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Growth and yield modelling for optimal multi-objective forest management of eastern Mediterranean *Pinus brutia*

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Academic dissertation

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ABSTRACT

Pinus brutia is a major element of the Mediterranean forest landscape. It plays an important ecological and socioeconomic role by providing wood and non-wood forest products and ecosystem services. Despite its regional relevance, information is lacking for scientific management of *P. brutia*. The aim of this thesis is to address several gaps in knowledge in the prediction of *P. brutia* growth and yield in relation to contemporary multi-objective management planning. Individual-tree forest management-oriented models were fitted to predict stand dynamics of even- and uneven-aged *P. brutia* stands. Taper models and allometric biomass equations were fitted to enable the prediction of assortment volumes and aboveground biomass of *P. brutia*. Different prediction strategies based on mixed- and fixed-effects models in the absence and in the presence of model calibration were tested. The potential of using meta-analytical approaches was also inspected. The joint production of pine honeydew honey and timber was optimized. Although *P. brutia* tends to form even-aged stands and it is mainly managed using even-aged schedules, the prediction of semi-even-aged stand dynamics is more accurate if ingrowth is considered within the framework of uneven-aged modelling approach. In the absence of calibration, marginal predictions of timber assortments based on mixed-effects taper equations are competitive with those from fixed-effects models. The calibration of generalized mixed-effects biomass meta-models with minimal sampling effort results in more accurate predictions than local models developed from much larger datasets. The economic profitability of *P. brutia* forest management is the highest in healthy stands growing on good sites unaffected by *Marchalina hellenica*. In infested stands growing on good sites, honey production cannot compensate for the volume increment loss caused by the scale insect. On the contrary, on poor and medium sites, joint production of honey and timber can result in higher economic profit than wood production in healthy stands.

Keywords: stand dynamics, mixed-effects, calibration, biomass and carbon, optimization, non-wood forest product, forest planning

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Joensuu, December 2013

LIST OF ORIGINAL ARTICLES

This doctoral thesis is based on the following six articles, which are referred to in the text by the Roman numerals I-VI. Articles I, II, III and IV are reproduced with the kind permission of the publishers. Articles V and VI are the author's versions of submitted manuscripts.

I de-Miguel S., Pukkala T., Shater Z., Assaf N., Kraid B., Palahí M. (2010). Models for simulating the development of even-aged *Pinus brutia* stands in Middle East. Forest Systems 19(3): 449-457.
doi:10.5424/fs/2010193-9046

II de-Miguel S., Pukkala T., Assaf N., Bonet J.A. (2012). Even-aged or uneven-aged modelling approach? A case for *Pinus brutia*. Annals of Forest Science 69(4): 455-465.
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III de-Miguel S., Mehtätalo L., Shater Z., Kraid B., Pukkala T. (2012). Evaluating marginal and conditional predictions of taper models in the absence of calibration data. Canadian Journal of Forest Research 42(7): 1383-1394.
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IV de-Miguel S., Pukkala T., Assaf N., Shater Z. (2014). Intra-specific differences in allometric equations for aboveground biomass of eastern Mediterranean *Pinus brutia*. Annals of Forest Science 71(1): 101-112.
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Sergio de Miguel Magaña was primarily responsible for the study design, execution, data analysis and writing of all papers. In papers II, III and VI, data analysis was performed together with Prof. Timo Pukkala. In paper III, data analysis was also conducted together with Dr. Lauri Mehtätalo. The other co-authors contributed by collecting field data or commenting the manuscripts of the articles.

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ABBREVIATIONS

BAL	basal area of trees larger than the subject tree
dbh	diameter at breast height
Ddom	dominant diameter
Dmean	stand mean diameter at breast height
EA	even-aged
G	stand basal area
Hdom	dominant height
IPCC	Intergovernmental Panel on Climate Change
LC	lack of correlation
MCDA	multi-criteria decision analysis
MSD	mean squared deviation
NPV	net present value
NU	nonunity slope
REDD	Reducing emissions from deforestation and forest degradation
RMSD	root mean squared deviation
SB	squared bias
SD	standard deviation
SEV	soil expectation value
SI	site index
SK	skewness
SRA	strategic research agenda
T	stand age
UA	uneven-aged

1 INTRODUCTION

1.1 *Pinus brutia* forests

1.1.1 Worldwide distribution of P. brutia

Mediterranean forests cover approximately 25.5 million hectares (FAO 2013). Approximately, 25% of the Mediterranean forest area is covered by pines. This proportion becomes much higher in the eastern Mediterranean rim and North Africa where pine forests represent, in average, 75% of the total forest cover (Barbéro et al. 1998). *Pinus brutia* Ten., commonly known as Turkish red pine, Turkish pine, Brutian pine or Calabrian pine, is native to the eastern Mediterranean region, where it constitutes the most widespread coniferous ecosystem. It is also the most abundant non-broadleaved forest type in terms of forest cover in the whole Mediterranean basin. The total area covered by *P. brutia* is commonly estimated at 4 million hectares in the literature (Le Houerou 1981; Quézel 2000; Fady et al. 2003; Boydak et al. 2006). Based on more recent information, the area covered *P. brutia* within its native range could be estimated at more than 6 million hectares: around 5.8 million hectares in Turkey (MFWA 2012), 175,000 hectares in Cyprus (Pantelas 1986), 196,000 hectares in Greece (Skordilis and Thanos 1997), around 50,0000 hectares in Syria (IPGRI 2001) and around 17,000 hectares in Lebanon (Dalsgaard 2005). According to this information, *P. brutia* forests in Turkey, Cyprus, Greece, Syria and Lebanon represent, respectively, 26, 90, 6, 11 and 13 percent of the national forest cover. In addition, the species is also sparsely present in other countries out of its natural distribution area (i.e., Italy, Israel, France, Morocco, Australia), as a consequence of its introduction as a plantation species (Biger and Liphschitz 1991; Schiller and Mendel 1995; Barbéro et al. 1998; Quézel 2000).

1.1.2 Ecological and economic importance of P. brutia

P. brutia forests constitute a major element of the eastern Mediterranean landscape and play a key ecological and socioeconomic role. As most Mediterranean wooded lands, *P. brutia* forests are multipurpose ecosystems that provide multiple wood and non-wood products and services (EFI 2010). They are of great economic importance for the forestry sector since they represent the main source of timber products in some Mediterranean countries (Gezer 1985; Fischer et al. 2008). *P. brutia* provides a number of timber assortments such as sawlogs, sawn wood, pulpwood and fuelwood, which are used in construction, wood and paper industry, carpentry, as well as for producing charcoal and forest biomass-based energy (Pantelas 1986; Fady et al. 2003; Petrakis et al. 2007; Tolunay et al. 2008). Furthermore, non-wood forests products from *P. brutia* forests, such as pine honey, mushrooms, resins, and medicinal and aromatic plants (Sabra and Walter 2001; Yeşil et al. 2005; Satil et al. 2011; Kızılarslan and Sevg 2013) are relevant from the socioeconomic point of view. They can represent more than 40 percent of forests' total economic value and they are crucial for rural livelihoods (Croitoru and Liagre 2013). In addition, pine forests constitute a key habitat for biodiversity (Ne'eman and Trabaud 2000) hosting a number of eastern Mediterranean endemisms such as the Krüper's Nuthatch (*Sitta* *krueperi*) (Frankis 1991) and the scale insect *Marchalina hellenica* (Hatjina and Bouga 2009).

The interaction between *M. hellenica* and *P. brutia* constitutes a paradigmatic example that symbolizes the complexity of the ecological and socioeconomic trade-offs that occur in these pine forest ecosystems. Namely, the sap-sucking scale insect causes a weakening of infested trees and stands, which reduces forest growth and may lead to tree mortality. Since *P. brutia* forests are mostly publicly owned, this is perceived by the forestry sector as a threat to forest health and productivity. On the other hand, honeybees feed on the honeydew secretions of *M. hellenica* and produce a valuable non-wood forest product commonly known as pine honey (Yeşil et al. 2005). The beekeeping sector is mostly privately managed business and, therefore, beekeepers perceive the scale insect as a beneficial feature of the forest system.

P. brutia forests are also key ecosystems in relation to global change. As a fast-growing fire-prone pine (Boydak 2004), carbon sequestration and storage in its biomass is important for climate change mitigation and REDD policies. In terms of adaptation to climate change, its ability of withstanding aridity and continentality brings special interest to this species (Fischer et al. 2008), also in regions beyond the boundaries of the Mediterranean basin where the climate might become more Mediterranean-like in the future (FAO 2013).

As most Mediterranean ecosystems, *P. brutia* forests are fragile and vulnerable ecosystems historically affected by an intense anthropogenic pressure and harsh climatic conditions. In view of the undergoing global changes in climate, land uses, societies and lifestyles, *P. brutia* forests need to be properly and adaptively managed in order to meet the social demands for forest goods and services at multiple scales (global, regional and local) (FAO 2013).

1.2 Stand structure, dynamics, silviculture and management of *P. brutia*

P. brutia is a fire-prone fast-growing light-demanding species that can regenerate well after wild fires and usually grows in pure stands (Boydak 2004). Thus, completely unmanaged and non-harvested *P. brutia* forests tend to form even-aged stands as a result of the recurrent fire regime typical of the ecological and socioeconomic Mediterranean conditions. This is the case for instance of pine forest ecosystems in Syria, where the strict forest protection policy started during the 1950s has prevented any large-scale forest management or harvesting of *P. brutia* forests for decades (Shater et al. 2011).

When intensively managed for timber production (i.e., in Turkey), *P. brutia* is mostly managed under even-aged management schemes using regeneration methods that mainly consist of thinning from below and clearcutting, as well as of shelterwood and strip clearcut methods. In combination with natural regeneration or planting, such forest management schemes also tend to form even-aged stand structures (Boydak 2004). However, in other Mediterranean countries such as Cyprus or Lebanon, *P. brutia* forests have been historically “managed” until relatively recent times by applying selective cutting or thinning from above with the aim of harvesting the dominant and most profitable trees (Pantelas 1986; Assaf 2010). Such forest harvesting practices have led to more complex, uneven-sized and multi-layered stands ranging from two-aged to rather uneven-aged structures. It is, in fact, common that, under natural conditions, forest stands form semi-even-aged structures, that is, gradations between the strict even-aged and uneven-aged structures, which also occur in forest ecosystems other than *P. brutia* (Smith et al. 1996; González 2005).

Stand structure is an important feature in forest management planning. On one hand, a given stand structure is the result of tree growth and mortality dynamics, and of certain silvicultural practices. In turn, it determines the future stand dynamics and affects future forest management. Continuous regeneration and ingrowth play an important role in semi-even-aged pine stand dynamics. The structural heterogeneity of multi-layered uneven-sized stands is an important determinant of high bird diversity in pine forests (Izhaki 2000) as compared to typical even-aged stands. On the other hand, in the fire-prone *P. brutia* forests, vertical and horizontal continuity of vegetation may entail higher fire risk and severity than in even-aged stands (González et al. 2006).

Stand density and structural heterogeneity may have an influence on aboveground tree biomass allocation patterns. This may, in turn, have an impact on forest carbon balance and on nutrient cycles by affecting litter production and decomposition (Arianoutsou and Radea 2000), as well as carbon stock in tree biomass components and pinewood assortments (Naidu et al. 1998; Jenkins et al. 2003; Henry et al. 2011). Stand density and forest cover also affect understory plant diversity (Kutiel 2000), which is in turn tightly related to the potential use of Mediterranean pine forests as complementary sylvopastoral systems. In addition, taking into account water scarcity within the Mediterranean basin, the modification of the canopy structure towards multi-layered stands by means of silvicultural treatments may increase water infiltration to the soil and improve water use efficiency by the trees (Gracia et al. 2011). Therefore, tools are needed for properly describing and predicting different features of *P. brutia* stand dynamics and their influence on relevant forest attributes.

1.3 Why to model *P. brutia* forests?

Society demands an increasing number of goods and services from forest ecosystems. Such demands represent a major driving factor determining forest management objectives and practices. Thus, forests need to be managed for the provision of wood and non-wood forest products, biodiversity conservation, bioenergy supply, carbon sequestration and storage, avoiding deforestation and forest degradation, preserving water resources, etc. In short, forests have to be managed as complex adaptive systems facing ecological and socioeconomic changes (Messier et al. 2013). In view of the complexity and multifunctionality that characterize *P. brutia* forests, there is a need for efficient forest management schemes based on scientific knowledge in order to ensure the provision of multiple wood and non-wood forest products and ecosystem services in a changing world. Therefore, there is a need for science-based tools and decision support systems in order to assist and enable adaptive forest management to properly face the changing environmental and socioeconomic conditions (EFI 2010).

However, such science-based tools are few for many countries and for many forest ecosystems. This has been the case for instance of *P. brutia* forests. Despite the ecological and economic importance of *P. brutia*, the scientific knowledge concerning its stand dynamics and yield prediction is scanty. In addition, there is little knowledge for predicting stand dynamics in transitional complex stand structures of light-demanding species naturally tending to form even-aged stands, as it is often the case for Mediterranean pine forests. Although the prediction of forest biomass and carbon is important for many purposes such as carbon balance calculations, fire risk management and fuelwood production, there is not much knowledge on the influence of forest management and stand structure on forest biomass allocation in eastern Mediterranean pine forests. Accurate prediction of tree-, stand- and forest-level biomass and carbon stock on large spatial scales is a topical issue within forest science (Jenkins et al. 2003; Muukkonen 2007). Furthermore, the implications of ecological interactions between stand dynamics and different features of *P. brutia* ecosystems (e.g., pests, wood and non-wood forest products) are not well known or fully understood.

1.4 Multi-objective forest management planning: managing for complexity

Contemporary multi-objective forest management planning, which is partly based on operational research approaches, constitutes a suitable framework for tackling the above-mentioned challenges at multiple scales (i.e., tree, stand, forest, landscape). Stand dynamics and management objectives can be integrated by means of model-based simulation procedures of stand development in combination with quantitative or numerical optimization methods. Under this approach, stand-level optimization constitutes the first meaningful planning level. The outcomes are useful for developing forest management instructions. Sometimes, the outputs from stand-level optimizations may be scaled up in order to produce optimal forest- or landscape-level management plans. However, it is more common to use combinatorial optimization techniques on those cases (Pukkala 2002). So far, optimization has received little attention in previous research on *P. brutia*, and is absent from the relatively recently published monographs dealing with the management and silviculture of this species (Ne'eman and Trabaud 2000; Boydak et al. 2006).

Based on sound forest growth and yield models, it is possible to conduct flexible simulations of stand dynamics under different growing conditions and management alternatives. In combination with socioeconomic data, the efficiency and the optimality of a given forest management schedule can be assessed. In this regard, multi-objective forest management planning tends more and more to reflect the multifuncionality of forest ecosystems. Hence, the joint provision of wood and non-wood forest products and ecosystem services is receiving increasing interest in research and forestry practice. By means of numerical optimization techniques, it is possible to provide an objective scientific basis for the selection of management alternatives that maximize or minimize the objective function that defines the forest management goals.

The basic features of contemporary multi-objective forest management planning are the following (Pukkala 2002):

- Models to predict tree- and/or stand-level dynamics, characteristics and attributes,
- Simulation of stand dynamics (i.e., growth and yield of wood and non-wood forest products and ecosystem services) in alternative forest management schedules (i.e., number of thinnings, thinning intensities, rotation lengths) based on the existing models,
- Quantitative optimization to integrate the simulation of complex forest systems and socioeconomic criteria in order to find the optimal management according to one or several forest management objectives (e.g., provision of non-wood forest products, timber assortments, ecosystem services) (Fig. 1).

1.5 Individual-tree forest management-oriented models

Science-based models for describing how forest stands develop and for predicting the yield of forest goods and ecosystem services constitute the basis of contemporary multi-objective forest management planning (Fig. 1).

