that high or low competition values have on biomass. The results showed that high competition values led to a decrease in biomass. Therefore, the competitive pressure of neighboring trees is probably an important factor influencing tree growth and biomass partitioning, especially for small trees. Indeed, according to Litton et al. [61] and Poorter et al. [62], biomass partitioning may vary with soil resource availability and with the ability of plants to withstand competition for light. Furthermore, according to the theory of biomass allocation, high competition may increase or reduce biomass allocation in plants [63,64]. Zhou et al. [33] found that the biomass ratio of roots and stems decreased with increasing intensity of competition from neighboring trees, while biomass at the level of branches and leaves increased.

Few previous studies were found in the literature that combined lidar and competition indices. Among the ones present in the literature, the ones of Lo et al. [42], Lin et al. [43], and Ma et al. [44] are the only ones slightly related to this work. In all these studies, competition indices were computed using ITCs automatically delineated on lidar data, in a similar way to our computation of the lidar metrics *CI_DBH_ITC* and *CI_H_ITC*. None of these studies analyzed the accuracy of the prediction of competition indices using lidar metrics or validated the predictions using field data. In contrast to the present study, these studies used lidar-predicted competition indices as metrics to predict trees attributes, such as DBH, volume, and carbon density.

Several studies have shown the relationship between radial growth and height growth of trees [65,66] and that the crown:height ratio may quantify competition among trees [67,68]. Therefore, the diameter and height of a tree are not only closely linked to light capture but also to the effects of water, nutrients, and soil conditions [33]. Moreover, according to the results of Zhou et al. [33], during growth, plants change how they are affected by the competition of neighboring plants, and their competitive effect on other plants. This suggests a close relationship between individual competition and tree growth.

In the workflow proposed in this study, some parameters were fixed in a way that could have influenced the final results. The main one was the search radius used to compute the competition indices. Many studies in the literature focusing just on the computation of indices using field data used a different radius for each area analyzed. This is possible if all the tree crowns are measured on the ground; however, that was not our case. Moreover, as we wanted to relate the indices to the lidar data in order to have the possibility of also predicting competition indices in areas not covered by field data, we needed to have a fixed value of the search radius. We chose 10 m as it was used before in other studies investigating forests with similar characteristics [53]. It is worth noting that we also carried out the same analyses using other values, computed in other ways, but the used radius was quite close to 10 m and the final results were very similar or the same.

The ITCs delineation could also have had an effect on the final results. Indeed, the higher the accuracy of the delineation, the more valuable ITC metrics are, and the more trees can be considered as subject trees in the area. The algorithm selected is a simple method when compared with the many algorithms in the literature [69], and has been used successfully in many other studies on forests with similar characteristics (e.g., [47,55]). It was effective for different forest scenarios in a previous study conducted on various forest sites in the Alps [70].

Despite the high potential of lidar technology for the estimation of vegetation parameters, it must be considered that lidar also has limitations. According to Rosette et al. [71], the ability to estimate vegetation parameters (tree height and DTM) decreases in the presence of high terrain slopes and high canopy coverage. Moreover, in very dense forests, it is only able to identify dominant trees, as in our study. Values of competition indices calculated using metrics derived from lidar can be biased due to the fact that small trees are not detected.

5. Conclusions

Our results showed that lidar metrics have a good capacity to predict competition indices. We developed a system that, after detecting individual tree crowns (ITCs) in the forest, on the basis of lidar metrics extracted in the neighborhood of the detected ITC, predicts two competition indices related to height and diameter at breast height (DBH). From the analyses, it emerged that the use of lidar metrics based on ITCs is important in prediction models. Moreover, we showed that all the information that can be extracted from lidar data should be used, as both plots and ITCs metrics were used in our models. Regarding the relationship between AGB and competition indices, it was observed that the AGB value decreases, increasing competition at both the DBH and height level. These results are probably related to the variation in the availability of soil-level resources and the ability of plants to withstand competition for light. The possibility of predicting competition indices in large areas opens interesting perspectives for forest management practices aimed at regulating species mixture, in particular for forests managed extensively with selective logging, typical of many mountain areas.

