

## Simulating regeneration and vegetation dynamics in Mediterranean coniferous forests

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### ARTICLE INFO

#### Article history:

Received 1 November 2009

Received in revised form 25 February 2010

Accepted 5 March 2010

Available online 1 April 2010

#### Keywords:

*Abies cephalonica*

*Pinus nigra*

*Pinus brutia*

Mediterranean conifers

Climate change

Cold stratification

Seed germination

Regeneration dynamics

Forest dynamics

Forest modelling

Gap dynamics

### ABSTRACT

This study aims to provide a quantitative framework to model the dynamics of Mediterranean coniferous forests by integrating existing ecological data within a generic mathematical simulator. We developed an individual-based vegetation dynamics model, constrained on long-term field regeneration data, analyses of tree-rings and seed germination experiments. The simulator implements an asymmetric competition algorithm which is based on the location and size of each individual. Growth is parameterized through the analysis of tree-rings from more than thirty individuals of each of the three species of interest. A super-individual approach is implemented to simulate regeneration dynamics, constrained with available regeneration data across time-since-disturbance and light-availability gradients. The study concerns an insular population of an endemic to Greece Mediterranean fir (*Abies cephalonica* Loudon) on the island of Cephalonia (Ionian Sea) and two interacting populations of a Mediterranean pine (*Pinus brutia* Ten.) and a more temperate-oriented pine (*Pinus nigra* Arn. ssp. *pallasiana*) on the island of Lesbos (NE Aegean Sea), Greece. The model was validated against plot-level observations in terms of species standing biomass and regeneration vigour and adequately captured regeneration patterns and overall vegetation dynamics in both study sites. The potential effects of changing climatic patterns on the regeneration dynamics of the three species of interest were subsequently explored. With the assumption that a warmer future would probably cause changes in the duration of cold days, we tested how this change would affect the overall dynamics of the study sites, by focusing on the process of cold stratification upon seed germination. Following scenarios of a warmer future and under the current model parameterization, changes in the overall regeneration vigour controlled by a reduction in the amount of cold days, did not alter the overall dynamics in all plant populations studied. No changes were identified in the relative dominance of the interacting pine populations on Lesbos, while the observed reduction in the amount of emerging seedlings of *A. cephalonica* on Cephalonia did not affect biomass yield at later stages of stand development.

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### 1. Introduction

Forests established at areas surrounding the Mediterranean basin have been managed, altered and studied by humans for more than 2000 years (Grove and Rackham, 2001). Coniferous forests are a substantial component of these long-term human dominated areas, with pine (to a greater) and fir (to a lesser extent) taxa being between the most dominant elements of vegetation. Ecosystems found at areas surrounding the Mediterranean Sea, are expected to experience significant changes in their structure, function and distribution due to global change related drivers (Sala et al., 2000).

Land use and climatic changes are considered the main threats for the viability of these ecosystems. Focusing on forest dynamics, numerous field observations (Arianoutsou et al., 2009; Peñuelas and Boada, 2003) and model projections (Arianoutsou, 2004; Fyllas and Troumbis, 2009; Mouillot et al., 2002; Pausas, 1999) have highlighted their vulnerability in terms of changes in the frequency of drought and fire events.

Although established forests are thought to exhibit a time-lag in their response to environmental changes, some processes like regeneration could present much faster responses. Additionally, it is well established that changes in recruitment processes have a direct effect on future vegetation patterns (Catovsky and Bazzaz, 2000; Good and Good, 1972; Kobe et al., 1995), with even short-term changes in the environmental conditions having long-term effects on forest composition (Brown and Wu, 2005). Thus, under-

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standing the potential response of regeneration dynamics to suites of global change related environmental shifts could provide valuable insight in modelling potential changes in the functioning of forest ecosystems.

The representation of regeneration dynamics in current vegetation models is rather weak (Price et al., 2001). For example, in forest gap dynamics simulators (Botkin, 1993), recruitment is assumed to take place at the saplings stage and each year a random number of new individuals up to 1.3 m height are “established” in the stand. In these models the regeneration algorithms have only evolved very little since their original formulation (Botkin et al., 1972). Species-specific recruitment vigour is filtered through abiotic and/or biotic parameters such as the annual number of growing degree days and/or a species-specific light availability threshold for successful establishment. Such formulations are paying less attention to the initial stages of seedling recruitment and could lead to biased predictions in terms of species persistence and/or diversity patterns (Bugmann, 2001). Different approaches to deal with the above issues have been suggested the last decade spanning from the “cohort” approach (Bugmann, 1996), to the inclusion of life history strategies that mediate both species persistence and recruitment density based on a set of functional characters (Fyllas et al., 2007; Pausas, 1999). The inclusion of seedlings-dynamics specific submodels could be a step forward; however, substantial increase in computational time could provide an obstacle to that direction especially when simulating large stand areas with seedling densities reaching up to 30 individuals per square meter per species. Thus, a realistic and computationally affordable way of representing regeneration dynamics in current vegetation simulators is needed, if we are to realistically represent plant diversity and key ecosystem processes in such quantitative schemes.