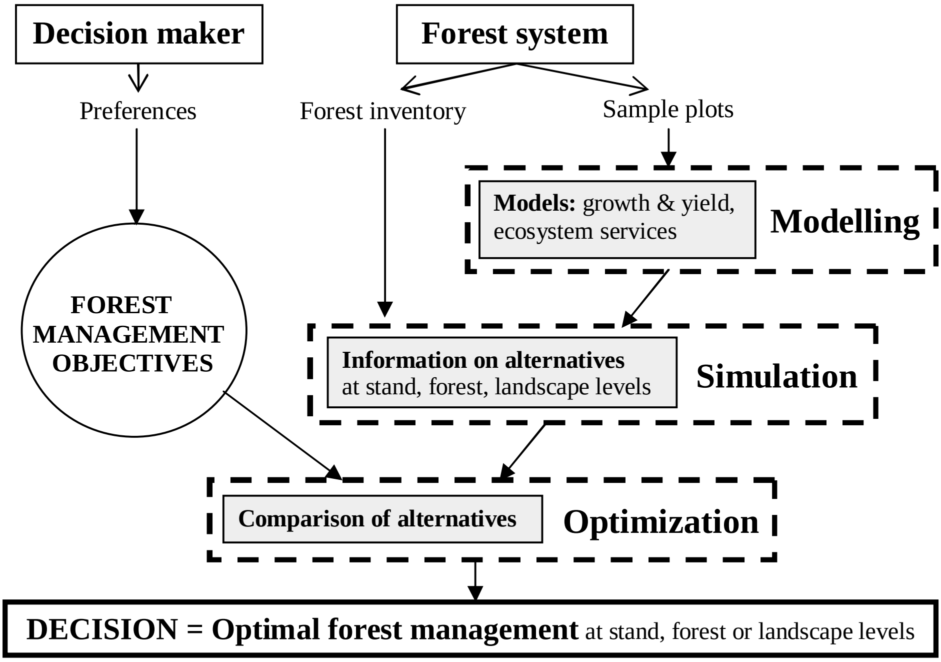

Figure 1. Flowchart of contemporary science-based forest management planning.

Among the existing modelling approaches (i.e., empirical, process-based or mechanistic, hybrid and gap or forest succession models) (Hasenauer et al. 2000), empirical growth and yield models, also called forest management-oriented models, have been widely used in forest management planning to predict stand dynamics and the yield of wood and non-wood products and ecosystem services (Vanclay 1994; Pretzsch 2010; Weiskittel et al. 2011; Bonet et al. 2012; Martínez-Peña et al. 2012; Burkhart and Tomé 2012). Such predictive models rely on statistical analyses, often under the form of regression techniques, aiming at predicting growth and yield from several predictor variables. They are based on the state-space approach (García 1994), which assumes that the variables describing the current state of a given forest system at any time include the required information for predicting the future evolution of the system (Fontes et al. 2010). Although these models rely to some extent on the stationarity of site conditions (Vanclay and Skovsgaard 1997; Skovsgaard and Vanclay 2008), they are also suitable to accurately predict stand dynamics under changing environmental conditions when based on a dynamic state-space approach (Nord-Larsen and Johannsen 2007; Nord-Larsen et al. 2009) or if productivity-environment relationships are developed (e.g., Seynave et al. 2005; Tyler et al. 1996).

Empirical forest growth and yield models can be broadly classified as: i) individual-tree models, if the basic modelling units are the individual trees within a stand, ii) size-class models (e.g., transition matrices) if the basic modelling units are, for instance, stand diameter classes containing several trees, iii) diameter-distribution models, if statistical probability functions are used to model the evolution of stand diameter distribution, and iv) whole-stand models, if the stand constitutes the modelling unit (Munro 1974; Weiskittel et al. 2011). Individual-tree growth modelling has several advantages compared to other modelling methods: i) it accounts for between-tree differential growth and survival rates as a result of inter- or intra-specific competition, ii) has a high resolution and enables flexible and detailed simulations of stand dynamics taking into account the aforesaid differential development of every tree (Pretzsch et al. 2002), iii) avoids the potential bias emerging from the mean tree approach typical of stand-level and some hybrid physiological modelling approaches as a consequence of Jensen's inequality (Duursma and Robinson 2003), and iv) by aggregation of individual-tree predictions it can also provide estimates of lower resolution (i.e., diameter class- and stand-level) in a similar way as size-class, diameter distribution and whole-stand models (Pretzsch et al. 2002). In addition, some other modelling approaches (i.e., diameter-distribution models) are not suitable for properly simulating all management alternatives and their impacts on forest stand dynamics, growth and yield.

Depending on whether the between-tree spatial distance is explicitly taken into account or not in model fitting and in the prediction of stand dynamics, individual-tree models can be distance-dependent or distance-independent (Weiskittel et al. 2011). Distance-dependent models are able to account for the between-tree competition in a more detailed and sophisticated way than distance-independent models. However, the distances between individual trees in a stand are usually unknown in forest management practice. Therefore, distance-independent models may be more widely applicable in forestry practice. On the other hand, increasing use of LIDAR in forest inventory would possibly broaden the applicability of distance-dependent approaches.

In addition, since different stand structures may reflect differences in stand dynamics, predictive individual-tree models need to be able to imitate and reproduce the expected stand dynamics according to the stand structure and species composition. In this regard, previous research has given little attention to exploring the most suitable modelling approaches for complex, transitional or intermediate stand structures between even-aged and uneven-aged stands.

Multi-objective forest management often needs to address issues related not only to the provision of wood products and timber assortments (i.e., sawnwood, pulpwood, firewood), but also in relation to carbon sequestration and storage. Since forest yield can be expressed in terms of either volume or biomass, taper models and biomass allometric equations are useful tools for predicting tree-level yield into different timber assortments and tree components. By aggregating individual-tree predictions, such models can be used for scaling up estimations of timber and biomass production at multiple scales (i.e., stand, forest, landscape, country). In fact, according to the IPCC guidelines (IPCC 2006), currently under review, the accounting of biomass and carbon stock for Tier 2 (national level) and Tier 3 (local level forest modelling) levels should be based on sound allometric equations.

Large-scale prediction has much ado with the generalisation of biomass and carbon estimates (e.g., Jenkins et al. 2003; Muukkonen 2007; Somogyi et al. 2007). In a nutshell, to what extent are our results applicable elsewhere or generalizable into larger scales? From the modelling perspective this can be partly tackled from a number of approaches ranging from sampling design issues, to data acquisition methods and basic statistical modelling theory. Thus, from the sampling point of view, it is desirable that the modelling data are collected from a wide range of possible growing conditions in terms of site characteristics, stand structure and geographical distribution. Concerning data acquisition, most forest research relies on the analysis of field data, regardless of whether those field measurements are processed within the framework of primary or secondary analysis (Glass 1976). Furthermore, it is possible to directly rely on the outcomes of previous forest modelling research, i.e., already published models for different geographical areas and growing conditions, to generate data for large-scale models. These latter kinds of data are often called pseudo-data or pseudo-observations, and the models developed from them may be called meta-models, as they fall into the research field of meta-analysis (Glass 1976; Jenkins et al. 2003; Muukkonen 2007).

Model validation against independent data is probably the most robust way to prove whether model predictions are accurate and precise enough beyond the range of the modelling data. In addition, modelling theory offers the possibility to account for the variation arising from different hierarchical levels of the data. This can be conducted by means of mixed-effects models which implicitly assume that the modelling data represent only a sample of a larger population. Mixed-effects may be calibrated to different growing sites and conditions with little resampling effort (Pinheiro and Bates 2000).

1.6 The state of the art of *P. brutia* growth and yield modelling

Despite the relevance of *P. brutia* in the Mediterranean region, the scientific knowledge on *P. brutia* growth, yield and management is rather scanty. Differences in stand structure, growing conditions and tree shape among locations and provenances (e.g., Isik et al. 1999; Zianis et al. 2011) prevent the extrapolation of local results to broader areas.

The complete set of equations provided by Palahí et al. (2008) to predict *P. brutia* stand dynamics on an individual-tree basis was limited to a small area in Dadia National Park (north-eastern Greece). In addition to the restricted geographical area, the study failed to provide an ingrowth model to properly simulate uneven-aged stand dynamics. In fact, according to Kitikidou et al. (2011), the scarcity of suitable data has prevented the development of sound individual-tree models in other Greek areas. The other available complete set of forest management-oriented models for even-aged *P. brutia* stands (Shater et al. 2011) was conducted within the framework of this PhD thesis. More recently, a couple of local site index models have been developed for areas in Greece and Cyprus (Kitikidou et al. 2011, 2012). In view of the relevance of *P. brutia* in Turkey, one would expect to find growth and yield models from that country. However, no such research papers can be found from international journals. The fact that none of the two main monographs on this species (Ne'eman and Trabaud 2000; Boydak et al. 2006) explicitly tackles the multi-objective forest management planning of *P. brutia* also indicates lacking knowledge for scientific management.

So far, the studies dealing with tree taper and biomass prediction of *P. brutia* are also scanty and restricted to geographically small areas in Turkey and a couple of Aegean islands in Greece. In addition, the existing papers on allometric biomass equations for *P. brutia* are based on rather small datasets presenting mainly medium-sized and small trees (Bilgili and Kucuk 2009; Durkaya et al. 2009; Zianis et al. 2011). Therefore, reliable estimations of aboveground biomass and carbon cannot be obtained for most regions throughout the natural distribution area of *P. brutia*. Concerning taper modelling of *P. brutia*, the existing rather localised studies are based on the evaluation of a limited number of models that in some cases result in biased predictions of stem volume, especially for large trees (Brooks et al. 2008; Özçelik et al. 2011; Özçelik and Brooks 2012).

1.7 Strategic research objectives for *P. brutia*

The international strategic research objectives for Mediterranean forests are in accordance with the above-mentioned concerns and challenges in relation to *P. brutia* ecosystems, as well as with their ecological and economic importance. They are also consistent with the contemporary multi-objective forest management planning approach. The Mediterranean

Forest Research Agenda 2010-2020 (EFI 2010) identifies the following meaningful research targets in relation to the aforementioned gaps in knowledge: i) to implement modelling approaches at multiple scales (e.g., tree- and ecosystem-level), ii) to use and develop new forest growth and yield models that can provide predictions on the provision of wood and non-wood products and ecosystem services, iii) to develop goal-based dynamic and adaptive silvicultural models to optimise the provision of relevant goods and services, iv) to develop new multi-objective forest planning models to solve multiple objective problems considering socioeconomic and ecological factors and adjacent resources at multiple scales, v) to develop advanced optimisation techniques capable of integrating bio-physical and socioeconomic paradigms, in dynamic modelling frameworks, vi) to monitor, understand and model interactions between forests and microorganisms and insects: symbionts, pathogens, pests, and vii) to design, implement and evaluate policy instruments to promote the optimal provision of market and non-market goods and services.

Since *P. brutia* forests are partly distributed throughout some EU countries of the eastern Mediterranean region, the above-mentioned research goals are also linked to the strategic objectives, research areas and forestry-value chains defined by the first Strategic Research Agenda (SRA), which was designed within the framework of the European Forest-Based Sector Technology Platform (FTP – Forest Technology Platform). Among the strategic research objectives identified by the SRA, the following ones would respond to the challenges of *P. brutia* forests: i) enhancing the availability and use of forest biomass for products and energy, and ii) meeting the multifunctional demands on forest resources and their sustainable management. In addition, the following forestry-based value chains mentioned in the SRA are also related to the gaps in knowledge on *P. brutia*: i) commercialising soft forest values, ii) trees for the future, iii) forests for multiple needs, iv) advancing knowledge on forest ecosystems, and v) adapting forestry to climate change (FTP 2006; EFI 2010). Similar targets are defined also in the second strategic theme ("responsible management of forest resources") of the FTP's Strategic Research and Innovation Agenda for 2020, and more specifically, under the following research and innovation areas (FTP 2013): i) multi-purpose management of forests, ii) forest ecology and ecosystem services, and iii) enhanced biomass production.

1.8 Objectives of this PhD thesis

This PhD thesis aims at addressing several of the aforementioned research goals concerning *P. brutia* forests. Specifically, the objectives of this PhD thesis are to:

1. quantitatively describe and predict *P. brutia* stand dynamics based on individual-tree growth models (studies I and II);
2. provide reliable tree-level models for predicting *P. brutia* yield in terms of biomass and carbon, as well as in terms of timber assortment volumes (studies III, IV and V);
3. test the performance and potential of mixed-effects models in yield prediction both in the absence and in the presence of calibration data (studies III and V);
4. inspect the potential of using meta-analytical approaches to improve the predictions of empirical models (study V);
5. propose optimal forest management schedules for *P. brutia* forest stands (studies I and VI); and
6. optimize the joint production of pine honey (a non-wood forest product) and timber in *P. brutia* stands infested by the scale insect *M. hellenica* (study VI).

2 MATERIALS AND METHODS

2.1 Materials

2.1.1 Study area

The study region is the eastern Mediterranean rim which practically constitutes the natural distribution area of *P. brutia* (Fig. 2). Studies I, III and IV used data collected in Lebanese and Syrian *P. brutia* stands. Study II was based on data collected in *P. brutia* stands throughout Lebanon. Study V was based on existing models for different *P. brutia* populations in Greece, Turkey, Syria and Lebanon. Finally, study VI focused on Turkey and Greece, where all pine honey in the world is produced.

2.1.2 Data for individual-tree growth modelling

Data were collected from 133 circular plots placed throughout the natural distribution area of *P. brutia* in Middle East: 83 plots in Syria and 50 plots in Lebanon. All plots were used in study I of this PhD thesis, whereas only the Lebanese plots were used in study II. The sample plots were selected so as to capture the whole range of variation in site, stand age and stand density. The sample plots were established in stands where no forestry operations had been conducted at least during the previous 20 years. The plot radius was varied depending on the stand density in order to include approximately 75 trees in each plot.

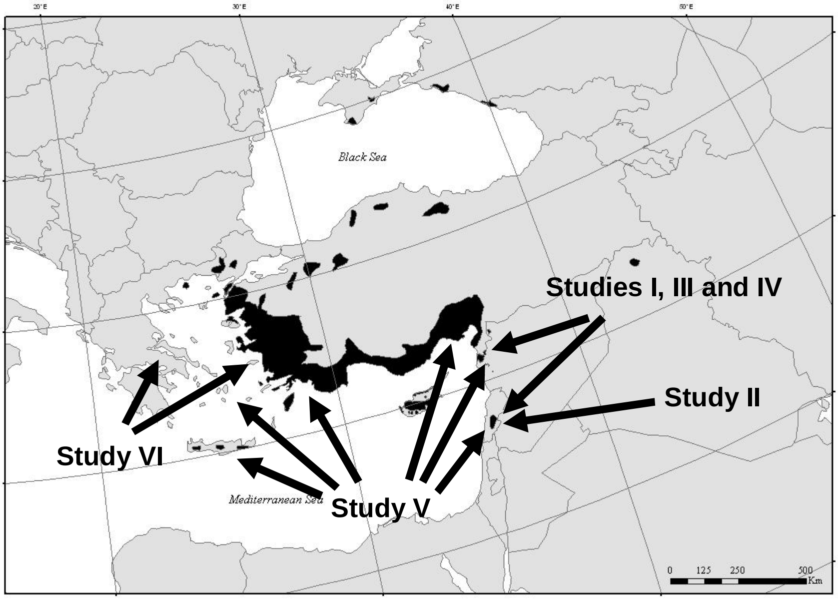

Figure 2. Natural distribution area of *Pinus brutia* (EUFORGEN 2009) and approximate location of the study areas of the papers included in this PhD thesis.

Diameter at breast height (dbh) and radial growth of one or two past 10-year periods were measured for every tree in the plots. Tree height and bark thickness were measured for 10 to 11 sample trees, and age was measured for 5 dominant trees. The following variables were recorded for every plot: altitude, slope, aspect, average soil depth (5 measurements per plot, one in the plot centre and four near the limits of the plot) and UTM coordinates of the plot centre. Additional stand and tree level variables (i.e., stand basal area, basal area of trees larger than the subject tree, mean dbh) were calculated for every plot as part of the data preparation process. Two plot-wise models were fitted to calculate the height and bark thickness of those trees for which these variables had not been measured in the field. Backdating was used to calculate tree and stand variables at the beginning of the two past 10-year growth periods assuming that the bark thickness-dbh and height-dbh relationships had remained constant along time.