Author Contributions: Conceptualization, S.V., D.G., L.F., R.T., V.G. and M.D.; Data curation, S.V. and L.F.; Formal analysis, S.V. and M.D.; Funding acquisition, D.G. and R.T.; Investigation, S.V. and M.D.; Methodology, S.V., D.G. and M.D.; Supervision, D.G., R.T., V.G. and M.D.; Writing—original draft, S.V. and M.D.; Writing—review and editing, S.V., D.G., L.F., R.T., V.G. and M.D.

Funding: This study is linked to activities conducted within the COST (European Cooperation in Science and Technology) Action CLIMO (Climate-Smart Forestry in Mountain Regions—CA15226) financially supported by the EU Framework Programme for Research and Innovation HORIZON 2020.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Jucker, T.; Avăcăriței, D.; Bărnoaiea, I.; Duduman, G.; Bouriaud, O.; Coomes, D.A. Climate modulates the effects of tree diversity on forest productivity. *J. Ecol.* **2016**, *104*, 388–398. [CrossRef]
2. Shi, H.; Zhang, L. Local Analysis of Tree Competition and Growth. *For. Sci.* **2003**, *49*, 938–955. [CrossRef]
3. Liang, H.; Huang, J.-G.; Ma, Q.; Li, J.; Wang, Z.; Guo, X.; Zhu, H.; Jiang, S.; Zhou, P.; Yu, B.; et al. Contributions of competition and climate on radial growth of Pinus massoniana in subtropics of China. *Agric. For. Meteorol.* **2019**, *274*, 7–17. [CrossRef]
4. Aakala, T.; Berninger, F.; Starr, M. The roles of competition and climate in tree growth variation in northern boreal old-growth forests. *J. Veg. Sci.* **2018**, *29*, 1040–1051. [CrossRef]
5. Contreras, M.A.; Affleck, D.; Chung, W. Evaluating tree competition indices as predictors of basal area increment in western Montana forests. *For. Ecol. Manag.* **2011**, *262*, 1939–1949. [CrossRef]
6. Coomes, D.A.; Allen, R.B. Effects of size, competition and altitude on tree growth. *J. Ecol.* **2007**, *95*, 1084–1097. [CrossRef]
7. Ford, K.R.; Breckheimer, I.K.; Franklin, J.F.; Freund, J.A.; Kroiss, S.J.; Larson, A.J.; Theobald, E.J.; HilleRisLambers, J. Competition alters tree growth responses to climate at individual and stand scales. *Can. J. For. Res.* **2017**, *47*, 53–62. [CrossRef]