In their review of the recruitment algorithms used in forest gap dynamics simulators, Price et al. (2001) identified several drivers that are currently weakly represented, but are important for the overall model behaviour under current and future climatic conditions. Modellers have started dealing with these issues; for example van der Meer et al. (2002) have adjusted seed production based on the climatic conditions of the previous years. Seed cold stratification/chilling, is an important regeneration variable (Grime et al., 1981; Venable and Lawlor, 1980) which is expected to shift as a result of an increase in daily temperature under global change scenarios (Frich et al., 2002; Goubanova and Li, 2007). In boreal tree species dynamics models, chilling requirements are usually included by calculating the sum of days that are between  $-5$  and  $5^{\circ}\text{C}$ , and have been proven to increase the accuracy of simulations (Burton and Cumming, 1995; Nitschke and Innes, 2008). The effect of chilling on seed germination seems to be less important for temperate rain forest, with more than half of the studied species being indifferent to a chilling treatment (Figuerola, 2003). The picture is less clear for the Mediterranean region, with some studies showing no or negative chilling effect on seed germination for mid-mountain plant taxa (Luna et al., 2008) and others identifying a positive effect on species found at relative low altitude ranges (Skordilis and Thanos, 1995). Here we address the above issue by conducting germination experiments for the three study species (*Abies cephalonica* Loudon, *Pinus brutia* Ten. and *Pinus nigra* Arn. ssp. *pallasiana*) and subsequently feed in the recruitment algorithm with these data.

The aim of this paper is to describe a simulation framework for the dynamics of Mediterranean coniferous forest, by integrating a generic mathematical model with species-specific data obtained from both field and experimental studies. Similar data are available in the literature for other tree taxa and thus the proposed model could potentially easily be re-parameterized for other areas of interest. We developed an individual-based, spatially explicit model of vegetation dynamics and validated its predictive ability

against field observations from the study sites. We subsequently forced the model under two downscaled IPCC climatic change scenarios and tested whether temperature oriented changes in recruitment density of *A. cephalonica*, *P. nigra* and *P. brutia* populations, realised through shifts in the period of cold stratification, could potentially affect the overall forest dynamics.

## 2. Materials and methods

We developed a new spatially explicit individual-based vegetation model and parameterized its (a) regeneration, (b) growth and (c) mortality algorithms using field and experimental data for three coniferous species of interest. The model uses the competition algorithm described in detail in Berger and Hildenbrandt (2000) and further discussed in Section 2.2. The growth and mortality submodels are based on previously published simulators (Fyllas et al., 2007; Fyllas and Troumbis, 2009), and have been re-parameterized based on tree-rings analyses (Section 2.3). These two processes are modelled on an annual basis. We additionally incorporated a new “recruitment” model which integrates the rationale of gap dynamics (Section 2.2) with regeneration data from permanent plots at two study sites (Section 2.3), again on an annual basis. Finally, a stochastic climate submodel provides daily values for temperature and precipitation under both baseline and climate change scenarios (Section 2.4).

The outputs analysed here are the stand level basal area ( $\text{m}^2/\text{ha}$ ) and the density of seedlings (number/ha) between 0.1 and 1.3 m tall. Additional population density and size class distribution results are provided in the [Supplementary Data](#) file. The new model is built in Java and all analyses and graphs were performed in R (R Core Development Team, 2008).

### 2.1. Study sites

The first study area is located at the western part of Greece ( $38^{\circ}09'\text{N}$ ,  $20^{\circ}38'\text{E}$ ) on the island of Cephalonia in the Mt. Aenos National Park (Politi et al., 2009). *A. cephalonica* [the predominant species of the Park (Forestry Department of Cephalonia, 1996)] extends from approximately 700–1600 m a.s.l., on a calcareous substrate with a poor understory in most of the area (Table 1). Twenty permanent sampling plots,  $100\text{ m}^2$  each, were established at 11 different locations over an altitudinal gradient from 1000 to 1600 m. Within each plot, ten subplots of  $1\text{ m}^2$  were randomly selected and set for monitoring seedling recruitment and dynamics. Subplots were regularly monitored over a four-year period (Politi et al., 2009). The second study area is found on the island of Lesbos ( $39^{\circ}12'\text{N}$ ,  $26^{\circ}05'\text{E}$ ) at the north-eastern part of Greece, and provides a good example of pine-to-pine interaction across an elevation gradient (Fyllas et al., 2008). Along an altitude of 500–800 m a.s.l., 100 plots ( $100\text{ m}^2$  each) were censused for recording the regeneration dynamics of two Mediterranean pines (*P. brutia* and *P. nigra* ssp. *pallasiana*). In general, *P. brutia* represents a more drought-tolerant light-demanding functional type, while *A. cephalonica* and *P. nigra* are able to regenerate on lower light levels although they are less drought-tolerant and depends on the presence of mature individuals for adequate flow of regeneration material (Fyllas et al., 2008; Ordoñez et al., 2005; Politi et al., 2009).

### 2.2. Model description

The state variable of each individual is the diameter at breast height (*dbh*) from which allometric equations are used to estimate its height. A tree is defined as a cylinder with single layer cyclic foliage at its top, and species-specific allometric equations are used to estimate each individual's foliage area as a function of its diameter at breast height (*dbh*) (Fyllas et al., 2007). Additionally each

**Table 1**  
Study sites and available field and laboratory measurements.

	Mt. Aenos, Cephalonia, Ionian Sea	Mt. Parakoila-Anemotia, Lesbos, NE Aegean Sea
Coordinates	38°09'N, 20°38'E	39°12'N, 26°05'E
Altitudinal gradient (m a.s.l.)	700–1600	500–800
Mean annual temperature (°C)	12.6	14.8
Total annual precipitation (mm)	1070	479
Soil substrate	Limestone	Cambisols
Dominant coniferous species	<i>Abies cephalonica</i>	<i>Pinus brutia</i> and <i>P. nigra</i> ssp. <i>pallasiana</i>
Number of plots	20 (200 monitoring subplots)	102
Time course of regeneration measurements	2004–2008	2005–2006
Measurement of light availability	Hemispherical pictures	Hemispherical pictures
Number of tree cores analysed	<i>A. cephalonica</i> : 32	<i>P. brutia</i> : 52 and <i>P. nigra</i> : 30

tree has a specific suite of xy coordinates used to estimate neighbourhood competition effects, as well as light availability at any point within the simulated stand, as further discussed below. Simulation plots are defined by their altitude and area, while latitude and aspect are not explicitly taken into account in the current version of the model (but see Fyllas et al., 2009). All simulations start from bare ground, with a constant elevation and area, and the main source of variation comes from climatic variability as generated from the stochastic climate submodel.