2.1.3 Data for volume and biomass modelling

Data were collected from 201 felled trees of different sizes and shapes were felled throughout the natural distribution area of *P. brutia* in Middle East: 100 trees in Syria and 101 trees in Lebanon. The trees represented different site qualities, stand densities, and stand ages. Every tree was measured for outside bark diameter at breast height (1.3 m). Each tree was felled at stump height (10 cm above ground level), and the total length of the stem (total height from ground to tip) was measured from the felled trees. Stem diameter was measured at relative heights of 1%, 5%, 10%, 20%, 30%, 40%, 50%, 60%, 70%, 80%, and 90% of the total tree height. A cubic spline function was fitted for each tree to calculate the stem diameter at 10-cm intervals. The volume of each10-cm disc was calculated with the cylinder formula and summed to obtain the total “true” stem volume.

For taper modelling purposes (study III), the 100 sample trees from Syria were used as modelling data, whereas the 101 trees measured in Lebanon were used as an independent dataset for model validation of the selected stem profile equation.

For the first study on allometric aboveground biomass equations (study IV), the dry matter content of *P. brutia* was determined from samples of branches and needles of about 1.5 kg each taken from felled trees. The samples were dried in an oven at 105 ºC until they reached constant weight. The dry matter content of branches and needles was multiplied by the corresponding fresh biomass of every sample tree in order to calculate the dry biomass for these two components (branches and foliage). Since needles were not separated from branches, the proportion of branches of the total fresh biomass of tree crown was calculated from p(branch) = 0.6 + 0.003*dbh (Montero et al. 2005).

To determine the basic density of the tree stem, stem disks were taken from felled trees of different sizes and at different tree heights. The samples were also dried in an oven until constant weight, and the basic density was calculated by dividing the obtained dry weight by the fresh volume of the disk. Then, the mean basic density of all samples was calculated. The stem dry biomass of every tree stem was then computed by multiplying the total “true” stem volume by the mean basic density.

The study on allometric biomass meta-models (study V) used pseudo-observations as modelling data. Pseudo-observations were derived from existing allometric biomass equations throughout the natural distribution area of *P. brutia*. In addition to the equations developed in study IV for Middle East, those developed by Zianis et al. (2011) in Greece, together with those developed by Bilgili and Küçük (2009) and Durkaya et al. (2009) in Turkey, completed the list of equations from which the pseudo-data were derived. The pseudo-observations were generated based on the systematic part of the models assuming normally distributed residuals with mean equal to zero and variance equal to the reported variance. This procedure aimed at recovering the within- and between-location variability of the original field measurements. Five pseudo-observations were randomly generated for each 2-cm diameter class for the whole diameter range of the original datasets reported in the reference studies.

2.1.4 Data for economic optimization of stand management

Study VI used the results of studies I and III for predicting and simulating *P. brutia* growth and yield. The additional data requirements for this study consisted of: i) annual pine honey production, and ii) prices and production costs of timber assortments and pine honey. Since honey yield estimates per hectare can vary considerably, a sensitivity analysis accounting for the effect of pine honey production on optimal forest management was conducted by using the following honey yields: 30 kg ha^{-1} yr^{-1}, 60 kg ha^{-1} yr^{-1} and 90 kg ha^{-1} yr^{-1}. The price assigned to pine honey was 7 US$ kg^{-1}. The stumpage prices of different timber assortments (i.e., sawlogs, pulpwood and firewood) provided by *P. brutia* stands were also considered in the analysis (Table 1). Site preparation and tending costs in years 5 and 10 were set to 200 US$ ha^{-1} each. The costs associated to pine honey production were 2 US$ kg^{-1}. The economic information of wood and non-wood forest products was obtained from the literature (e.g., Saner et al. 2003; Pak et al. 2010) as well as from Turkish forestry experts and official records.

2.2 Methods for individual-tree growth modelling

2.2.1 Model sets for predicting even-aged and uneven-aged stand dynamics

Individual-tree growth models were developed for both even-aged (EA) and uneven-aged (UA) *P. brutia* stands. Individual-tree modelling of even-aged *P. brutia* stand dynamics for Middle East countries (studies I and II) was based on models for dominant height, diameter-increment, height-diameter relationship and self-thinning. Country effects accounting for the geographical isolation between the Syrian and Lebanese *P. brutia* populations were considered in model fitting by using a country indicator variable. All models were fitted using nonlinear least squares regression analysis. Individual-tree modelling of uneven-aged *P. brutia* stand dynamics (study II) was based on models for ingrowth, diameter-increment, and height-diameter relationship.

Since only one measurement of dominant height was available from each plot, site quality was assessed by using the guide curve method in order to produce anamorphic site index curves (Clutter et al. 1983). Several functions among those compiled by Kiviste et al. (2002) were fitted in nonlinear regression analysis when searching a suitable site index model. The index age used for calculating site index was selected according to the rotation period typically applied in managed even-aged *P. brutia* stands, that is, 50 years (e.g., Bettinger et al. 2013).

Table 1. Stumpage prices and minimum dimensions of different timber assortments.

Assortment	Stumpage price (US$ m^{-3})	Min. top diameter (cm)	Min. piece length (m)
Sawlog	90	19	2
Pulpwood	45	8	1
Firewood	10	4	0.5

The diameter-increment modelling aimed at predicting the future 10-year diameter growth. Variables representing site productivity, tree size and competition were used as predictors. Under the even-aged modelling approach, site index was used to describe site quality. Since stand age is undefined in uneven-aged forestry (a stand does not have a single age) and dominant height may be modified through forest management, site productivity was described via soil and topographic variables.

In height-diameter modelling of even-aged stands, the total tree height was expressed as a function of diameter at breast height, dominant height and dominant diameter based on the power equation model form of Stoffels and van Soest (1953) modified by Tomé (1989), which constrains the model to pass through the point determined by dominant diameter and dominant height. Since dominant height and diameter are not meaningful predictors under the uneven-aged framework, the height-diameter equation was an adaptation of the "Hossfeld I modified" function.

Stand-level survival of *P. brutia* trees was modelled by means of a self-thinning model in accordance with Reineke's model form (Reineke 1933) and the –3/2 power rule (Yoda et al. 1963). The model was fitted using the number of living trees per hectare in the densest sample plots as the response variable. Stand mean dbh and site index were tested as predictors. For that purpose, the sample plots were first divided into three site quality classes (good, medium and poor) according to site index. The plots that were assumed to be on the self-thinning limit were selected separately in each site index category, which resulted in 40 plots for modelling the self-thinning limit. Since nowadays *P. brutia* stands are seldom thinned in Syria and Lebanon, a high proportion of plots were at the self-thinning limit mainly in Syria, which could be verified in the field: dead, dying and weakened trees were common in the densest plots. Since sample plots were temporary (i.e., measured only once for past growth), it was not possible to develop an individual-tree mortality model.

Under the uneven-aged modelling approach, ingrowth modelling was conducted by means of a two-equation model that predicts the number of trees that pass the 10-cm dbh limit during the next 10-year period, and the mean diameter of those trees at the end of the 10-year period.

2.2.2 Simulation of even-aged and uneven-aged stand dynamics

The fitted growth models were used to simulate stand dynamics of even-aged (studies I, II and VI) and uneven-aged (study II) *P. brutia* stands. The input data consists of a list of all trees growing in a given plot. The simulation procedure for a 10-year growth period in even-aged stands was as follows (Shater et al. 2011):

1. In addition to tree diameters, dominant height (Hdom) and stand age (T) need to be known.
2. Site index is calculated from Hdom and T using the site index model.
3. Stand age is incremented by 10 years, and a new Hdom is computed using the site index model,
4. Diameters are incremented using the diameter-increment model,
5. The stand mean dbh is calculated (Dmean),
6. The self-thinning limit is computed using the self-thinning model,
7. If the number of trees overpasses the self-thinning limit, trees are removed
8. Dominant diameter (Ddom) is computed and individual-tree heights are predicted using the height-diameter model,

9. The remaining tree characteristics (timber assortment volumes, biomass in different tree components) and stand attributes (stand volume, biomass, basal area, etc.) are computed.

The simulation procedure for a 10-year growth period in uneven-aged stands was as follows:

1. 10-year diameter increment is predicted for each tree and added to the current tree dbh,
2. The number and initial diameter of ingrowth trees is calculated using the two-equation ingrowth model,
3. Ingrowth trees are added to the stand,
4. New tree heights are computed based on the height-diameter model.

Survival was not simulated in study II, where the simulation period was short. This choice was necessary since the backdated characteristics of current survivors were used as input data; there was no mortality in the data. In addition, the Lebanese stands of study II were seldom near the self-thinning limit.

2.2.3 Comparing even-aged and uneven-aged modelling

As a result of study I, it was observed that while Syrian pine stands were rather even-aged, the plots sampled in Lebanon presented higher structural heterogeneity ranging from even-aged to uneven-aged stands (Fig. 3). To analyse which modelling approach may be more suitable to predict *P. brutia* growth and yield when dealing with such complex stand structures, the 50-plot Lebanese sample was split into two sub-samples of 25 plots containing, respectively, the most even-aged and the most uneven-aged stands. The stand classification was based on the standard deviation (SD) and skewness (SK) of the diameter distribution. SD was selected because high standard deviations of dbh are indicative of “uneven-agedness”, even if the diameter distribution is bell-shaped. In turn, positive SK describes the degree of asymmetry of typical uneven-aged, inverse J-shaped diameter distributions. Standard deviation plus two times skewness (SD+2 SK) was used to bisect the plots as even-aged and uneven-aged. As a result, a 50-plot sample containing all the stands, as well as two 25-plot sub-samples containing the most even-aged and the most uneven-aged stands, were obtained to evaluate the performance of the two modelling approaches in stand volume prediction. Stand volume was estimated through aggregation of individual-tree stem volumes using the taper model developed in study III.

A 20-year growth simulation was conducted separately on the 50-plot sample and the two 25-plot sub-samples. The even-aged and uneven-aged model sets were used separately to simulate a 20-year growth period in every sample stand using the known backdated stand conditions 20 years ago as the starting point for the simulation process, and running the simulation until the current stand conditions.

The performance of each modelling approach was evaluated by comparing the simulation-based stand volume predictions with the observed values in three different ways: (a) assuming that all the stands were either uneven-aged or even-aged, that is, testing the predictions of each modelling approach against the observed values in all the 50 stands (“overall-performance”); (b) testing the predictions of each approach against the measured values of the 25 stands corresponding to the same stand structure as the approach (“self-performance”); and (c) testing the predictions of each approach against the measured values of the 25 stands corresponding to the opposite stand structure (“cross-performance”).

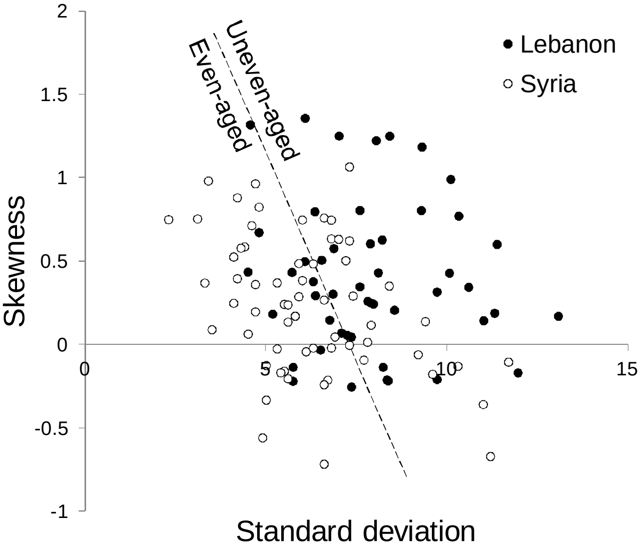

Figure 3. Differences in stand structure between Lebanese and Syrian *P. brutia* forests according to skewness and standard deviation of the stand diameter distribution.

2.3 Methods for volume and biomass modelling

2.3.1 Comparing volume prediction strategies based on taper modelling

A taper model for *P. brutia* in Middle East was developed within study III. Alternative volume prediction strategies based on fixed- and mixed-effects models in the absence of calibration were compared: 1) marginal predictions from a marginal (fixed-effects) model, 2) conditional predictions from a conditional (mixed-effects) model with random effects equal to zero, and 3) mean predictions from a mixed-effects model over the distribution of random effects (marginal predictions from a conditional model).

Candidate taper equations with different numbers of parameters (from 1 to 10) were selected from the literature. Because volume prediction was the main purpose of this study and tree volume is the integral of cross-sectional stem area over the tree height, the models were fitted for squared dbh (d^2). These models provide unbiased predictions for tree cross-sectional area and volume (Bruce et al. 1968; Prodan et al. 1997; Gregoire et al. 2000). The best model for each number of parameters was selected aiming at identifying a single best equation.

Since marginal predictions from fixed-effects models have been shown to be often more accurate when the aim is prediction (e.g., Pukkala et al. 2009; Guzmán et al. 2012; de-Miguel 2013), the fixed-effects least squares modelling approach guided the model selection procedure. Once the best model was selected, a nonlinear mixed-effects model was fitted and compared with the fixed-effects model. For that, the effects of different parameters on the shape of the taper curve and their random variation were analyzed. Based on this analysis, the parameters that were tree-specific were identified, and the best combination of random parameters according to the likelihood ratio test was selected.

Whereas volume predictions under strategy 1 and 2 can be directly obtained by numerically integrating the taper equation resulting from model fitting, the implementation of strategy 3 required Monte-Carlo calculation consisting of 20,000 realizations of model parameters drawn from the multivariate normal distributions of the random parameters taking into account the covariance matrix of the random effects. The taper curve for each simulated vector of random effects was integrated numerically to compute the volume. Finally, the mean over the 20,000 predictions was computed as the marginal prediction of tree volume. All three prediction strategies were evaluated in the modelling data (Syria) and validated using an independent data set gathered from another country (Lebanon) aiming at a generalized taper equation meaningful to Middle East.

2.3.2 Allometric modelling of aboveground biomass

Study IV was devoted to the assessment and inspection of differences in tree-level aboveground biomass prediction for *P. brutia* in Middle East. A number of models among the most utilized in previous research dealing with biomass prediction (e.g., Zianis et al. 2005) were tested. Two alternative models were provided for each aboveground tree component: one using the best combination of the available predictors (i.e., dbh, tree height and crown length), and the other using dbh as the only predictor. Predictions at the tree, stand and forest levels were based on the latter model form.

The equations presented in this study were fitted under the intrinsically linear form, which assumes an additive error in model fitting (Návar 2010), and using generalized least squares nonlinear regression analysis. Such an approach is supposed to prevent the "additivity problem" (Parresol 2001) arising from the mismatch between the sum of biomass component-specific predictions and total aboveground biomass estimates (Snowdon 2000). In addition, yielding predictions for the response variable on its original scale avoids the use of bias corrections factors (e.g., Baskerville 1972).

A power-type variance function describing the heteroscedasticity found in the model residuals was used to homogenize the residual variance:

$$\operatorname{var}(e_i) = \sigma^2 \cdot |y|^{2\cdot\delta} \tag{1}$$

where σ^2 is the error variance, y represents a variance covariate given by the fitted values of the model, and δ is the variance function coefficient.

2.3.3 Generalizing biomass models to the natural distribution area of P. brutia

Study V focused on providing generalized meta-models for predicting aboveground biomass of *P. brutia* on large spatial scales by calibrating those models to location-specific conditions. The hierarchical structure of the meta-modelling data (i.e., pseudo-observations generated based on existing models developed for different locations) was taken into account by means of a mixed-effects modelling approach. The widely used allometric model with dbh as the only predictor was selected due to lacking local information for relating other tree attributes (e.g., height) to dbh and because tree attributes other than dbh may not be available in large-scale biomass prediction. Thus, the power-type equation form using diameter at breast height as the single predictor of tree biomass was selected to conduct the meta-analysis. The linearized version of the power-type equation was favoured instead of the nonlinear form to enable the straightforward calibration procedure within the context of linear prediction without linear approximations of nonlinear functions. Therefore, the logarithmic transformation of the biomass model was selected to conduct the meta-analysis.