8. Ledermann, T. Evaluating the performance of semi-distance-independent competition indices in predicting the basal area growth of individual trees. *Can. J. For. Res.* **2010**, *40*, 796–805. [CrossRef]
9. Radtke, P.J.; Westfall, J.A.; Burkhart, H.E. Conditioning a distance-dependent competition index to indicate the onset of inter-tree competition. *For. Ecol. Manag.* **2003**, *175*, 17–30. [CrossRef]
10. Larocque, G.R. Examining Different Concepts for the Development of a Distance-Dependent Competition Model for Red Pine Diameter Growth Using Long-Term Stand Data Differing in Initial Stand Density. *For. Sci.* **2002**, *48*, 24–34. [CrossRef]
11. Kahriman, A.; Şahin, A.; Sönmez, T.; Yavuz, M. A novel approach to selecting a competition index: The effect of competition on individual-tree diameter growth of Calabrian pine. *Can. J. For. Res.* **2018**, *48*, 1217–1226. [CrossRef]
12. McTague, J.; Weiskittel, A. Individual-Tree Competition Indices and Improved Compatibility with Stand-Level Estimates of Stem Density and Long-Term Production. *Forests* **2016**, *7*, 238. [CrossRef]
13. Metz, J.; Seidel, D.; Schall, P.; Scheffer, D.; Schulze, E.-D.; Ammer, C. Crown modeling by terrestrial laser scanning as an approach to assess the effect of aboveground intra- and interspecific competition on tree growth. *For. Ecol. Manag.* **2013**, *310*, 275–288. [CrossRef]
14. Sun, S.; Cao, Q.V.; Cao, T. Evaluation of distance-independent competition indices in predicting tree survival and diameter growth. *Can. J. For. Res.* **2019**, *49*, 440–446. [CrossRef]
15. Kuehne, C.; Weiskittel, A.R.; Waskiewicz, J. Comparing performance of contrasting distance-independent and distance-dependent competition metrics in predicting individual tree diameter increment and survival within structurally-heterogeneous, mixed-species forests of Northeastern United States. *For. Ecol. Manag.* **2019**, *433*, 205–216. [CrossRef]
16. Hui, G.; Wang, Y.; Zhang, G.; Zhao, Z.; Bai, C.; Liu, W. A novel approach for assessing the neighborhood competition in two different aged forests. *For. Ecol. Manag.* **2018**, *422*, 49–58. [CrossRef]
17. Stadt, K.J.; Huston, C.; Coates, K.D.; Feng, Z.; Dale, M.R.T.; Lieffers, V.J. Evaluation of competition and light estimation indices for predicting diameter growth in mature boreal mixed forests. *Ann. For. Sci.* **2007**, *64*, 477–490. [CrossRef]
18. Biging, G.S.; Dobbertin, M. Evaluation of Competition Indices in Individual Tree Growth Models. *For. Sci.* **1995**, *41*, 360–377. [CrossRef]
19. Tomé, M.; Burkhart, H. Distance-Dependent Competition Measures for Predicting Growth of Individual Trees. *For. Sci.* **1989**, *35*, 816–831.
20. Dale, V.H.; Doyle, T.W.; Shugart, H.H. A comparison of tree growth models. *Ecol. Model.* **1985**, *29*, 145–169. [CrossRef]
21. Thorpe, H.C.; Astrup, R.; Trowbridge, A.; Coates, K.D. Competition and tree crowns: A neighborhood analysis of three boreal tree species. *For. Ecol. Manag.* **2010**, *259*, 1586–1596. [CrossRef]
22. Lang, A.C.; Härdtle, W.; Bruelheide, H.; Geißler, C.; Nadrowski, K.; Schuldt, A.; Yu, M.; von Oheimb, G. Tree morphology responds to neighbourhood competition and slope in species-rich forests of subtropical China. *For. Ecol. Manag.* **2010**, *260*, 1708–1715. [CrossRef]
23. Purves, D.W.; Lichstein, J.W.; Pacala, S.W. Crown Plasticity and Competition for Canopy Space: A New Spatially Implicit Model Parameterized for 250 North American Tree Species. *PLoS ONE* **2007**, *2*, e870. [CrossRef]
24. King, D.A.; Davies, S.J.; Supardi, M.N.N.; Tan, S. Tree growth is related to light interception and wood density in two mixed dipterocarp forests of Malaysia. *Funct. Ecol.* **2005**, *19*, 445–453. [CrossRef]
25. Wyckoff, P.H.; Clark, J.S. Tree growth prediction using size and exposed crown area. *Can. J. For. Res.* **2005**, *35*, 13–20. [CrossRef]
26. Lu, H.; Mohren, G.M.J.; den Ouden, J.; Goudiaby, V.; Sterck, F.J. Overyielding of temperate mixed forests occurs in evergreen-deciduous but not in deciduous-deciduous species mixtures over time in the Netherlands. *For. Ecol. Manag.* **2016**, *376*, 321–332. [CrossRef]
27. Forrester, D.I.; Theiveyanathan, S.; Collopy, J.J.; Marcar, N.E. Enhanced water use efficiency in a mixed Eucalyptus globulus and Acacia mearnsii plantation. *For. Ecol. Manag.* **2010**, *259*, 1761–1770. [CrossRef]
28. Brassard, B.W.; Chen, H.Y.H.; Cavard, X.; Laganière, J.; Reich, P.B.; Bergeron, Y.; Paré, D.; Yuan, Z. Tree species diversity increases fine root productivity through increased soil volume filling. *J. Ecol.* **2013**, *101*, 210–219. [CrossRef]