### 2.2.1. Competition, growth and mortality

The developed model implements a generic competition algorithm (Berger and Hildenbrandt, 2000). It basically estimates the competition strength that each individual is experiencing, as a member of a plant community with a given size and location. As discussed in detail in Berger and Hildenbrandt (2000) each tree ( $i$ ) has a spatially explicit Zone Of Influence [ $ZOI_i$  (derived from its size)], within which it affects its neighbours ( $j$ ). Furthermore the strength of this influence is controlled by the distance of the interacting tree ( $j$ ) to the center of  $ZOI$  of tree  $i$ , where the effect is maximum. This generic competition model has been used for intuitively estimating the strength of competition for multiple resources, both above and below ground (Berger et al., 2008). As in Berger and Hildenbrandt (2000), we hypothesize that a unified competition metric is reducing the optimum growth ( $G_{max}$ ) of each individual, a modelling technique extensively implemented in gap dynamics models (Botkin, 1993; Shugart, 1984). The estimation of optimum growth for our study species is described in the next paragraph, with the use of species-specific tree-rings analyses. Finally, mortality is modelled at the individual level, with trees that achieve low annual growth having a higher probability to die (Fyllas et al., 2007). Species-specific low-growth thresholds ( $G_T$ ) are estimated from the analysed tree-rings data as described in Section 2.3.

### 2.2.2. Regeneration

Special attention was paid to a realistic simulation of recruitment dynamics. A two-step regeneration algorithm has thus been developed and integrated into the simulator. This submodel combines the rationale of gap-phase regeneration with available field data of species-specific recruitment along levels of light availability (Coates, 2002). At the same time it also takes into account available experimental data relating species-specific seed germination with the duration of cold stratification (see Section 2.3). Specifically each year a maximum number of viable seeds ( $SO_{max}$ ) are assigned to each species, assumed to be proportional to the area of the plot. Subsequently, an annual number of new seedlings ( $sdl$ ) is estimated by the multiplication of  $SO_{max}$  with a germination coefficient ( $Rc$ , ranging from 0 to 1) as a function of the annual number of cold days ( $ancd$ ), viz. days with mean temperature lower than 5 °C. The derivation of species-specific  $Rc$  curves is based on experimental data as described in the next section.

The second step in the regeneration submodel simulates the ability of successful seedling recruitment at the saplings size class. The annual number of new seedlings provides a source of new recruits at the age of one year which is added in a pool of available seedlings ( $sdlPool$ ) for each species. Seedlings are maintained in the seedlings pool until the age of 10 years, when they are eventually added at a specific location as saplings ( $spl$ ). Until that stage seedlings do not have specific coordinates, but are rather considered as a pool of potential recruits. In order for a seedling to increase its age (for example from years 1 to 2) it has to pass a species-specific threshold of light availability, as expressed by a leaf area index threshold ( $LAI_T$ ). At each time step light availability is computed for each member of the seedlings pool, by selecting a random location within the plot and estimating a local leaf area index ( $LAI_L$ ) at a cyclic area of 10 m radius.  $LAI_L$  is computed as the sum of foliage area of all established individuals (bigger or equal to the sapling stage) within the cyclic area, divided by the area of the circle. No three-dimensional description of the canopy is pursued, and thus if a mature tree falls within the local cyclic area, its entire canopy is assumed to shade the seedling under consideration. This algorithm is essentially “scanning” the soil surface estimating a level of light availability at random points. If  $LAI_L < LAI_T$ , then the specific seedling is surviving in the current time step. In contrast, with existing gap models, where an aggregated level of available incoming radiation at the soil surface is estimated, our approach is following a random sampling procedure which could potentially identify more than one gap within the simulated plot area, and thus lead to realistic simulations of areas bigger than the gap scale.

### 2.3. Model parameterization

Experimental and field data were used to parameterize three key processes, namely regeneration, growth and mortality, modelled as described above.

#### 2.3.1. Regeneration

Experimental data were used to model species germination efficiency as a function of cold days, defined here as days with an average temperature lower than 5 °C. For *A. cephalonica* and *P. nigra*, seeds were collected from the study sites and treated under a common germination protocol in the lab. Following the methodology described in Thanos and Skordilis (1987) seeds were pre-treated with fungicide. Cold stratification was performed at  $4 \pm 1$  °C for one up to six weeks. Three Petri dishes containing 20 seeds each was used for each cold stratification time period. Germination tests were carried out at  $20 \pm 2$  °C in temperature control chambers in the dark. Seeds were moistened with deionised water and their germination was recorded daily, using as criterion the appearance of a radicle protrusion (Skordilis and Thanos, 1997; Thanos and Skordilis, 1987). The above data along with those published by Skordilis and Thanos (1997) for *P. brutia*, were used to develop germination curves as a function of cold stratification