Thus, the selected model form was:

$$\ln y_{ij} = (\beta_0 + b_{0i}) + (\beta_1 + b_{1i}) \cdot \ln(d_{ij}) + e_{ij} \tag{2}$$

where y_{ij} is dry biomass of the corresponding component (stem, crown or foliage) of tree j in location i (kg tree^{-1}), d_{ij} is diameter at breast height (cm), β_0 and β_1 are fixed-effects regression coefficients, b_{0i} and b_{1i} are the parameters accounting for between-location random effects and e_{ij} is residual variance. It is assumed that both random effects and residual are independent, normally distributed random variables with $(b_{0i}, b_{1i})'= \mathbf{b}_i \sim MVN(0, \mathbf{D})$ and $e_{ij} \sim NID(0, \sigma^2)$. Parameters β_0, β_1, $\mathbf{D}$ and σ^2 were estimated using restricted maximum likelihood as implemented in the *nlme* package (Pinheiro and Bates 2000) of R-environment (R Development Core Team 2011). Baskerville's bias correction factor (Baskerville 1972) was used to back-transform aboveground biomass estimates into their original scale (kg tree^{-1}).

The meta-model calibration procedure was based on the prediction of random effects using the best linear unbiased predictor (BLUP) (Lappi 1991), which requires destructive sampling of at least one tree from the location of interest for measuring the biomass components. Thus, the logarithmic aboveground biomasses measured from trees in location i are pooled into vector $\mathbf{y}_i$, and they follow the model

$$\mathbf{y}_i = \boldsymbol{\mu} + \mathbf{Z}\mathbf{b}_i + \mathbf{e}_i \tag{3}$$

where $\boldsymbol{\mu}$ is the fixed part of the mixed-effects model, $\mathbf{b}_i$ is a vector of random effects accounting for between-location differences, $\mathbf{Z}$ is the design matrix including those measured predictors which have a random coefficient, and $\mathbf{e}_i$ is a vector of random residuals. Let us define the variance-covariance matrix of the random effects var($\mathbf{b}_i$)=$\mathbf{D}$ and var($\mathbf{e}_i$)=$\mathbf{R}$, where $\mathbf{R}=\sigma^2\mathbf{I}$. $\mathbf{D}$ is, therefore, a square $n \times n$ matrix with n equal to the number of random parameters. In this case, the design matrix $\mathbf{Z}$ is a $2 \times n$ matrix.

The mean and variance of a vector including both random effects and observations are (McCulloch and Searle 2001)

$$\begin{bmatrix} \mathbf{b}_i \\ \mathbf{y}_i \end{bmatrix} \sim \left(\begin{bmatrix} 0 \\ \boldsymbol{\mu} \end{bmatrix}, \begin{bmatrix} \mathbf{D} & \mathbf{D}\mathbf{Z}' \\ \mathbf{Z}\mathbf{D} & \mathbf{Z}\mathbf{D}\mathbf{Z}' + \mathbf{R} \end{bmatrix} \right) \tag{4}$$

The Best Linear Unbiased Predictor (BLUP) of the random effects for the location of interest, $\mathbf{b}_i$, can be then computed as follows:

$$\textbf{BLUP}\ (\mathbf{b}_i) = \hat{\mathbf{b}}_i = \mathbf{D}\mathbf{Z}'(\mathbf{Z}\mathbf{D}\mathbf{Z}' + \mathbf{R})^{-1}(\mathbf{y}_i - \boldsymbol{\mu}) \tag{5}$$

with the prediction variance of

$$\textbf{var}\ (\hat{\mathbf{b}}_i - \mathbf{b}_i) = \mathbf{D} - \mathbf{D}\mathbf{Z}'(\mathbf{Z}\mathbf{D}\mathbf{Z}' + \mathbf{R})^{-1}\mathbf{Z}\mathbf{D} \tag{6}$$

An independent dataset was used in model validation. Different sampling strategies were tested using Monte-Carlo simulation by generating 10,000 sampling realizations per sampling strategy. The sampling strategies tested were the following: i) completely random sampling of 1,2,3,...,*n* trees, ii) stratified random sampling of 2,4,6,...,*n* trees within two strata (dbh≤23, dbh≥23), and, iii) stratified random sampling of 3,6,9,...,*n* trees within three strata (dbh≤18, 18<dbh≤30, dbh>30). The dbh thresholds to determine the partitioning of the independent dataset into tree-size categories was set so as to have the same number of trees per tree-size category. At every iteration, the independent dataset was split into two sub-datasets. The first sub-dataset contained nineteen sample trees randomly selected for model validation purposes. Of the remaining 20 trees, 1 to 20 trees were selected according to the applied sampling strategy for model calibration using BLUP. At each iteration, an ordinary least squares (OLS) linear model was also fitted to the calibration sub-dataset. This procedure aimed at comparing the differences in terms of predictive performance between the calibrated linear mixed-effects meta-model and the equivalent OLS linear model based on the same sample of trees. The performances of the meta-models and the corresponding OLS models were then assessed by comparing observed *versus* predicted biomass estimates.

2.4 Criteria used in model selection, comparison, evaluation and validation

In studies I to IV, the selection of the best individual-tree growth and yield models was based on the following criteria: a) agreement with current biological knowledge, b) logical behaviour of the models in extrapolations and long-term simulations, c) simplicity and robustness, d) accuracy and precision, e) statistical significance (p-value < 0.05) of model parameters, f) non-biasness, g) homocedasticity and normal distribution of residuals, h) acceptable levels of multicollinearity, and i) sensitivity analysis of model predictions to changes in the parameter values. The statistics used for model selection were the coefficient of determination (R^2), residual standard error (RSE), Akaike's information criterion (AIC), and Bayesian information criterion (BIC). Likelihood-ratio tests were carried out in order to assess whether the improvement of model fitting arising from adding more predictors to a null model was statistically significant.

Model comparisons, evaluation and validation in studies II to V were also partly based on the partitioning of the mean square deviation (MSD) into squared bias (SB), nonunity slope (NU) and lack of correlation (LC) (Gauch et al. 2003). Such a partitioning enables a proper assessment of all sources of discrepancy between observed and predicted values with respect to the perfect fit.

When needed (i.e., studies II and III), a multi-criteria decision analysis (MCDA) was conducted based on the above-mentioned criteria to produce a ranking in order to facilitate the decision-making on the best modelling approach (Render and Stair 1992). Accordingly, a performance index (rank sum) was computed for each model or modelling approach by adding the rates for the different criteria used in model selection and evaluation.

2.5 Methods for optimizing stand management

Study VI optimized the management of even-aged *P. brutia* stands in the joint production of timber and pine honey. The distance-independent individual-tree models developed within study I were used to simulate stand growth. The taper model provided within study III was used to estimate the volume of different timber assortments and total tree volume.

The negative effect of *M. hellenica* on tree growth in infested stands was subtracted from tree growth predictions for healthy stands based on the quantitative information provided by Yeşil et al. (2005). Thus, based on the simulation of stand dynamics for healthy *P. brutia* stands (i.e., in the absence of the scale insect) detailed in section 2.2.2, the procedure for simulating 10-year growth periods in pine stands infested by *M. hellenica* was as follows:

1. The following equations published by Yeşil et al. (2005) were used to calculate diameter increment of infested and healthy trees as a function of stand age:

   $$\Delta d_{\text{infested}} = -0.2479 \times \ln(T) + 1.3557 \tag{7}$$

   $$\Delta d_{\text{non-infested}} = -0.1909 \times \ln(T) + 1.2399 \tag{8}$$

   where $\Delta d_{\text{infested}}$ and $\Delta d_{\text{non-infested}}$ is diameter increment of infested and non-infested *P. brutia* trees (cm), and T is stand age (yr).

2. The ratio between dbh increment in infested and non-infested trees was modelled as a function of stand age. This ratio was used as a correction factor accounting for the growth reduction caused by *M. hellenica* in subsequent simulation steps (CF_{infested})

   $$CF_{\text{infested}} = 1 - 0.0039 \times T \tag{9}$$

3. The dbh growth prediction for non-infested stands (Δd) based on the diameter increment models of study I was multiplied by the aforesaid growth correction factor in order to simulate 10-year diameter growth of infested trees ($\Delta d_{\text{corrected}}$)

   $$\Delta d_{\text{corrected}} = CF_{\text{infested}} \times \Delta d \tag{10}$$

4. The dominant height increment ($\Delta H_{\text{corrected}}$) resulting from the dominant height model fitted in study I was multiplied by the same factor

   $$\Delta H_{\text{corrected}} = CF_{\text{infested}} \times (H_{T2} - H_{T1}) \tag{11}$$

   where H_{T1} is predicted dominant height at the current stand age, H_{T2} is predicted dominant height at the end of the next simulation step.

5. The site index was updated after every simulated growth period ($SI_{\text{corrected}}$) using the site index model provided in study I

   $$SI_{\text{corrected}} = \frac{H_{T1} + \Delta H_{\text{corrected}}}{HG_{T2}} \times HG_{50} \tag{12}$$

   where HG_{T2} is guide curve value at the end of the next simulation step and HG_{50} is the guide curve value at the reference age (50 years).

Since specific quantitative information regarding the impact of *M. hellenica* on tree vigour is lacking, it was assumed that tree mortality occurring at the stand level followed the self-thinning model fitted within study I for healthy stands. Since increasing site index increases the self-thinning limit, infestation by *M. hellenica* increases mortality via its negative effect on site index. In simulation, trees having lower growth rates had a higher mortality rate (Vanclay 1994). The stand age at which pine honey production started in stands infested by *M. hellenica* was set to 35 years, when the infestation of trees is, in average, more likely to be relevant enough (Yeşil et al. 2005). In the absence of detailed scientific information, it was assumed that, in a given stand, pine honey yield remains constant over time until the final cut.

The simulation stands considered in this study VI represented even-aged structures and different site productivities according to site index: good site (SI = 22.2 m), medium site (SI = 14. 8 m) and poor site (SI = 9.7 m). The initial stand density was 1800 trees ha^{-1}. The initial stand age was 10 years for the good and medium site quality and 15 years for the low-productivity site. It was assumed that infestation by *M. hellenica* started at the initial stand age and was considered to be intensive enough for honey production at 35 years. Forest management schedules typical of even-aged forestry (i.e., low thinning and final cut at the end of the rotation period) were the silvicultural operations allowed in simulation.

Simulation of both healthy and infested *P. brutia* stands was run together with an optimization procedure so as to obtain the optimal management schedules for the joint production of wood and non-wood forest products (i.e., timber assortments and pine honey) (Fig. 4). The optimization method was based on Hooke and Jeeves (1961) nonlinear programming algorithm, a direct search method that uses exploratory and pattern search alternatively. The objective function to be maximized was soil expectation value (SEV) (Price 1989) which, in even-aged forestry, expresses the value of a forest stand as a sum of discounted net cash flow over an infinite number of rotations. SEV is based on net present value (NPV) (Hartman 1976) and was calculated as follows using a 3% discount rate:

$$SEV = \frac{NPV}{1-\frac{1}{(1+i)^T}} = \frac{\sum_{t=0}^{T}\frac{Rw_t - Cw_t}{(1+i)^t} + \sum_{t=0}^{T}\frac{Rh_t - Ch_t}{(1+i)^t}}{1-\frac{1}{(1+i)^T}} \tag{13}$$

where Rw_t is revenues from all wood assortments in year t (US\$ ha^{-1}), Cw_t is timber production costs in year t (US\$ ha^{-1}), Rh_t is revenues from pine honey in year t (US\$ ha^{-1}), Ch_t is pine honey production cost in year t (US\$ ha^{-1}), i is discount rate (percentage divided by 100), and T is rotation length (yr).

The optimized decision variables were: (a) for the first thinning, number of years since regeneration/planting, (b) for 2 to n thinnings, number of years since previous thinning, (c) basal area removal in every thinning (%), and (d) number of years since the last thinning to the final cut. The best combination of number of thinnings and decision variables that maximised SEV was selected as the optimal schedule for different management scenarios.

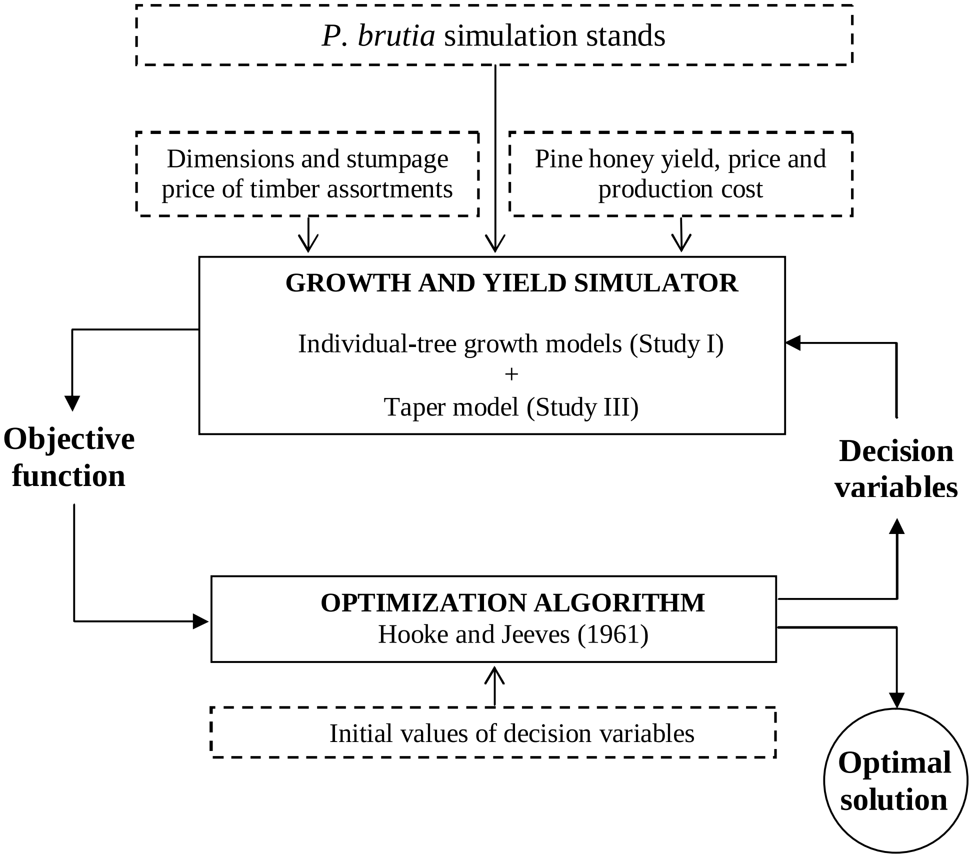

Figure 4. Flowchart of the stand-level simulation and optimization procedure.

3 RESULTS

3.1 Individual-tree models for simulating stand dynamics

3.1.1 Models for simulating even-aged stand dynamics

The set of individual-tree growth models for predicting even-aged *P. brutia* stand dynamics in Middle East are displayed in Table 2. These models were fitted within study I based on pooled data from Syria and Lebanon. Country-level differences were found when modelling dominant height development, 10-year diameter increment and self-thinning limit. Thus, the regional models for *P. brutia* stand dynamics are country-sensitive.

The following two supplementary models for 10-year diameter increment and height-diameter relationship were fitted within study II for the particular case of Lebanese *P. brutia* stands using additional predictors, some of which were not available for Syria. The additional two models are

$$i_d = e^{2.989 + 0.020\,SI - 0.393\ln(T) - 0.012\,G - 0.455\frac{\ln(BAL+20)}{d} - 0.114\ln(slope) + 0.045\ln(depth) - 0.020\,soil_1 G - 0.016\,soil_2 G} \quad (18)$$

$$h = Hdom\left(\frac{d}{Ddom}\right)^{0.657 - 0.095\ln\left(\frac{d}{Ddom}\right) - 0.133\ln(depth) + 0.002\,T} \quad (19)$$

where *slope* is terrain slope (%), *depth* is average soil depth (cm), $soil_1$ is dolomitic sand and $soil_2$ is sand, and the rest of symbols have the same meaning as reported in Table 2.