29. Bosela, M.; Tobin, B.; Šebeň, V.; Petráš, R.; Larocque, G.R. Different mixtures of Norway spruce, silver fir, and European beech modify competitive interactions in central European mature mixed forests. *Can. J. For. Res.* **2015**, *45*, 1577–1586. [CrossRef]
30. Fox, T.R.; Jokela, E.J.; Allen, H.L. The Development of Pine Plantation Silviculture in the Southern United States. *J. For.* **2007**, *105*, 337–347. [CrossRef]
31. Davidson, R.L. Effect of Root/Leaf Temperature Differentials on Root/Shoot Ratios in Some Pasture Grasses and Clover. *Ann. Bot.* **1969**, *33*, 561–569. [CrossRef]
32. Sebastià, M.-T. Plant guilds drive biomass response to global warming and water availability in subalpine grassland. *J. Appl. Ecol.* **2006**, *44*, 158–167. [CrossRef]
33. Zhou, W.; Cheng, X.; Wu, R.; Han, H.; Kang, F.; Zhu, J.; Tian, P. Effect of intraspecific competition on biomass partitioning of Larix principis-rupprechtii. *J. Plant Interact.* **2018**, *13*, 1–8. [CrossRef]
34. Lin, Y.; Huth, F.; Berger, U.; Grimm, V. The role of belowground competition and plastic biomass allocation in altering plant mass-density relationships. *Oikos* **2014**, *123*. [CrossRef]
35. Cahill, J.F., Jr.; Casper, B.B. Investigating the relationship between neighbor root biomass and belowground competition: Field evidence for symmetric competition belowground. *Oikos* **2000**, *90*, 311–320. [CrossRef]
36. Petersen, K.S.; Ares, A.; Terry, T.A.; Harrison, R.B. Vegetation competition effects on aboveground biomass and macronutrients, leaf area, and crown structure in 5-year old Douglas-fir. *New For.* **2008**, *35*, 299–311. [CrossRef]
37. Badreldin, N.; Sanchez-Azofeifa, A. Estimating Forest Biomass Dynamics by Integrating Multi-Temporal Landsat Satellite Images with Ground and Airborne LiDAR Data in the Coal Valley Mine, Alberta, Canada. *Remote Sens.* **2015**, *7*, 2832–2849. [CrossRef]
38. Hansen, E.; Gobakken, T.; Bollandsås, O.; Zahabu, E.; Næsset, E. Modeling Aboveground Biomass in Dense Tropical Submontane Rainforest Using Airborne Laser Scanner Data. *Remote Sens.* **2015**, *7*, 788–807. [CrossRef]
39. Sheridan, R.; Popescu, S.; Gatziolis, D.; Morgan, C.; Ku, N.-W. Modeling Forest Aboveground Biomass and Volume Using Airborne LiDAR Metrics and Forest Inventory and Analysis Data in the Pacific Northwest. *Remote Sens.* **2014**, *7*, 229–255. [CrossRef]