**Table 2**  
Species parameters used in this study. See text for details.

Parameter	<i>Abies cephalonica</i>	<i>Pinus brutia</i>	<i>Pinus nigra</i>	Source data
<b>Regeneration submodel</b>				
Date of seed dispersal	October*	May–June <sup>^</sup>	March–May <sup>^</sup>	*Politi et al. (2007)
Date of seed germination	April*	October <sup>^</sup>	May–June <sup>^</sup>	<sup>^</sup> Skordilis and Thanos (1995)
<i>a</i> (germination curve)	7.03*	48.25 <sup>^</sup>	32.88*	*This study
<i>b</i> (germination curve)	0.61*	0.28 <sup>^</sup>	2.77*	<sup>^</sup> Skordilis and Thanos (1995)
<i>c</i> (germination curve)	0.008*	0.001 <sup>^</sup>	–0.056*	
<i>LAI<sub>T</sub></i>	4.5*	4 <sup>^</sup>	3 <sup>^</sup>	*Politi et al. (2009) <sup>^</sup> Fyllas et al. (2008)
<b>Growth submodel</b>				
<i>a</i> (growth curve)	1.55	2.73	2.20	This study
<i>b</i> (growth curve)	0.0500	–0.0224	–0.0291	
<i>c</i> (growth curve)	–0.0010	0	0	
<b>Mortality submodel</b>				
<i>G<sub>T</sub></i> (growth threshold)	0.2	0.6	0.3	This study

period. The analysed lab data revealed a stronger dependence of fir on cold stratification and a weaker but still significant dependence of *P. brutia*. Species-specific germination curves provide a germination coefficient  $R_C$ , which multiplied with  $SO_{max}$  gives the annual number of emerging seedlings.  $R_C$  was modelled as a quadratic function of annual cold days (*ancd*), which were used as a proxy of effective cold stratification between the seed dispersal and seed germination period; i.e.  $R_C = a + bx + cx^2$  with *a*, *b* and *c* coefficients estimated from lab data based regressions. A random length of the period between seed dispersal and germination is selected each year which is based on the currently observed respective dates (Table 2). The coefficients of the three  $R_C$ –*ancd* curves are given in Table 2, with the germination curves presented in Supplementary Data (Fig. A.1).

The second step of the recruitment model is based on the estimation of a light availability level for each seedling in the seedlings pool. Available light is decreasing with increasing LAI following a negative exponential function (Monsi and Saeki, 2005). At the same time different species seem to have different levels of shade tolerance, with fast growing species being relatively less shade tolerant and slow growing species being relatively more shade tolerant (Sánchez-Gómez et al., 2006). Based on our dataset, we used the maximum value of LAI under which living seedlings were found for each species as the species-specific LAI threshold ( $LAI_T$ —Fig. A.2). The fast growing *P. brutia* illustrated the lowest LAI threshold ( $LAI_T \approx 3$ ) below which effectively no new recruits were observed. *P. nigra* had a relatively higher LAI threshold ( $LAI_T \approx 4$ ) and *A. cephalonica* illustrated the highest one ( $LAI_T \approx 4.5$ ).

### 2.3.2. Growth and mortality

Tree-rings data for more than 30 individuals for the three species were used to fit a  $G_{max} = f(dbh)$  curve and estimate the  $G_T$  threshold. Increment cores were taken at 130 cm above ground in order to match the central growth variable, i.e. *dbh* in the model. Sampled individuals were located outside the stand, in order to exclude light competition effects on annual growth. For the first case, we plotted annual tree-ring increment against individual's previous years *dbh*, thus each individual is represented by a number of points expressing its annual growth along its life cycle (Fig. A.3). We then used the maximum value of *dbh* increment to fit an optimum growth curve,  $G_{max} = e^{a+bx+cx^2}$ , where *a*, *b* and *c* species-specific coefficients (Table 2). Finally the species-specific  $G_T$  threshold was estimated as the minimum annual *dbh* observed value along its life cycle, hypothesizing that this low growth is a proxy of a sufficient resource acquisition and allocation. For the three study conifers  $G_T$  is also shown in Table 2. Below this threshold trees are experiencing a higher mortality probability expressed with an exponential function as described in Fyllas et al. (2007).

### 2.4. Scenarios and simulations

The simulator uses a built in climate generator as described in Fyllas and Troumbis (2009). Climatic profiles are generated using available baseline data from local weather stations (for Lesbos: <http://catastrophes.geo.aegean.gr/ATMOS/lesvos.asp> and for Cephalonia: <http://kefalonias.chi.civil.ntua.gr/wkef/el/index>). In particular daily temperature and precipitation are sampled from a normal and a log-normal distribution, respectively using the monthly average and standard deviation estimates. Additionally, two climate change scenarios that follow a warming trend were implemented for a period of 100 years, after which climate is assumed to stabilize to a new warmer and drier annual profile (Fyllas and Troumbis, 2009). IPCC climate change scenarios A1 and B2 lead to a mean annual increase of 4.3 and 2.8 °C, respectively according to downscaled HADCM3 projections for Greece (Mitchell et al., 2004).