Table 2. Models for predicting even-aged *P. brutia* stand dynamics in Middle East.

Models	Equations	
Dominant height	$Hdom = \dfrac{T^{2.522}}{52.766 + (0.055 + 0.01Lebanon)T^{2.522}}$	(14)
10-year dbh increment	$i_d = e^{-0.391-(0.019-0.007\,Lebanon)BAL + 1.050\ln SI - 0.125\sqrt{G} - 0.083\sqrt{d}}$	(15)
Height-diameter	$h = Hdom\left(\dfrac{d}{Ddom}\right)^{0.516-0.173\frac{d}{Ddom}}$	(16)
Survival (self-thinning)	$N_{\max} = e^{11.649-1.639\ln D_n + (0.026-0.016\,Lebanon)SI}$	(17)

Note: *d* is dbh(cm), i_d is 10-year dbh increment (cm), *G* is stand basal area (m^2/ha), *BAL* is stand basal area of trees larger than the object tree (m^2/ha), *Hdom* is dominant height (mean height of the 100 thickest trees per hectare, m), *Ddom* is dominant diameter (cm), *T* is stand age (yr), *SI* is site index (m), $N_{\max}$ is maximum number of living trees per hectare, *h* is tree height (m), D_n is stand mean diameter (cm), and *Lebanon* is an indicator variable (country dummy) expressing country effects (0 = Syria; 1 = Lebanon).

Among the tested dominant height models, Hossfeld IV showed the best fit according to statistical and biological criteria. Dominant height follows an s-shaped asymptotic development that attains the asymptote when the stand is about 50 years old. In the diameter increment models, tree size is represented by diameter at breast height and age, site quality by site index, slope, soil depth and soil type, and competition by stand basal area and basal area in larger trees. Whereas site index contributes positively to tree diameter increment, all the other predictors entail a reduction of radial growth. Diameter increment is higher in younger trees (low diameters) and it gradually decreases as the diameter increases. Site index also has a positive effect on survival. The country dummy results in lower dominant height in Lebanon than in Syria, as well as in a reduction of the maximum number of living trees per hectare in Lebanese stands with respect to Syrian ones. In contrast, the country dummy diminishes the effect of tree-level intra-specific competition in *P. brutia* stands growing in Lebanon.

3.1.2 Models for simulating uneven-aged stand dynamics

The set of individual-tree growth models for predicting uneven-aged *P. brutia* stand dynamics in Lebanon were fitted within study II and are displayed in Table 3. Stand basal area is the main predictor for the mean diameter of ingrowth trees and the number of ingrowth trees per hectare. The higher the stand basal area, the lower is the number and diameter of ingrowth trees. In the diameter increment model, tree size is represented by dbh, and site quality is represented by altitude, slope, soil depth and soil type, whereas competition is represented by stand basal area and basal area in larger trees. Variables representing competition and tree size as well as describing challenging site conditions for trees have negative signs in the equations (causing a reduction in 10-year diameter increment). Variables that contribute to improved site quality have a positive sign. The altitude and its logarithmic transformation illustrate an increasing–decreasing trend with a maximum in some point along the altitudinal range. The height–diameter equation is an adaptation of the "Hossfeld I modified" function.

Table 3. Models for predicting uneven-aged *P. brutia* stand dynamics in Middle East.

Models	Equations	
Number of ingrowth trees	$F_{in} = e^{6.932 - 0.423\sqrt{G} - 0.016\,slope}$	(20)
Mean dbh of ingrowth trees	$D_{in} = e^{2.667 - 0.013\,G}$	(21)
10-year dbh increment	$i_d = e^{0.676 - 0.202\sqrt{G} + 0.006\,depth - 0.176\ln(slope) - 0.001\,alt + 0.402\ln(alt) - 0.049\frac{BAL}{d} - 0.120\,soil_1\sqrt{G} - 0.058\,soil_2\sqrt{G}}$	(22)
Height-diameter	$h = \dfrac{(5.122 + 0.015\,depth - 0.001\,alt - 0.408\,soil_2)^2}{\left(1 + \dfrac{7.226}{d}\right)^2}$	(23)

Note: *d* is dbh (cm), i_d is 10-year dbh increment (cm), *G* is stand basal area (m^2/ha), D_{in} is mean diameter of the ingrowth trees at the end of the 10-year period (cm), F_{in} is number of ingrowth trees at the end of the 10-year period (trees ha^{-1}), *slope* is terrain slope (%), *depth* is average soil depth (cm), *alt* is altitude above sea level (m), *BAL* is stand basal area of larger trees (m^2/ha), *h* is tree height (m), and $soil_1$ and $soil_2$ are indicator variables for dolomitic sand and sand, respectively.

3.1.3 Comparison of uneven- and even-aged modelling approaches

When the measured and predicted values were compared assuming all *P. brutia* sample stands either as uneven-aged or as even-aged (referred to as overall-performance), the mean squared deviation (MSD) was practically the same for both modelling approaches (only 0.21 m^3ha^{-1} difference). However, the predictions based on the EA approach had higher squared bias (SB). The UA models met much better the nonunity slope principle (smaller NU). The regression line of the UA approach almost crossed the origin, and its slope was closer to 1.

When the predictions based on one of the modelling approaches were compared with the measured values of plots representing the opposite stand structure (referred to as cross-performance), the MSD was considerably lower for the UA approach. In addition, the UA approach was less biased and performed better according to the NU criterion. Similarly to the overall-performance, the EA approach tended to underestimate wood production (mainly in intermediate and low stocking stands), whereas the UA approach tended to overestimate it.

When predictions based on one of the modelling approaches were compared with the measured values of those stands representing the same stand structure as the modelling approach (referred to as self-performance), the MSD was considerably lower for the EA approach. However, this approach was much more biased (underestimation) and performed worse also with respect to the NU criterion. In fact, the simulation based on the UA set of models was almost non-biased. Consequently, the regression line was closer to the origin, and the slope was closer to 1 when the UA modelling approach was used to predict the growth of the most uneven-aged stands.

The lack of correlation (LC) was higher (worse) for the UA approach for all performance types. Based on the aforesaid results, the UA modelling approach was ranked better according to the overall- and cross-performance due to the smaller MSD, SB and NU. Regarding the self-performance, both modelling approaches were ranked equal, as the EA approach presented lower MSD and LC, but the UA one was less biased and better met the NU criterion. Thus, the global performance (aggregation of the scores obtained for each performance type) was better for the UA modelling approach, i.e., it turned out to be the most suitable way to simulate and predict semi-even-aged *P. brutia* stand dynamics (Fig. 5).

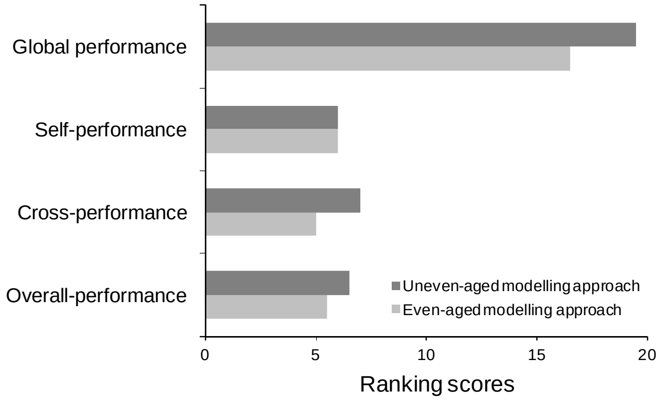

Figure 5. Performance of EA and UA modelling approaches in wood production of semi-even-aged *P. brutia* stands.

3.2 Taper and biomass models

3.2.1 Taper models

In general, the higher the number of parameters, the better was the statistical fitting of stem profile models fitted in study III. Nevertheless, this trend was not systematic since some equations with few parameters performed very well and some equations with more parameters did not. The “1995 equation” referred to as Kozak II (1997) was selected as the best taper model for *P. brutia* in Middle East among more than thirty candidate equations. Although Kozak II had originally 8 parameters, it was found that two of them were not significant for the equation fitted to *P. brutia* stem data. Therefore, two 6-parameter versions of Kozak II model were finally fitted using fixed- and mixed-effects modelling (Table 4) the latter including a power-type variance function to account for the heteroscedasticity of the residuals. The residual variance of the mixed-effects model was assumed to follow the model

$$\operatorname{var}(e_{ki}) = \sigma^2 D_k^{2\delta} \tag{24}$$

where σ^2 is the error variance, D_k is dbh and δ is the variance function coefficient.

The general form of the selected taper model based on Kozak “1995 equation” is

$$d_{ki}^2 = \left(D_k^{b_2} H_k^{b_3+\beta_{1k}} \left[\frac{1-\sqrt{q_{ki}}}{1-\sqrt{t_{ki}}} \right]^{b_4 \left(\frac{1-\sqrt{q_{ki}}}{1-\sqrt{t_{ki}}} \right)^{0.1} + (b_5+\beta_{2k}) q_{ki}^4 + (b_6+\beta_{3k}) \arcsin\left(1-\sqrt{q_{ki}}\right) + b_8 D_k \left(\frac{1-\sqrt{q_{ki}}}{1-\sqrt{t_{ki}}} \right)} \right)^2 + e_{ki} \tag{25}$$

where d_{ki} is the i^{th} diameter measurement of tree k measured at height h_{ki}, D_k and H_k are the dbh and total height of tree k, q_{ki} is h_{ki}/H_k, t_{ki} is $1.3/H_k$, b_2 to b_8 are fixed parameters, β_1, β_2, and β_3 are random parameters accounting for the between-tree variation in the lower, top, and middle parts of the stem, respectively, and e_{ki} is residual.

Table 4. Estimates of regression parameters of the fixed- and mixed-effects Kozak II (1997) models for *P. brutia* in Middle East.

Parameter	Fixed-effects model	Mixed-effects model
b_2	0.9693	0.9771
b_3	0.0347	0.0238
b_4	0.2818	0.4189
b_5	0.9272	0.7630
b_6	0.8227	0.5068
b_8	-0.0050	-0.0018
$\operatorname{var}(\beta_1)$	-	0.0133^2
$\operatorname{var}(\beta_2)$	-	0.2247^2
$\operatorname{var}(\beta_3)$	-	0.1695^2
$\operatorname{corr}(\beta_1, \beta_2)$	-	-0.851
$\operatorname{corr}(\beta_1, \beta_3)$	-	0.184
$\operatorname{corr}(\beta_2, \beta_3)$	-	0.360
σ^2	4691	0.214^2
δ	-	1.51

The utilized variance function realistically described the heteroscedasticity of the residual variance, and the random effects reduced the correlation of residuals at successive heights compared with the fixed-effects model.

3.2.2 Biomass models and intra-specific differences in biomass allocation

Study IV found between-country differences for all aboveground biomass components. On the other hand, no statistically significant differences were found for the total aboveground biomass of *P. brutia*. Without accounting for the country-effects, the regional models using pooled data from Syria and Lebanon resulted in biased predictions in Syria and Lebanon (Fig. 6), whereas they were unbiased for Middle East.

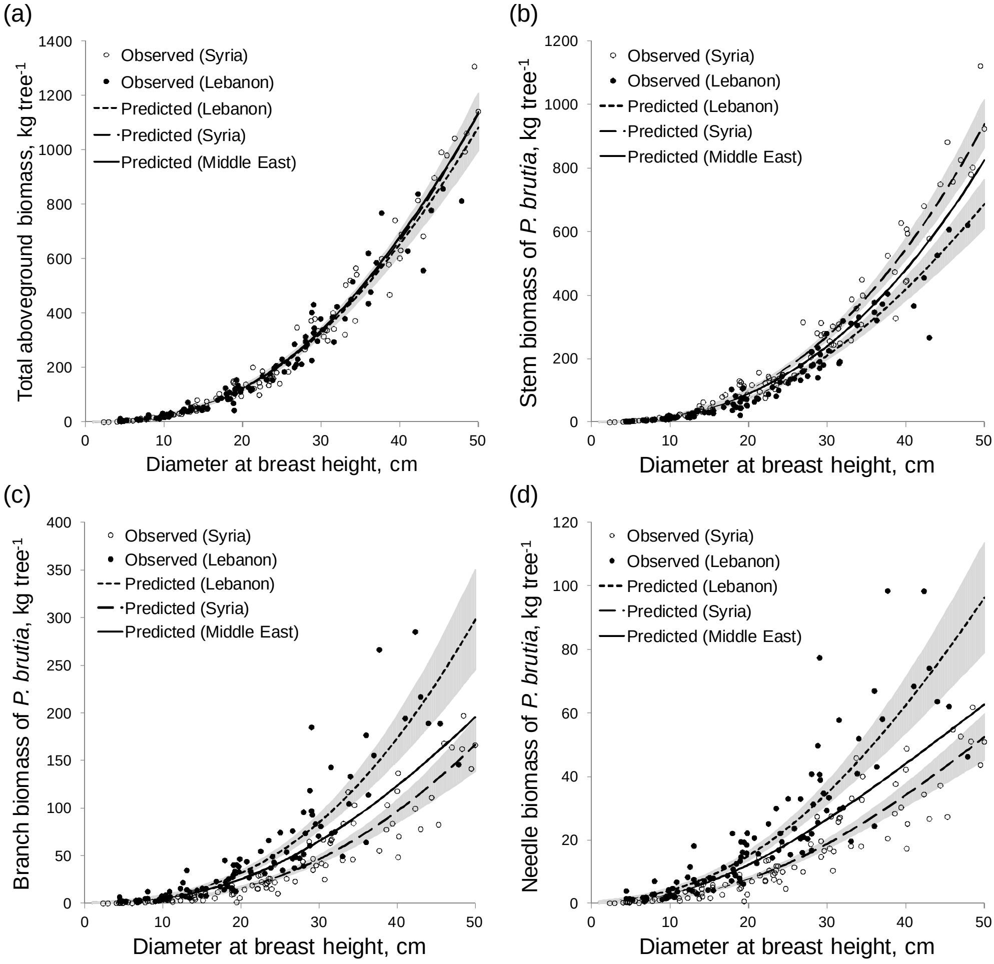

Figure 6. Country-specific relationships between dbh and total (a), stem (b), branch (c) and needle (d) biomass. The 95% confidence intervals for country-specific allometric models are shown by the grey areas around the model predictions. The thick solid line represents the predictions of the regional model based on pooled data (Lebanon + Syria).

For that reason, fitting separately country-specific models (Table 5) was finally considered as the most suitable approach to get unbiased estimates at both the country and the regional scales.

Table 5. Country-specific models for aboveground biomass components (Ne: needles, Br: branches, Cr: crown, St: stem) considering all predictors and only dbh, where *y* is dry biomass (kg tree^{-1}), *d* is dbh (cm), *h* is tree height (m), *cl* is crown length (m), δ is the variance function coefficient, and RSE is the residual standard error.