40. Popescu, S.C.; Wynne, R.H.; Scrivani, J.A. Fusion of Small-Footprint Lidar and Multispectral Data to Estimate Plot-Level Volume and Biomass in Deciduous and Pine Forests in Virginia, USA. *For. Sci.* **2004**, *50*, 551–565. [CrossRef]
41. Simonson, W.; Ruiz-Benito, P.; Valladares, F.; Coomes, D. Modelling above-ground carbon dynamics using multi-temporal airborne lidar: Insights from a Mediterranean woodland. *Biogeosciences* **2016**, *13*, 961–973. [CrossRef]
42. Lo, C.-S.; Lin, C. Growth-Competition-Based Stem Diameter and Volume Modeling for Tree-Level Forest Inventory Using Airborne LiDAR Data. *IEEE Trans. Geosci. Remote Sens.* **2013**, *51*, 2216–2226. [CrossRef]
43. Lin, C.; Thomson, G.; Popescu, S. An IPCC-Compliant Technique for Forest Carbon Stock Assessment Using Airborne LiDAR-Derived Tree Metrics and Competition Index. *Remote Sens.* **2016**, *8*, 528. [CrossRef]
44. Ma, Q.; Su, Y.; Tao, S.; Guo, Q. Quantifying individual tree growth and tree competition using bi-temporal airborne laser scanning data: A case study in the Sierra Nevada Mountains, California. *Int. J. Digit. Earth* **2018**, *11*, 485–503. [CrossRef]
45. Yu, X.; Hyyppä, J.; Litkey, P.; Kaartinen, H.; Vastaranta, M.; Holopainen, M. Single-Sensor Solution to Tree Species Classification Using Multispectral Airborne Laser Scanning. *Remote Sens.* **2017**, *9*, 108. [CrossRef]
46. Scrinzi, G.; Galvagni, D.; Marzullo, L. *I Nuovi Modelli Dendrometrici Per la Stima Delle Masse Assestamentali in Provincia di Trento*. 2010. Available online: http://sito.entecra.it/portale/public/documenti/sff_modelli_dendrometrici.pdf?lingua=EN (accessed on 15 September 2019).
47. Dalponte, M.; Coomes, D.A. Tree-centric mapping of forest carbon density from airborne laser scanning and hyperspectral data. *Methods Ecol. Evol.* **2016**, *7*, 1236–1245. [CrossRef]
48. *IPCC Guidelines for National Greenhouse Gas Inventories*. Agriculture, Forestry and Other Land Use. 2006. Available online: https://www.ipcc-nggip.iges.or.jp/public/2006gl/ (accessed on 15 September 2019).
49. Wang, D.; Tang, S.-C.; Hsieh, H.-C.; Chung, C.-H.; Lin, C.-Y. Distance-dependent competition measures for individual tree growth on a Taiwania plantation in the Liuguei area. *Taiwan J. For. Sci.* **2012**, *27*, 215–227.
50. Hegyi, F. A simulation model for managing jack-pine stands. In *Growth Models for Tree and Stand Simulation*; Fries, J.R., Ed.; Royal College of Forestry: Stockholm, Sweden, 1974; pp. 74–76.