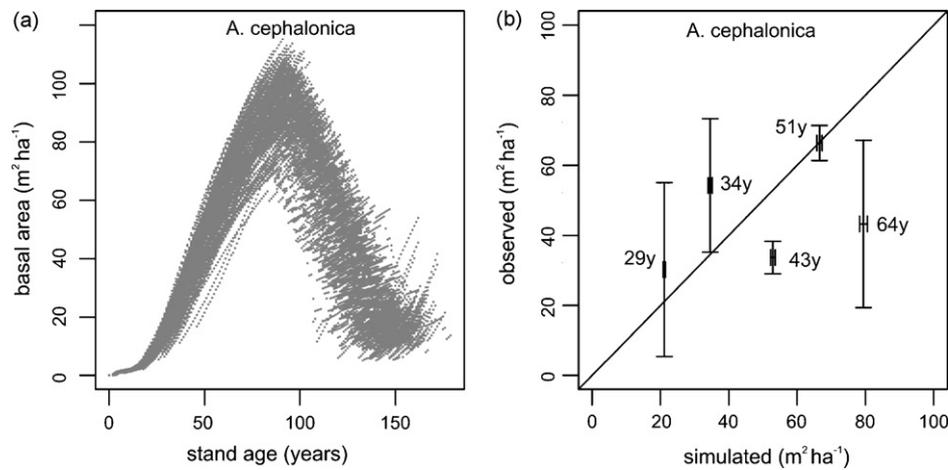
In this study we did not include the effects from potentially changing fire regime, as we were mainly interested to explore the climate effects solely on vegetation dynamics, due to modified regeneration patterns. It should also be noted that climate effects on growth of mature individuals cannot be simulated in this version of the model, as growth is parameterized using current climate tree-rings analyses.

For each of the study sites we performed 50 iterations for both baseline (BL) and climate change (CC) conditions, starting in all cases from bare ground. On Cephalonia the simulated plots were found at the lower (950 m a.s.l.) part of the National Park. For the Lesbos study site, plots were located in a pure *P. brutia* (400 m a.s.l.), mixed *P. brutia*–*P. nigra* (650 m a.s.l.) and pure *P. nigra* (750 m a.s.l.) forest. In all cases climatic data were extrapolated using a 6.5 °C km<sup>–1</sup> temperature lapse rate, while no trend with altitude was assumed for precipitation.

## 3. Results

### 3.1. Baseline simulations

Results from the baseline climate simulations on Mt. Aenos are summarised in Fig. 1. A unimodal relationship between *A. cephalonica* biomass (expressed as basal area per ha) and the age of the stand (as indicated by the age of the oldest individual) emerged (Fig. 1a). The peak of standing biomass was found at approximately the age of 80 years (Fig. 1a). Simulated against observed values of total *A. cephalonica* basal area per hectare along different stages of stand development is depicted in Fig. 1b. As expected much higher variability was recorded in the field compared with model predictions, where the main sources of variance are climatic variability

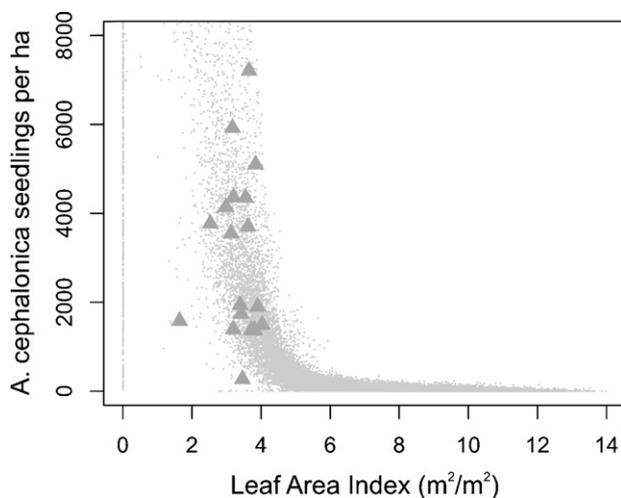


**Fig. 1.** Vegetation dynamics under baseline climate simulations for forest stands on Cephalonia at 950 m a.s.l. (a). Stand age estimated from the age of the oldest individual in the plot. Comparison between observed and simulated basal area ( $\pm$ standard error) is shown in panel (b). Values represent the mean stand age per decade from field measurements and 50 model iterations. Straight line in panel (b) illustrates the perfect fit line of one to one correspondence. Note the very low variation in simulated basal area.

and stochasticity in the mortality algorithm. However, a relative good behaviour of the model was identified for this monospecific forest, with the perfect fit line passing within the cloud of field observations.

Regeneration dynamics are summarised by plotting the number of seedlings maintained in the seedling pool of each species against stand's mean LAI. We note that the absolute values of  $SO_{max}$  did not affect the behaviour of the model; rather the relative species proportions seem to be more important in a set of explorative simulations. In Fig. 2 we plot both field observations and model simulations. For *A. cephalonica* simulated recruitment densities were well within the observed ranges in the field. Simulations suggest a higher seedling density at relatively lower stand LAI with a gradual decline of the seedling pool size with increasing LAI.

For the second area of study, the model illustrated a good predictive ability along the elevation gradient (Figs. 3 and 4), ranging from *P. brutia* to mixed *P. brutia*–*P. nigra* and pure *P. nigra* stands. At lower altitude *P. brutia* is dominating the plots and achieves a maximum basal area at around the stand age of 60 years (Fig. 3a) with the



**Fig. 2.** Regeneration dynamics under baseline climate simulations for forest stands on Cephalonia at 950 m a.s.l. Grey dots illustrate model outputs for *A. cephalonica* seedlings pool size and grey triangles *A. cephalonica* seedlings density field observations. Leaf area index (LAI) was estimated through hemispherical pictures in the field (one sided), while model estimations of LAI were made through the permutation method described in the text. Model outputs from 50 iterations.