Country	Component	Model	
Syria	Ne	$y = e^{-2.905 + 7.582 \cdot \frac{d}{d + 19.782} + 0.581 \cdot cl}$	(26)
	Ne	$y = e^{-2.302 + 8.865 \cdot \frac{d}{d + 20.790}}$	(27)
	Br	$y = e^{-1.794 + 10.665 \cdot \frac{d}{d + 21.660} + 0.845 \cdot \ln cl - 0.824 \cdot \ln h}$	(28)
	Br	$y = e^{-1.652 + 10.395 \cdot \frac{d}{d + 26.816}}$	(29)
	Cr	$y = e^{-1.838 + 8.570 \cdot \frac{d}{d + 24.443} + 0.593 \cdot \ln cl}$	(30)
	Cr	$y = e^{-1.203 + 9.925 \cdot \frac{d}{d + 25.316}}$	(31)
	St	$y = e^{-3.371 + 1.835 \cdot \ln d + 0.937 \cdot \ln h}$	(32)
	St	$y = e^{-2.698 + 2.440 \cdot \ln d}$	(33)
Lebanon	Ne	$y = e^{0.078 + 10.665 \cdot \frac{d}{d + 26.492} - 0.855 \cdot \ln h}$	(34)
	Ne	$y = e^{-0.820 + 8.279 \cdot \frac{d}{d + 26.854}}$	(35)
	Br	$y = e^{0.625 + 12.203 \cdot \frac{d}{d + 30.900} - 0.855 \cdot \ln h}$	(36)
	Br	$y = e^{-0.253 + 9.921 \cdot \frac{d}{d + 33.376}}$	(37)
	Cr	$y = e^{1.096 + 11.737 \cdot \frac{d}{d + 29.832} - 0.855 \cdot \ln h}$	(38)
	Cr	$y = e^{0.215 + 9.422 \cdot \frac{d}{d + 31.814}}$	(39)
	St	$y = e^{-1.372 + 8.100 \cdot \frac{d}{d + 25.960} + 0.920 \cdot \ln h}$	(40)
	St	$y = e^{-0.622 + 10.187 \cdot \frac{d}{d + 21.196}}$	(41)

The widely used exponential model presented better fitting only for stem biomass of Syrian trees. Most of the selected biomass models were of the form

$$y = e^{b_0 + b_1 \cdot \frac{d}{d + b_2} + c \cdot X} \tag{42}$$

where d is the diameter at breast height (cm), b_0 to b_2 are model parameters, c is a vector containing the regression coefficients of predictors other than dbh, and X is a vector containing predictors other than dbh.

Crown length was a significant predictor of crown biomass components in dense even-aged Syrian stands, whereas it was not among the best predictors in the more sparse and uneven-aged stands of Lebanon. Using tree height as an additional predictor improved most biomass models.

The contribution of each tree component to the total aboveground biomass varied according to tree size (Fig. 7). Thus, the proportion of stem biomass (so-called harvest index) is lower in small or young trees, whereas the proportion of crown biomass diminishes as trees grow. A medium-sized pine growing in a Syrian unthinned even-aged stand is expected to have 30% more biomass in its stem than a medium-sized tree growing in a sparse and more irregular Lebanese stand. On the contrary, a medium-sized tree growing in Lebanon is expected to have 88.5% more biomass in its crown than a medium-sized tree in a Syrian stand.

3.2.3 Mixed- vs. fixed-effects volume modelling in the absence of calibration

In study III, three different prediction strategies (strategy 1: fixed-effects model; strategy 2: conditional prediction of mixed-effects model; strategy 3: marginal prediction of mixed-effects model) based on non-calibrated mixed- and fixed-effects taper models were tested in volume prediction.

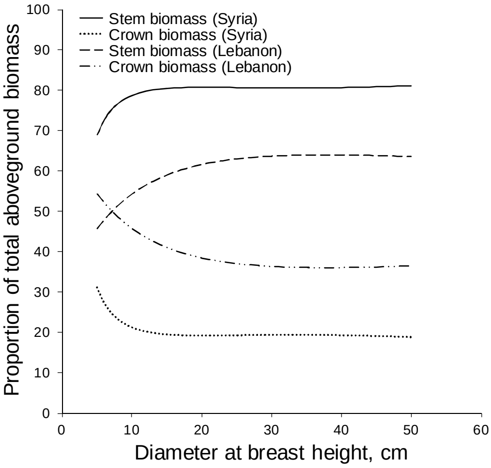

Figure 7. Contribution of crown and stem components to total aboveground tree biomass as a function of tree size (dbh) in Syria and Lebanon.

Although the errors in prediction were low for all three prediction strategies (less than 0.060 m^3 in the modelling data and less than 0.040 m^3 in the validation data), there were differences in the way they performed. Regarding the total discrepancy from perfect fit (MSD), strategy 1 performed better in model evaluation, followed by strategy 3. Strategy 3 performed equally well as strategy 1 in terms of MSD in model validation (independent data set). Strategy 2 had the highest MSD and nonunity slope in both model evaluation and validation, and it was the most biased in model evaluation as well. Strategies 2 and 3 were less biased in model validation than strategy 1. In contrast, strategy 1 was the least biased in model evaluation and the best in terms of the nonunity slope criterion in both model evaluation and validation, followed by strategy 3. For deviations from perfect fit due to scattering, strategy 3 was the best approach in model evaluation and as good as strategy 2 in model validation, whereas strategy 1 was the worst in both cases (Table 6, Figure 8).

Table 6. Results of model evaluation (against the modelling data) and validation (against independent data) in volume (m^3) prediction according to the different prediction strategies in the absence of calibration. The best value of each criterion is in boldface.

Evaluation (modelling data)	MSD	SB	NU	LC
Strategy 1	**0.00226**	**0.00001**	**0.00018**	0.00207
Strategy 2	0.00333	0.00028	0.00096	0.00209
Strategy 3	0.00284	0.00015	0.00063	**0.00206**
Validation (independent dataset)	MSD	SB	NU	LC
Strategy 1	**0.00150**	0.00002	**0.00005**	0.00144
Strategy 2	0.00156	**0.00000**	0.00014	**0.00141**
Strategy 3	**0.00150**	**0.00000**	0.00010	**0.00141**

Note: MSD is the mean squared deviation accounting for the total discrepancy from perfect fit when comparing predicted vs. observed values, SB is the squared bias, NU is the nonunity slope and LC is the lack of correlation. SB, NU and LC represent additive sources of discrepancy which sum up to the MSD.

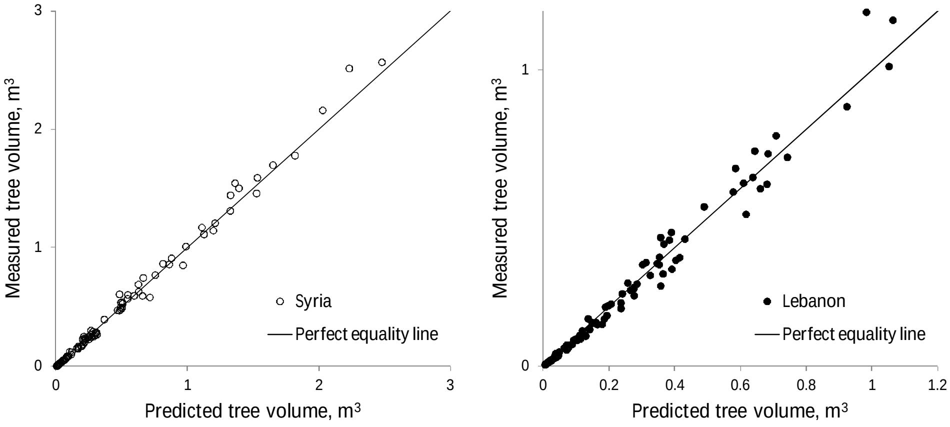

Figure 8. Predictions with strategy 3 vs. measured stem volume with the Kozak II model in the modelling (Syria) and independent (Lebanon) datasets.

3.2.4 Mixed-effects vs. OLS biomass modelling in the presence of calibration

Study V was devoted to developing a method for generalizing biomass models via meta-analysis. Based on existing equations, mixed-effects meta-models for predicting stem, crown and foliage biomass of *P. brutia* trees were developed (Table 7).

The fixed part of the meta-models provides a prediction for a typical location or dataset. The predicted stem biomass based on the fixed part of the mixed-effects meta-model clearly overestimated the values predicted by the original allometric equations developed for Greece, and resulted in clear underestimation when compared to the original equations of Syria and southern Turkey. Similarly, the fixed part of the crown biomass meta-model clearly overestimated the pseudo-observations of Syria and southern Turkey, and resulted in clear underestimation when compared to the original models for Lebanon and Greece. Finally, regarding foliage biomass, the pseudo-observations of north-western Turkey were clearly overestimated by the fixed part of the mixed-effects meta-model, whereas those of Lebanon and southern Turkey were underestimated. Comparing the predictions of the original allometric equations and the predictions provided by the OLS model fitted to the whole independent dataset shows that the trees of the validation dataset had higher stem biomass than predicted by any of the original equations. On the other hand, crown and foliage biomass were, in average, within the range of predictions of the reference studies (Fig. 9).

The influence of sampling strategy used in meta-model calibration on the accuracy of biomass predictions was negligible for all aboveground tree components. On the contrary, the corresponding OLS models were more sensitive to sampling strategy in such a way that the stratified sampling based on three tree-size categories provided the most accurate predictions of aboveground biomass followed by the two-category stratified sampling, whereas random sampling was the worst approach (Fig. 10a, 10b and 10c). Conditional stem and foliage biomass predictions of the mixed-effects meta-model based on calibration were better in terms of root mean squared deviation (RMSD) than the corresponding OLS model. These differences in RMSD diminished when the number of sample trees involved in meta-model calibration and OLS fitting increased. Regarding crown biomass, the calibrated mixed-effects meta-model performed better when sample size was lower than 12 to 14 trees, depending on the sampling strategy. Increasing the number of trees used in calibration always resulted in an improvement of the predictive accuracy of the calibrated meta-models. The predictive performance was always worse than for any calibrated model except for one case (Fig. 10d). The reduction in MSD of calibrated mixed-effects meta-models with increasing sample size was basically due to the reduction of the squared bias. In contrast, the improvement in the predictive performance of the corresponding OLS fittings with increasing sample size was due to a reduction in both bias and non-unity slope.

Table 7. Estimates of the fixed and random parameters of the mixed-effects meta-models for different aboveground tree biomass components.

Tree biomass component	Fixed parameters		Random parameters			Residual
	β_0	β_1	var(b_0)	var(b_1)	corr(b_0 , b_1)	var(e_{ij})
Stem	-2.697	2.345	0.345	0.031	-0.925	0.058
Crown	-2.612	2.076	0.195	0.002	-0.858	0.170
Foliage	-3.127	1.757	0.515	0.022	-0.513	0.148

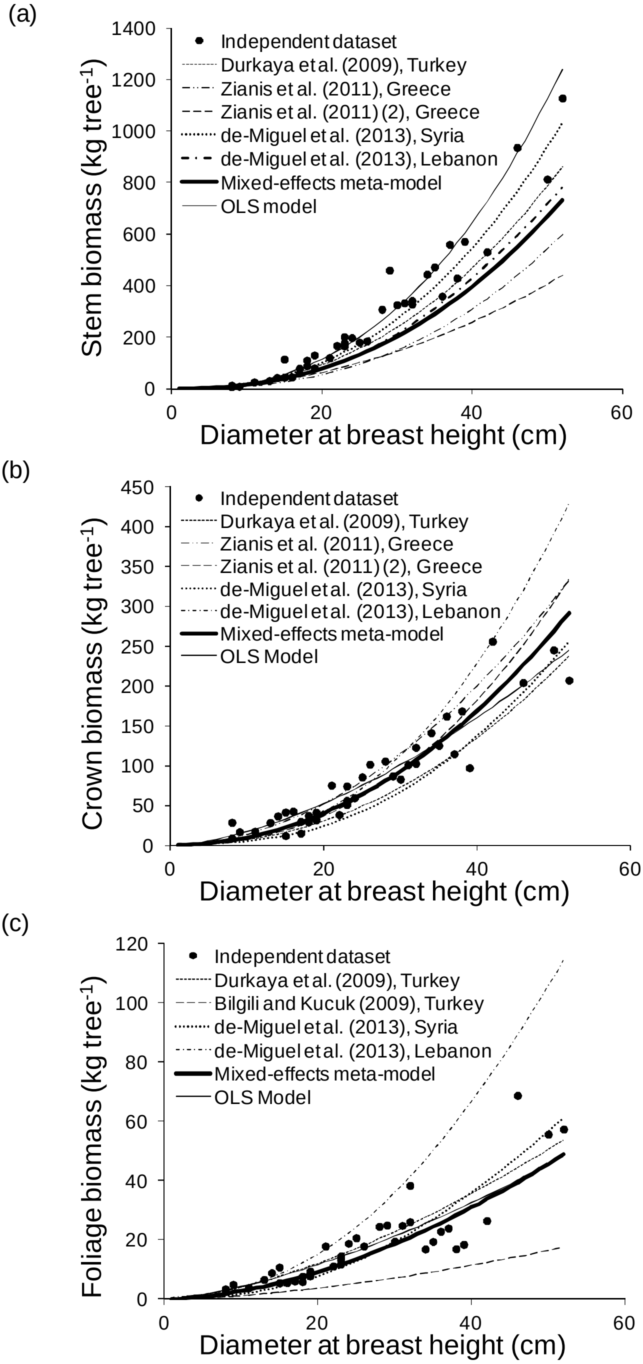

Figure 9. Stem (a), crown (b) and foliage (c) biomass independent dataset used in model calibration/validation (dots) and predicted biomass by the original allometric equations, by the fixed part of the mixed-effects meta-model, and by the OLS fitting to the independent dataset.

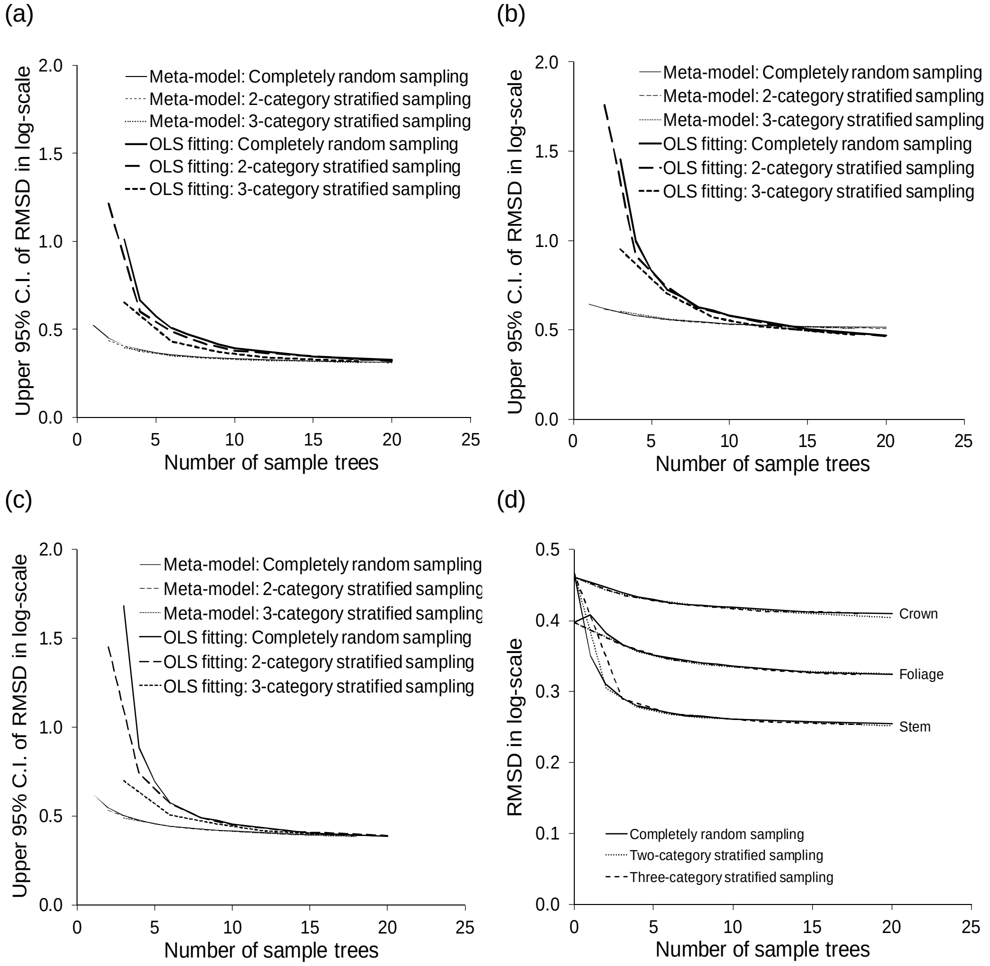

Figure 10. Predictive performance of the calibrated (a) stem, (b) crown and (c) foliage mixed-effects meta-models and the local OLS models for different sample sizes and sampling strategies. The lines represent the upper bound of the 95% confidence interval of the Root Mean Square Deviation (RMSD) computed from 10,000 realizations per sample size and sampling strategy via Monte-Carlo simulation. Sub-figure d represents the average RMSD in biomass prediction of the mixed-effects meta-models. When the number of sample trees is zero, the prediction is based on the fixed part of the mixed-effects meta-model.