51. Papaik, M.J.; Canham, C.D. Multi-model analysis of tree competition along environmental gradients in southern New England forests. *Ecol. Appl.* **2006**, *16*, 1880–1892. [CrossRef]
52. Canham, C.D.; LePage, P.T.; Coates, K.D. A neighborhood analysis of canopy tree competition: Effects of shading versus crowding. *Can. J. For. Res.* **2004**, *34*, 778–787. [CrossRef]
53. Szwagrzyk, J.; Szewczyk, J.; Maciejewski, Z. Shade-tolerant tree species from temperate forests differ in their competitive abilities: A case study from Roztocze, south-eastern Poland. *For. Ecol. Manag.* **2012**, *282*, 28–35. [CrossRef]
54. Dalponte, M. *Package 'itcSegment'*; 2018; pp. 1–12. Available online: https://cran.r-project.org/web/packages/itcSegment/index.html (accessed on 15 September 2019).
55. Dalponte, M.; Frizzera, L.; Ørka, H.O.; Gobakken, T.; Næsset, E.; Gianelle, D. Predicting stem diameters and aboveground biomass of individual trees using remote sensing data. *Ecol. Indic.* **2018**, *85*. [CrossRef]
56. Jucker, T.; Caspersen, J.; Chave, J.; Antin, C.; Barbier, N.; Bongers, F.; Dalponte, M.; van Ewijk, K.Y.; Forrester, D.I.; Haeni, M.; et al. Allometric equations for integrating remote sensing imagery into forest monitoring programmes. *Glob. Chang. Biol.* **2017**, *23*. [CrossRef]
57. Zhao, K.; Suarez, J.C.; Garcia, M.; Hu, T.; Wang, C.; Londo, A. Utility of multitemporal lidar for forest and carbon monitoring: Tree growth, biomass dynamics, and carbon flux. *Remote Sens. Environ.* **2018**, *204*, 883–897. [CrossRef]
58. Kuhn, M. Building Predictive Models in R Using the caret Package. *J. Stat. Softw.* **2008**, *28*. [CrossRef]
59. Valbuena, R.; Hernando, A.; Manzanera, J.A.; Görgens, E.B.; Almeida, D.R.A.; Mauro, F.; García-Abril, A.; Coomes, D.A. Enhancing of accuracy assessment for forest above-ground biomass estimates obtained from remote sensing via hypothesis testing and overfitting evaluation. *Ecol. Model.* **2017**, *366*, 15–26. [CrossRef]
60. Lipovetsky, S. How Good is Best? Multivariate Case of Ehrenberg-Weisberg Analysis of Residual Errors in Competing Regressions. *J. Mod. Appl. Stat. Methods* **2013**, *12*, 242–255. [CrossRef]
61. Litton, C.M.; Raich, J.W.; Ryan, M.G. Carbon allocation in forest ecosystems. *Glob. Chang. Biol.* **2007**, *13*, 2089–2109. [CrossRef]
62. Poorter, H.; Niklas, K.J.; Reich, P.B.; Oleksyn, J.; Poot, P.; Mommer, L. Biomass allocation to leaves, stems and roots: Meta-analyses of interspecific variation and environmental control. *New Phytol.* **2012**, *193*, 30–50. [CrossRef]
63. Temesgen, H.; LeMay, V.; Mitchell, S.J. Tree crown ratio models for multi-species and multi-layered stands of southeastern British Columbia. *For. Chron.* **2005**, *81*, 133–141. [CrossRef]
64. Toma, B. Prediction equations for estimating tree height, crown diameter, crown height and crown ratio of Parkia biglobosa in the Nigerian guinea savanna. *Afr. J. Agric. Res.* **2012**, *7*, 6541–6543. [CrossRef]
65. Waring, R.; Thies, W.; Muscato, D. Stem Growth per Unit of Leaf Area: A Measure of Tree Vigor. *For. Sci.* **1980**, *26*, 112–117.
66. Rodríguez, R.; Espinosa, M.; Hofmann, G.; Marchant, M. Needle mass, fine root and stem wood production in response to silvicultural treatment, tree size and competitive status in radiata pine stands. *For. Ecol. Manag.* **2003**, *186*, 287–296. [CrossRef]
67. Rottmann, M. Waldbauliche Konsequenzen aus Schneebruchkatastrophen. *Schweiz. Z. Forstwes.* **1985**, *136*, 167–184.
68. Vospernik, S.; Monserud, R.A.; Sterba, H. Do individual-tree growth models correctly represent height:diameter ratios of Norway spruce and Scots pine? *For. Ecol. Manag.* **2010**, *260*, 1735–1753. [CrossRef]
69. Zhen, Z.; Quackenbush, L.; Zhang, L. Trends in Automatic Individual Tree Crown Detection and Delineation—Evolution of LiDAR Data. *Remote Sens.* **2016**, *8*, 333. [CrossRef]
70. Eysn, L.; Hollaus, M.; Lindberg, E.; Berger, F.; Monnet, J.-M.; Dalponte, M.; Kobal, M.; Pellegrini, M.; Lingua, E.; Mongus, D.; et al. A benchmark of lidar-based single tree detection methods using heterogeneous forest data from the Alpine Space. *Forests* **2015**, *6*, 1721–1747. [CrossRef]
71. Rosette, J.; North, P.R.J.; Rubio-Gil, J.; Cook, B.; Los, S.; Suarez, J.; Sun, G.; Ranson, J.; Blair, J.B. Evaluating Prospects for Improved Forest Parameter Retrieval From Satellite LiDAR Using a Physically-Based Radiative Transfer Model. *IEEE J. Sel. Top. Appl. Earth Obs. Remote Sens.* **2013**, *6*, 45–53. [CrossRef]