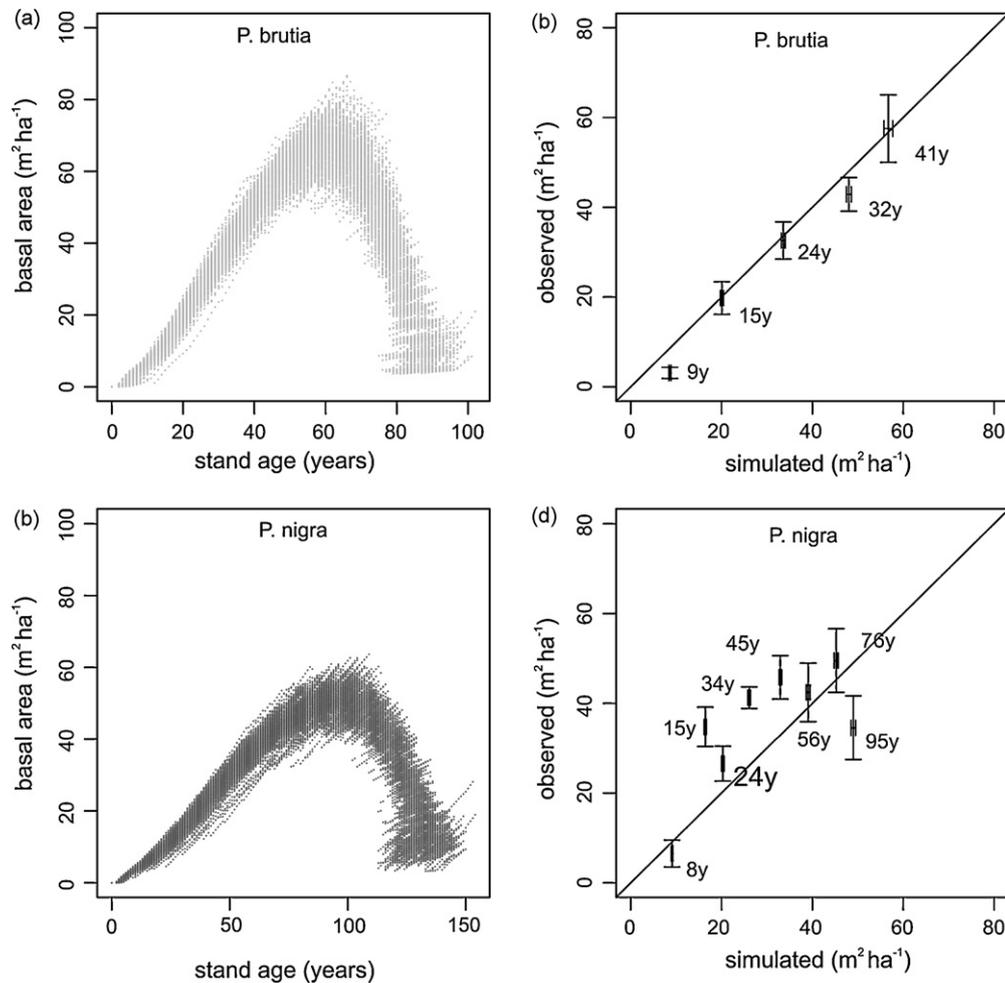
model presenting a very good behaviour against the observed data (Fig. 3b). At altitudes greater than 750 m a.s.l., *P. nigra* dominates the stands and illustrate a maximum basal area value at a stand age of 100 years (Fig. 3c). For these plots the model slightly underestimated the overall basal area for stand ages between 15 and 45 years (Fig. 3d). At mid-range altitudes (650 m a.s.l.) the model simulated a gradual dominance change from *P. brutia* to *P. nigra*. This vegetation shift is simulated to occur at a stand age of 70 years when *P. brutia* dominated canopy starts to decline (Fig. 4a) and more shade tolerant saplings of *P. nigra* start to grow (Fig. 4c). Simulation results were within both the observed species-specific (Fig. 4b and d) and total basal area values (Fig. 4f), and the identified change was mainly an effect of *P. nigra*'s relatively lower mortality threshold and higher shade tolerance. These simulations also agree with our field observation of higher *P. nigra* regeneration vigour under favorite mixed stands conditions, in the absence of fire (Fyllas et al., 2008). However for the mixed stands the overall model performance was the least informative when compared with the field observations.

Regeneration dynamics in study area on Lesbos are illustrated in Fig. 5. In all three forest types seedling densities were adequately simulated. As expected *P. brutia* seedlings density declines faster with increasing mean stand LAI compared with *P. nigra* in both monospecific (Fig. 5a and d) and mixed stands (Fig. 5b and c).

Simulations of stand development in terms of population density are provided in Supplementary Data B, for *A. cephalonica* (Fig. B.1), *P. brutia* (Fig. B.2) and *P. nigra* (Fig. B.3) dominated stands. The cyclic nature of patch dynamics introduced through the gap dynamics regeneration submodel, is indicated by the successive peaks in stems density. The frequency of regeneration peaks is controlled by the longevity of each species and spans from around 100 years for *P. brutia* to 200 for *A. cephalonica*. Furthermore, the size class distribution in specific time steps is also provided. All three species followed a similar distribution with a positive skew at the initial stages of stand development (time steps 30 and 40 for *A. cephalonica*, Fig. B.1), which gradually shifts to a negative skew (time step 100—*A. cephalonica* at maturity) and finally returns to a positive skew when mature trees start to die and light is available for recruitment of new individuals.

### 3.2. Climate change simulations

Simulation under a warmer climate showed no significant changes in the overall species abundance and process of stand



**Fig. 3.** Vegetation dynamics under baseline climate simulations for single dominance forest stands on Lesbos at 400 m a.s.l. (a) and 750 m a.s.l. (c). Stand age estimated from the age of the oldest individual in the plot. Comparisons between observed and simulated basal area ( $\pm$ standard error) at *P. brutia* dominated (400 m a.s.l.) (b) and *P. nigra* dominated (750 m a.s.l.) (d) stands. Values represent the mean stand age per decade from field measurements and 50 model iterations. Straight lines (in panels b and d) illustrate the perfect fit line of one to one correspondence. Note the very low variation in simulated basal area.