3.3 Optimal management of even-aged *P. brutia* stands for timber production

Simulation based on the individual-tree growth models provided in study I allowed us to determine the mean annual increment (MAI) and the current annual increment (CAI) curves. Volume was estimated using the fixed-effects taper model of study III. If wood production is maximized in the absence of thinning, the optimal rotation length is the age at which the MAI and CAI curves cross. According to the simulations, the optimal rotation length in a medium-quality site is about 50 years, and site productivity, as described by the maximum MAI, is around 4.5 $m^3ha^{-1}yr^{-1}$ (Fig. 11).

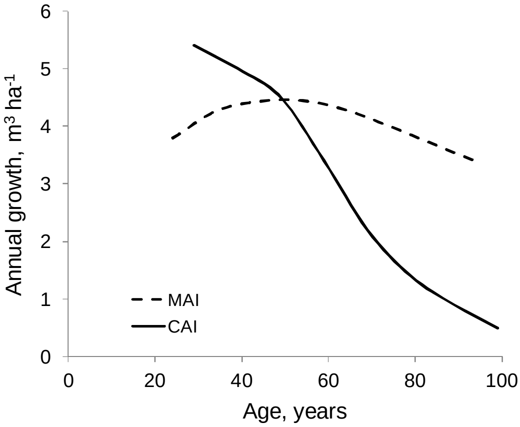

Figure 11. MAI and CAI and curves for even-aged *P. brutia* growing in an average site. MAI and CAI values have been calculated by simulating stand development based on the individual-tree growth and yield models provided in studies I and III.

However, management of *P. brutia* stands without thinning is not economically optimal. When stumpage prices of different timber assortments are taken into account, optimal management schedules for *P. brutia* stands require one to two thinnings depending on site productivity (study VI). Thus, in good sites, maximal economic profit (as described by the soil expectation value calculated with 3% discount rate) is obtained when the forest management schedule uses a 40-year rotation length and one thinning. For medium- and poor-quality sites, the optimal number of thinnings is two and the optimal rotation length is 49 and 71 years, respectively. In all cases, the optimal thinning intensity is close to 30% of stand volume and basal area. When thinnings are applied, wood yield increases as compared to management without thinning (Table 8, Fig. 12).

Fuelwood yield is of minor importance and rather similar across site qualities at the end of the rotation, if economic profit is maximized. On the contrary, pulpwood and sawnwood yield increases as site productivity improves. In medium and poor sites, pulpwood is the most important timber assortment whereas, in good sites, sawlog production is slightly higher than pulpwood production (Fig. 13).

Table 8. Soil expectation value (3% discount rate), rotation length and wood production in the optimal management of *P. brutia* stands growing on good, medium and poor sites.

	Good site (SI= 22.2 m)	Medium site (SI= 14. 8 m)	Poor site (SI= 9.7 m)
SEV, US$ ha^{-1}	15065	5290	941
Rotation length, yr	40	49	71
Wood yield, m^3 ha^{-1} yr^{-1}	12.9	5.9	2.3

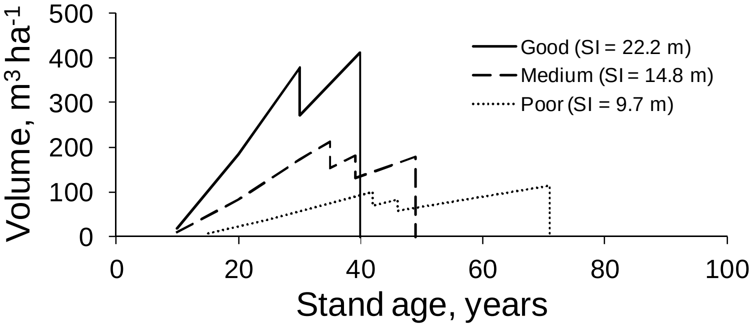

Figure 12. Optimal stand management schedules for *P. brutia* growing on good, medium and poor sites when soil expectation value with 3% discount rate is maximized. Calculations are based on the individual-tree growth and yield models developed in studies I and III.

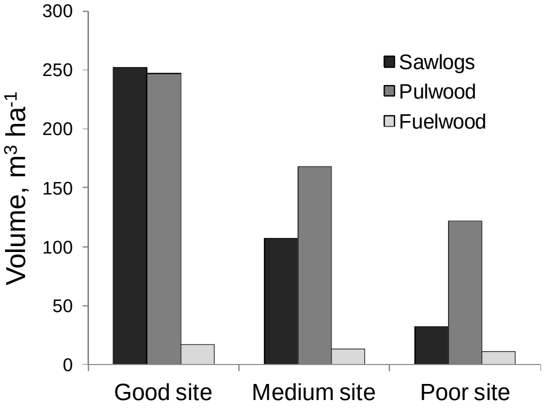

Figure 13. Timber assortments produced during the rotation representing optimal management of *P. brutia* stands growing on good, medium and poor sites.

3.4 Optimal joint production of pine honeydew honey and timber

Pine honey production requires the infestation of *P. brutia* trees by the scale insect *M. hellenica*. The simulated effect of *M. hellenica* infestation according to the models provided in study I, taking into account the impact of the scale insect on tree growth (Yeşil et al. 2005), resulted in a reduction of tree growth and survival. The effect of insect infestation on stand-level growth and mortality increased as stands grew older (Fig. 14).

The importance of pine honey on the optimal joint production of honey and timber varied according to site quality and honey productivity. In good sites, the contribution of pine honey to the overall economic profitability under the alternative honey production scenarios (30, 60 and 90 kg ha^{-1} yr^{-1} starting at stand age of 35 years) represented, respectively, 4%, 10% and 15% of the soil expectation value. The reduction in total soil expectation value due to the presence of the scale insect was 16%, 11% and 6%, respectively. The loss in timber-related soil expectation value was not compensated for by means of honey production. In medium-quality sites, soil expectation value was higher in healthy stands than in the presence of *M. hellenica* only when the honey production of infested stands was 30 kg ha^{-1} yr^{-1}. Honey productivity of 60 or 90 kg ha^{-1} yr^{-1} resulted in higher economic profit than obtained in the absence of the scale insect. In poor sites, the soil expectation value was higher in the presence of *M. hellenica* for all honey production scenarios. The contribution of pine honey to the total soil expectation value of poor sites ranged from 82% to 97% with increasing honey productivity, and the economic profit was 2 to 6 times higher in infested *P. brutia* stands than obtained in healthy stands (Table 9, Fig. 15).

Both site quality and pine honey productivity had a strong impact on optimal stand management. The optimal management consisted of only one thinning if stands growing on good sites were healthy, or if infested stands had a honey productivity of 30 kg ha^{-1} yr^{-1}. In all other cases, the optimal number of thinnings was two. The intensity of most thinnings was around 30% of stand volume and basal area. Integrating honey yield into stand management optimization had a modest influence on rotation length in good sites; optimal rotations were always shorter than 50 years regardless of the amount of honey produced. In medium sites, the optimal rotation length in the absence of *M. hellenica* increased up to by 49% when alternative honey yield scenarios were considered. In poor sites, the optimal rotation length doubled, as compared to healthy stands, when pine honey productivity was assumed to be 90 kg ha^{-1} yr^{-1}. Differences in optimal rotation length between good, medium and poor sites also became larger when the honey production of infested stands was taken into account (Table 8, Table 9, Fig. 16).

Longer rotation lengths due to honey production entailed a reduction in mean annual wood production as compared to healthy stands. The reduction ranged from 14% to 39% depending on the annual honey production and site quality. Increasing honey production from 30 to 60 kg ha^{-1} yr^{-1} (starting at 35 years) doubled the mean annual honey yield during the whole rotation in the poor site, and resulted in approximately three times higher mean annual honey yield in the good and medium sites. Increasing honey production to 90 kg ha^{-1} yr^{-1} resulted in more than three times higher mean annual honey yield in the poor site and between four and five times higher yield in the good and medium sites.

Table 9. Soil expectation value (US$ ha^{-1}), rotation length (yr), pine honeydew honey production (kg ha^{-1} yr^{-1}) and timber production (m^{3} ha^{-1} yr^{-1}) for alternative optimal stand management schedules in infested *P. brutia* stands growing on good (G), medium (M) and poor (P) sites, and under different assumptions on honey productivity.

	30 kg ha^{-1} yr^{-1}			60 kg ha^{-1} yr^{-1}			90 kg ha^{-1} yr^{-1}		
	G	M	P	G	M	P	G	M	P
SEV$_{total}$	12669	4867	2019	13356	6038	3644	14100	7441	5471
SEV$_{wood}$	12179	3839	366	11967	3422	214	12017	3144	129
SEV$_{honey}$	490	1028	1652	1389	2616	3429	2083	4296	5324
Rotation	41	54	99	45	66	112	45	74	141
Timber prod.	11.1	4.7	1.7	10.7	4.4	1.7	10.7	4.3	1.4
Honey prod.	4.1	10.4	19.3	12.8	27.9	41.3	19.2	47.1	67.6

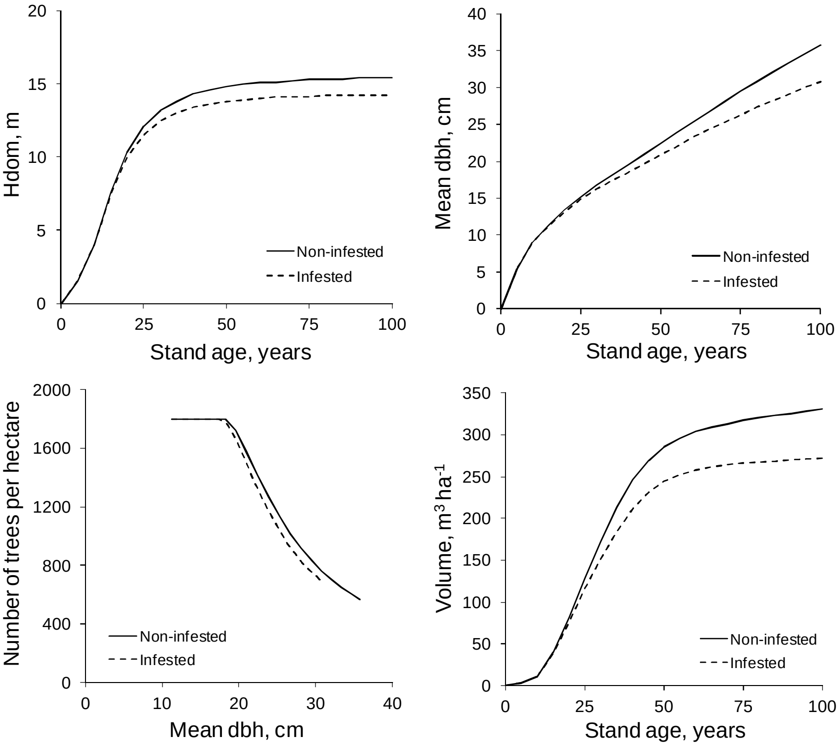

Figure 14. Effect of *M. hellenica* on growth, survival and yield of *P. brutia* according to the models fitted in studies I and III, and taking into account the impact of the scale insect on tree growth (Yeşil et al. 2005).

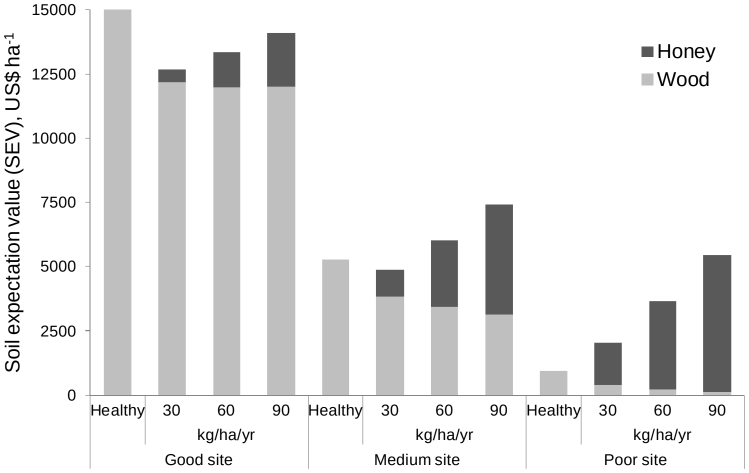

Figure 15. Economic profitability (soil expectation value) of timber production in healthy and infested *P. brutia* stands in relation to the joint production of pine honey and timber in pine stands infested by *M. hellenica*. Honey production begins at stand age of 35 years.

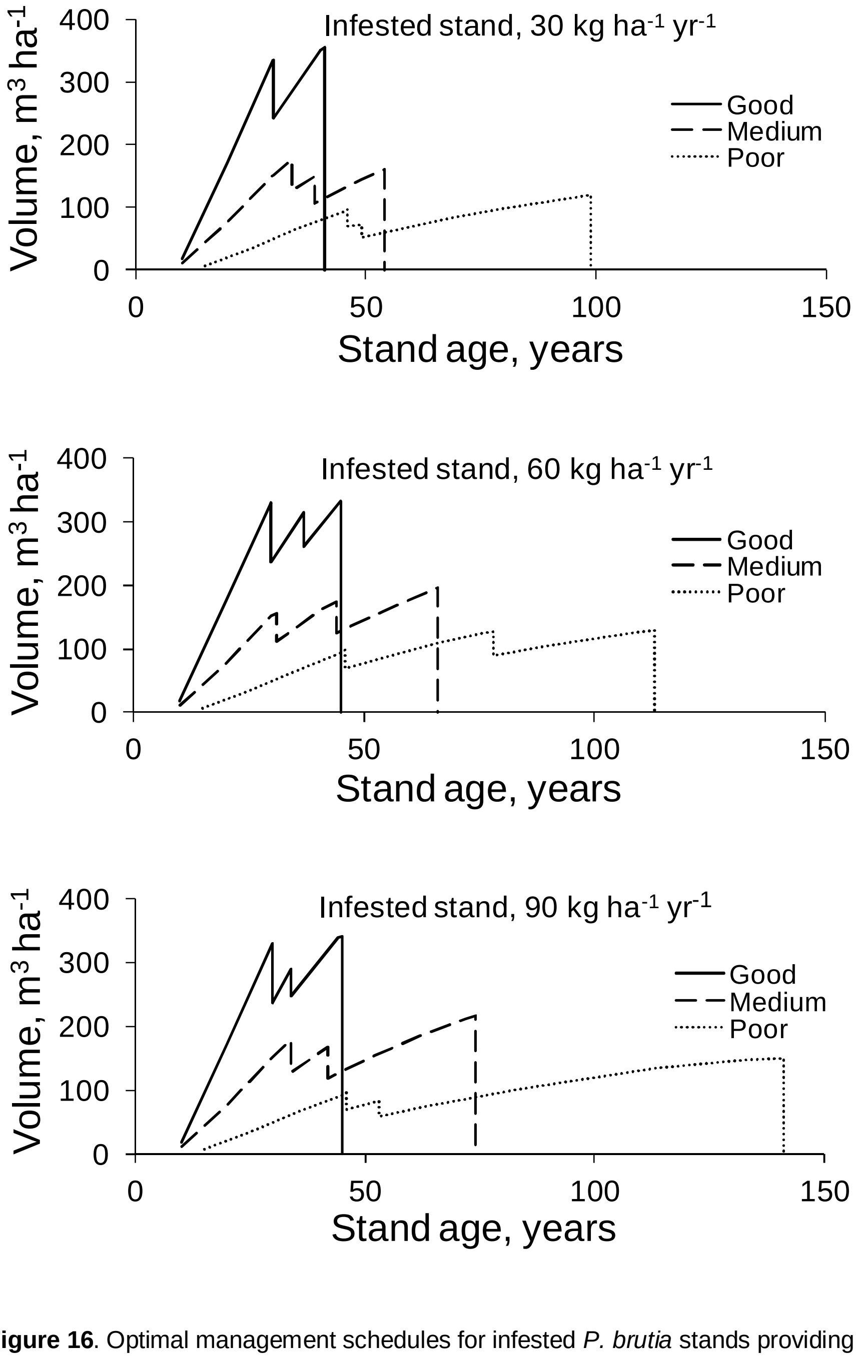

Figure 16. Optimal management schedules for infested *P. brutia* stands providing joint production of pine honey and timber products, growing on good (SI = 22.2 m), medium (SI = 14.8 m) and poor sites (SI = 9.7 m) and under different assumptions on pine honey productivity (30, 60 and 90 kg ha^{-1} yr^{-1}).