GENERAL DISCUSSION AND CONCLUCIONS

Discussions and conclusions

Overall, results highlighted the response of trees to climate variations and competition processes in mountain forests in Italy. Dendrochronological analyzes and remote sensing (e.g., lidar) were used to understand the effects of competition processes on tree growth of European beech (Fagus *sylvatica* L.), Norway spruce (*Picea Abies* L.) and silver fir (*Abies alba* Mill.). In the first work, correlation and response functions revealed the influence of climate on radial growth and the different responses of European beech and silver fir in mixed and pure stands (chapter 1). The research results showed no significant differences between the two species, and between plots (mixed vs. pure). However, a significant impact of site conditions (sites at different latitudes) was found, maximum temperatures influencing the two species differently along the latitudinal gradient. Different responses between Trentino and Molise and Calabria were probably related to the area of distribution of European beech and silver fir. In fact, Molise and Calabria represent the southern distribution limits of both species. Although European beech and silver fir are highly susceptible to summer drought, both species recovered readily from the extreme events that occurred during the summer. In these mountain areas, water supply is not limiting the growth of these species. The absence of differences between mixed and pure stands was probably related to small size of beech trees in mixed plots, which may have limited the benefits of niche separation and complementarity. Less complementarity between the two species, and therefore less exploitation of resources, may explain the absence of significant differences between the responses to the climate in mixed vs. pure plots. However, it is important to note that, in this study both dominant and co-dominant trees were sampled. Therefore, the poor correlations and responses between climatic variables and the radial growth of trees could be due to the lower sensitivity of dominant and co-dominant trees to climatic variations.

Furthermore, even competitive interactions might buffer or amplify tree responses to climate and thus have an impact on stem radial growth. In fact, using mixed linear models, competitive interactions were found to have negatively influence on tree basal area increment (Chapter 2). In particular, high levels of competition were observed in Molise. High competition in Molise could be linked to the spatial distribution of trees (random in Molise vs. clustered in Calabria). The spatial distribution of trees might influence the intensity and strength of competitive interactions, especially in uneven-aged and uneven-structured stands. However, in mixed stands the strength and the result of competitive interactions could be influenced by site conditions. For example, the low stand density and complementary crown characteristics might reduce the impact of competition on basal area increment in mixed stands. In fact, the mixed stand in Molise showed a low level of competition compared to the corresponding pure stands. This suggests that differences in competition in these stands could depend on low stand density of mixed stand compared to the corresponding monoculture, particularly for European beech.

It is worth noting that the data set used in this model considered only European beech and silver fir as competitors within the six stands. Therefore, the effect of interactions between species on trees basal area increment did not take into account the influence of the other species, even if they were in a lower percentage.

The influence of competitive interactions on tree productivity, in terms of tree aboveground biomass, was studied through light detection and ranging (lidar) remote sensing technology (Chapter 3). The research results showed that both species-specific models (silver fir and Norway spruce) and general models correctly predicted the competition indices. Therefore, the lidar has a good ability to predict competition between trees. The competition indices estimated with the lidar were used to assess the influence of competition on biomass. Results suggest that high competition for resources may increase or reduce biomass allocation in plants. Despite the high potential of lidar technology in the ability to estimate vegetation parameters, it must be considered that it also has limitations. In very dense forests it is able to identify only dominant trees, therefore values of competition indices calculated using metrics derived from lidar can be biased due to the fact that small trees are not detected.

The choice of sustainable forestry options that consider the mixture of species should carefully ponder the environmental conditions of the site, in addition to the ecology of the species. Nevertheless, mixed forests cannot always be more productive and the interactions in these stands are not always less serious than monocultures. Therefore, before choosing the most suitable adaptive management strategy, several factors need to be considered, particularly those related to the structure and density of the forest stands. For example, a greater vertical stratification, and therefore a denser crown space filling, could lead to less competition for light, greater survival of small trees and complete light exploitation by crowns.