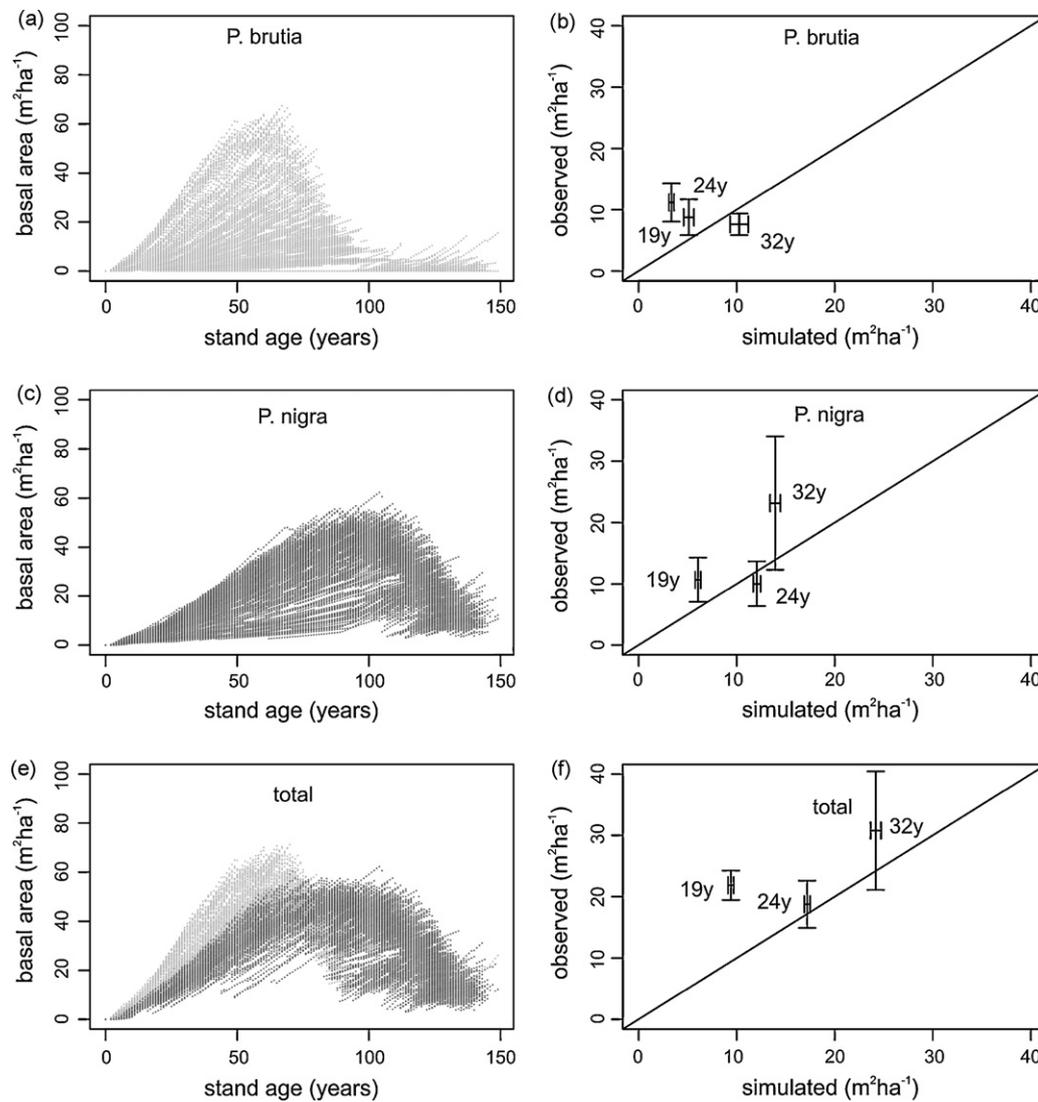
development, in both study sites. On Mt. Aenos, *A. cephalonica* illustrated a lower seedling density along a similar plot level LAI gradient (Fig. 6) under baseline and climate change scenarios. This was more or less expected as the endemic fir had the most sensitive germination curve derived from our lab experiments. Yet, according to our model parameterization, the presence of mature individuals seems to offer suitable conditions to ensure an adequate production and survival of seedlings able to retain a crucial recruitment rate that maintains the overall dynamics of these stands even under a warmer climate. At the drier and warmer Mediterranean climatic conditions of the altitudinal gradient on Lesbos, both stand development and seedling densities (Fig. 7) showed no significant shifts.

#### 4. Discussion

The integrated use of field measurements and theoretical vegetation dynamics models provides a powerful research framework towards better understanding ecosystem process and projecting their response to shifting environmental drivers. In this study, we presented a generalized simulation model, which could be relatively easily parameterized with species-specific data that are in general abundant in the ecological literature, at least for temperate and Mediterranean forests. The parameterization steps are of particular importance in the development of vegetation dynamics

simulators both at regional and global scales. Here we discuss the advantages and limitations of the approach followed in this study.