4 DISCUSSION

4.1 Individual-tree growth and yield modelling and simulation of *P. brutia*

The empirical individual-tree models and simulations of *P. brutia* stand dynamics based on studies I and II correspond to current scientific biological knowledge. Simulations reflect the ecology of a relatively fast-growing pioneer species (Boydak 2004). The fact that data for growth modelling were collected from temporary sample plots (i.e., measured only once) prevented the development of an individual-tree mortality model. Thus, in the absence of any other individual-tree mortality model tree, survival can be estimated by means of the self-thinning model, whose suitability for properly predicting mortality may be questioned. Alternatively, the equation provided by Palahí et al. (2008) may be used. Therefore, further research could aim at remeasuring the same sample plots in order to enable mortality prediction on an individual-tree basis. This could also allow for the validation of the growth models presented in this PhD thesis and, if needed, for their improvement.

It is clear that the EA modelling approach is the most suitable when dealing with strictly even-aged stands, and the UA approach is the most suitable for uneven-aged stands. However, it was not clear from previous research what is the best modelling approach when dealing with transitional or semi-even-aged stands. In this regard, study II shows that UA models produce more accurate predictions of wood production in semi-even-aged stands, even though model fitting may be statistically less accurate. This result arises from the fact that the assumptions of the EA modelling approach are more constraining, whereas the UA approach is less sensitive to slight deviations from the theoretical foundations of the method. Based on the principle of caution, the use of the UA modelling approach might be safer to predict growth and yield based on sound simulation of stand dynamics. The UA approach is also to be preferred since it enables higher flexibility in the simulation of forest management alternatives. Reliable UA models can be used to simulate any kind of thinning, whereas the EA approach assumes that the dominant trees are not removed in thinning (i.e., only thinning from below is allowed). Since there was no mortality in the modelling data, the lack of an individual-tree mortality model did not represent a shortcoming in this research.

Although not explicitly considered in studies I and II, due to the lack of appropriate climatic data, the growth models for *P. brutia* can accommodate the effect of changing environmental conditions on stand dynamics (Fontes et al. 2010). Since site index is a predictor of tree growth and survival in even-aged *P. brutia* stands, one possibility would be to relate site index to environmental variables (e.g., precipitation and temperature) (Seynave et al. 2005). Alternatively, the models for even-aged and uneven-aged stands could directly incorporate environmental variables as additional predictors. Snowdon et al. (1998) opted for incorporating climatic indices into growth models. Along the same line, another possibility to make the models climate-sensitive would consist of including a growth trend multiplier accounting for the environmental effects (Pukkala and Kellomäki 2012). Site productivity may be, in fact, affected by ecosystem features other than climate change. In this regard, study VI represents an example of how these models can be used to account for a changing environment caused by the infestation of *P. brutia* trees by the scale insect *M. hellenica*. Further research should model the impact of precipitation on *P. brutia* stand dynamics (Sarris et al. 2007). Then, the models provided in studies I and II could be used to derive stochastic or deterministic predictions of stand dynamics under different climate change scenarios. Developing site-specific models implicitly accounting for spatial or temporal changes in site quality (i.e., dynamic state-space approach) is a way of providing flexible empirical growth models to be used within the global change context (Fontes et al. 2010).

Between-country differences were found showing that dominant height development is slightly lower in Lebanon than in Syria, *BAL* has a smaller effect in Lebanon than in Syria, and site index has less influence on survival in Lebanon than in Syria. Such between-country variations are probably related to historical uses affecting stand structure and to differences in site conditions. Wood harvesting from *P. brutia* forests was allowed in Lebanon until 1991 whereas, in Syria, harvesting activities seem to have been stopped much earlier. Although no thinning or harvesting had been done in the sample plots within the measured past growth periods (up to 20 years), older forestry operations mainly consisting on selective cuttings may have led, in combination with forest fires, to more heterogeneous stand structures in Lebanon. Regeneration of the unmanaged Syrian forests most likely happened only after wildfire events, resulting in more homogeneous and even-aged stand structures. Thus, the slightly lower site index of Lebanese stands may arise from the past removal of dominant trees in selective cuttings as well as from poorer average site conditions due to the fact that Lebanon represents the southernmost limit of the native range of this species. *BAL* and site index have less influence, respectively, on radial growth and self-thinning limit in Lebanon. This is probably due to greater sampling error in these predictors arising from the higher heterogeneity of Lebanese *P. brutia* stands. Similarly, different regeneration methods could also explain differences found between even-aged *P. brutia* stands in Middle East (possibly regenerated after hard disturbances such as wild fires) and semi-even-aged Greek stands modelled by Palahí et al. (2008).

In combination with forest fires and environmental factors, past management may have led to significant differences in the amount of biomass and carbon accumulated in different tree components, although the total aboveground biomass of trees was nearly the same in both countries (study IV). Trees growing in uneven-aged stands have more biomass and carbon in their crown components (needles and branches) than trees growing in unthinned, even-aged Syrian stands. Since crown length was not significantly different between Syria and Lebanon, these results show that tree crowns are wider and/or denser in the uneven-aged Lebanese stands. Consequently, the biomass and carbon stored in the stem of trees is lower in uneven-aged than in even-aged stands. Due to such between-country differences, average regional biomass models not accounting for country effects will result in biased predictions at the country level. The harvest index found in Syrian even-aged *P. brutia* stands is fairly similar to the one reported for even-aged Norway spruce by Kuuluvainen (1991), whereas the harvest index of the multi-layered *P. brutia* stands in Lebanon is considerably lower. The results suggest that forest management-induced stand structure may have a significant influence on the way biomass and carbon are distributed within the tree since, depending on the resulting stand structure, trees adopt different ways to allocate biomass and carbon (Tinker et al. 2010).

These results are also consistent with current biological knowledge on stand dynamics of light-demanding species. Namely, trees growing in unthinned dense even-aged stands are expected to have longer stems and smaller crowns as a result of competition for light. Dominant trees growing under strong competition in even-aged stands are expected to have relatively small branch and foliage biomass (Návar 2009). In selectively cut uneven-aged stands, dominant trees experience less competition and can further develop their crowns (Naidu et al. 1998; Jenkins et al. 2003). This may happen especially when the stand density has been low for a long time. Due to the low shade tolerance of *P. brutia*, uneven-aged stands are not likely to be associated with high stand densities of the dominant canopy layer, but even-aged stands may have low density. This suggests that, to correctly predict crown dimensions, it is important to know the past competition rather than current stand structure (Hynynen 1995). Since stem taper and d/h ratio reflect the tree's past growing conditions it is recommendable to use both dbh and height in biomass prediction in simulations where different management regimes are possible (Chave et al. 2005), especially when dealing with fixed-effects models.

Mixed-effects may be more convenient for growth and yield modelling in a number of situations, as shown in studies III and V. This modelling approach is meaningful when dealing with correlated observations from hierarchically structured datasets according to given spatial or temporal grouping levels (Pinheiro and Bates 2000). Nevertheless, in studies I and II, least squares fitting assumed independence among observations. The reason for that choice is that it has been shown that fixed-effects models fitted via nonlinear least squares can perform better than non-calibrated mixed-effects models in the simulation of stand dynamics (e.g., de-Miguel et al. 2013). However, mixed-effects models could be used to provide, for instance, site-specific predictions within the framework of the dynamic state-space approach.

Studies III and V partly focused on providing new information and further insight into the performance of mixed-effects models in yield prediction, both in the absence and in the presence of model calibration. Study III shows that, in the absence of calibration, volume estimation based on marginal predictions of mixed-effects taper models can be competitive with the prediction of nonlinear least squares models. As suggested by Burkhart and Tomé (2012), population-averaged prediction based on mixed-effects models should not be based just on the fixed parameters of the model. In contrast, averaging the predictions over the estimated distribution of random effects seems a suitable alternative. However, further research should be devoted to fully understand the potential of such a prediction strategy since it does not seem to systematically result in better predictions than fixed-effects models (de-Miguel et al. 2013).

Study V shows the potential of calibrating mixed-effects allometric meta-models for providing reliable location-specific biomass prediction throughout large spatial scales with minimal sampling effort. The study represents a new methodological approach aiming at providing pan-Mediterranean aboveground biomass models for *P. brutia*. Study V shows that, for a given model form, calibration of mixed-effects meta-models can provide, with very little sampling effort, more accurate location-specific predictions than obtained with location-specific allometric equations fitted to larger datasets. Furthermore, deriving models directly from previous research by mixed-effects modelling has a potential for widespread use. The approach could also contribute to forest modelling disciplines other than biomass modelling (i.e., growth modelling) and should be the object of further research.

4.2 Forest management optimization

The empirical growth and yield models provided in this PhD thesis allow scientific forest management of eastern Mediterranean *P. brutia* stands and forests. They can be used to simulate alternative forest management schedules. In combination with economic data and optimization techniques, it is possible to propose optimal stand management schedules within the framework of multi-objective forest management planning. In this regard, study VI optimizes the management of even-aged *P. brutia* stands in the joint provision of wood and non-wood forest products (i.e., timber assortments and pine honeydew honey) taking into account changes in site productivity caused by the scale insect *M. hellenica.*

Simulation of stand dynamics of infested pine stands reproduces logically the influence of *M. hellenica* on the growth and mortality of *P. brutia* according to the currently available scientific information (Yeşil et al. 2005; Gallis 2007; Petrakis et al. 2010, 2011). Since the influence of the scale insect on *P. brutia* growth was based on tree-level measurements (Yeşil et al. 2005), the use of an individual-tree growth model made it possible to directly incorporate the negative effect of the scale insect on tree diameter increment. An additional impact of *M. hellenica* is its negative influence on site productivity through site index reduction. Since site index is a predictor in the diameter increment and survival models, the impact of *M. hellenica* on site quality also affects the survival rate and growth of pines.

The optimal rotation lengths for healthy stands are in line with the current knowledge for this pine species (Shater et al. 2011; Bettinger et al. 2013). The optimal schedules for pine stands growing on good sites are rather insensitive to infestation by the scale insect and honey production. As site quality decreases, the economic importance of honey increases, resulting in longer rotations for infested stands. The economic profitability of *P. brutia* forest management is the highest in pine stands growing on good sites that remain unaffected by *M. hellenica.* On very good sites, honey production in infested stands cannot compensate for the volume increment loss caused by the scale insect. The same occurs on medium sites when honey production is low. On the contrary, on poor sites, joint production of timber and honey results in higher economic profit than wood production in healthy stands, even when honey production is rather small. What is more, in those particular cases, pine honey alone may produce more profit than obtained from timber in healthy stands. In addition, if honey yield is at least 90 kg ha^{-1} yr^{-1}, honey-oriented forest management in poor sites may be as profitable as the traditional timber-oriented management in more productive sites. On medium sites, joint production of pine honey and timber is more profitable than timber production in healthy stands if honey production is greater than 30 kg ha^{-1} yr^{-1}. Therefore, from a strict economic perspective, the presence of *M. hellenica* might be regarded as economically harming in *P. brutia* stands growing on medium sites if honey yield is not very high (i.e., 30 kg ha^{-1} yr^{-1}), and on good sites if honey production is lower than approximately 100 kg ha^{-1} yr^{-1}. On the contrary, if honey yield is at least 10 to 15 kg ha^{-1} yr^{-1} on poor sites or at least 40 kg ha^{-1} yr^{-1} on medium sites, joint production of timber and pine honey results in higher economic profit than the traditional forest management in healthy stands.

In the absence of empirical results, some assumptions had to be made regarding the interactions between *P. brutia*, *M. hellenica* and honeybees. Further research should focus on improving our understanding about the effects of the scale insect on tree growth and mortality. This requires deeper knowledge on the interactions between host trees and the scale insect, and about the influence of tree vigour on sap flow and honeydew yield (Gounari 2006). Such knowledge may provide a better understanding of (i) which trees are "selected" by *M. hellenica,* (ii) what proportion of trees may be infested in pine stands affected by the scale insect, (iii) whether the infestation pattern may be influenced through forest management, and (iv) whether there is any relation between tree vigour, site quality and the amount of honeydew produced. This would enable better predictions of the availability of "raw material" for bees that produce pine honey (Gounari 2004).

M. hellenica is sensitive to changes in climatic conditions, mainly in temperature (Gounari 2006) which, in turn, may cause considerable fluctuations in honeydew and honey yields. Better knowledge on its weather sensitivity could improve honeydew yield predictions under different climatic scenarios. On the other hand, more insight into the efficiency of honeybees in processing honeydew to produce pine honey is needed. This would enable more detailed site-specific information concerning the potential pine honey productivity. Finally, considering forest ecosystem services potentially affected by *M. hellenica* infestation (e.g., biodiversity, recreational value, fire risk) (Gallis 2007; Petrakis et al. 2010) as well as other non-wood forest products (e.g., mushrooms) would probably affect the optimal management of *P. brutia* stands (Calish et al. 1978). Models for predicting the amounts of these goods and services are needed before they can be integrated in stand management optimization.

M. hellenica causes economic losses to those whose objective is to produce timber (i.e., the landowners). On the other hand, in combination with honeybees, the scale insect generates economic benefits to the beekeeping sector. For the society, which should maximize the total benefit produced by the forest, the insect may be harmful or useful, depending on the quantity of the losses in timber production as compared to the economic benefits of beekeeping. Based on the results of study VI, policy makers may consider alternative policy measures such as pine honey harvesting permits, taxation, royalties or public investments in rural development in relation to beekeeping. This study therefore provides valuable information for forest policy making in relation to sustainable multifunctional forestry and rural development with special focus on beekeeping communities.

The optimal uneven-aged management of *P. brutia* based on the UA models of study II was not inspected because *P. brutia* forests form even-aged structures when intensively managed. Nevertheless, further research could be devoted for instance to comparing even-aged *versus* uneven-aged *P. brutia* management by taking into account more complex additional interactions among different ecosystem features (e.g., other non-wood forest products, biodiversity, fire risk). For that purpose, new models would be required. In addition, since *P. brutia* forms sometimes mixed forests, mainly in combination with *Quercus* species, another topic for further research is the development of growth models for mixed *P. brutia* stands.

5 CONCLUSION

This PhD thesis provides a logical set of research papers that intend to shed light on a number of relevant issues for the management of *P. brutia* forest ecosystems. The topic is relevant as it addresses several of the strategic research objectives affecting *P. brutia* forests, from a European and a Mediterranean perspective, defined by the Strategic Research Agenda and the Strategic Research and Innovation Agenda for 2020 of the European Forest-Based Sector Technology Platform (FTP – Forest Technology Platform), as well as by the Mediterranean Forest Research Agenda 2010-2020 (EFI 2010).

The six studies that form this PhD thesis, together with this Dissertation, contribute to filling existing gaps in scientific knowledge concerning stand dynamics, provision of wood and non-wood forest products, biomass and carbon stock, as well as in relation to the optimal forest management of *P. brutia*.

The PhD thesis also provides further insight into several methodological issues, namely the suitability of alternative growth modelling approaches when dealing with transitional semi-even-aged forest stands, the performance of calibrated and non-calibrated mixed-effects models in volume and biomass prediction, the potential of meta-analysis in yield prediction, and the optimization of forest management in the joint production of wood and non-wood forest products taking into account the complex interactions among different elements of the forest ecosystem.

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