The dynamics of interacting plants at their early life stages are frequently considered important for the overall stand development and dynamics (Clark and Clark, 1992; Connell, 1989; Grubb, 1977). The gap dynamics theory has been extensively used both in conceptual and mechanistic models of vegetation dynamics (Smith and Huston, 1989). In simulation models it is usually implemented by assuming that under a gap with a specific size, species with different shade tolerance exhibit different establishment probabilities (Botkin, 1993; Shugart, 1984). However, common forest gap dynamics models usually make the assumption of a perfect height hierarchy in addition with horizontal homogeneity, i.e. they assume that within a gap all trees above a specific height (usually 1.3 m) contribute to the shading of smaller individuals. The above assumption sets an upper limit to the area that could be directly simulated ( $\leq$ gap size), and thus a number of iterations are usually employed in order to statistically scale up the results of gap models to larger areas (Bugmann et al., 2000; Ehman et al., 2002). At the same time this spatial homogeneity affects the species-specific germination success and seedling survival, by leading for example to an overestimation of canopy closure and thus could favor the establishment and maintenance of the more shade tolerant species (Bugmann, 2001). A 3D representation of the light environment could provide better light-availability gradients within the stand (Lexer and



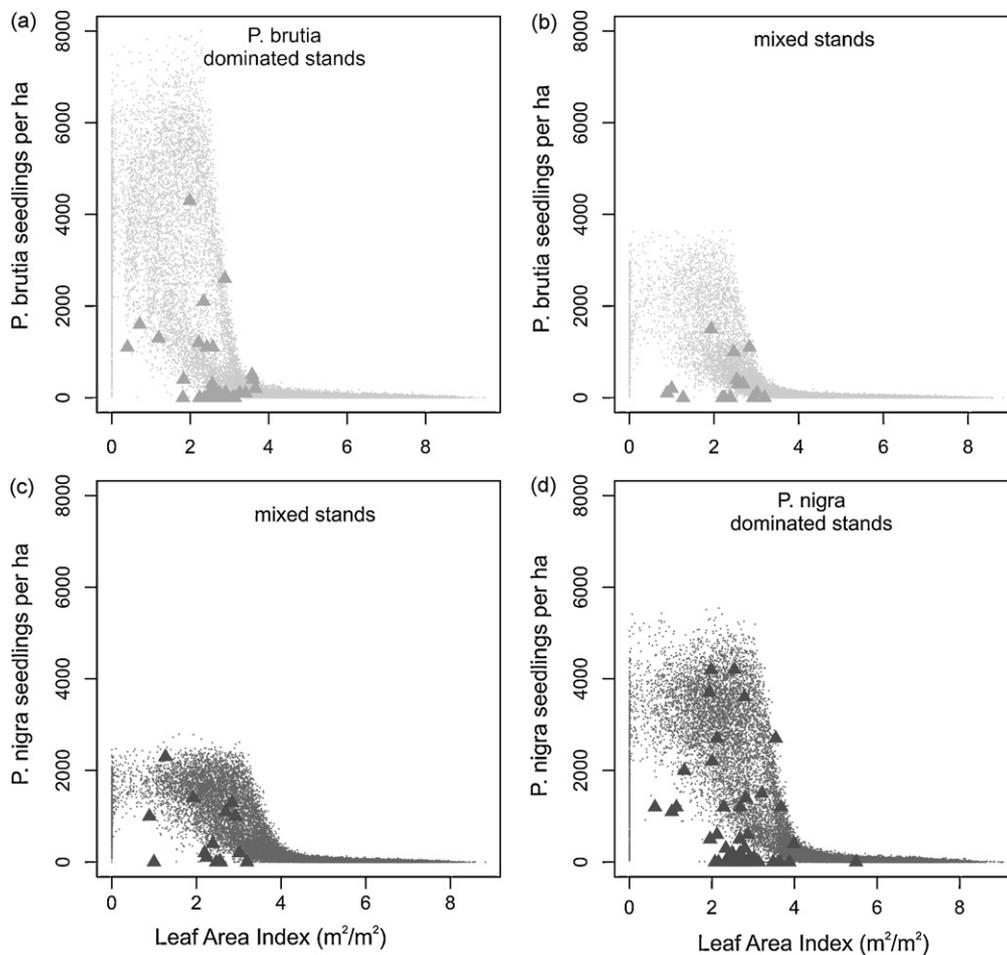
**Fig. 4.** Vegetation dynamics under baseline climate simulations for mixed forest stands on Lesbos at 650 m a.s.l., illustrating *P. brutia* (a), *P. nigra* (c) and total basal area (e). In panel e, different colours represent change in dominance from *P. brutia* (light grey) to *P. nigra* (dark grey) dominated stands. Comparisons between observed and simulated basal area ( $\pm$ standard error) for *P. brutia* (b) *P. nigra* (d) and total basal area (f) are shown. Values represent the mean stand age per decade from field measurements and 50 model iterations. Straight lines (in panel b, d and f) illustrate the perfect fit line of one to one correspondence. Note the very low variation in simulated basal area.

Hönninger, 2001; Weishampel and Urban, 1996; Williams, 1996); however it was not pursued here due to the increased computational cost. The two issues raised above have been dealt within our approach, by developing a nested spatial-explicit gap-regeneration algorithm. This algorithm runs for each new seedling within the plot and estimates a seedling-specific LAI based on its mature tree neighbours. Thus a potential high stand-level spatial heterogeneity, which is frequent in Mediterranean forests, could lead to an identification of several favorite microsites within the plot where seedlings could establish and grow up to the age of 10 when they are eventually treated as saplings. As a consequence, our model could be implemented in stands with a considerable larger size compared to the typical area of up to 0.1 ha used in gap models. It should be noted that this formulation of gap regeneration gave considerably better results in terms of seedlings density when compared against simulations using the common homogenous gap-level implementation, without substantially increasing the computational time.

Another common criticism of the representation of recruitment processes in gap dynamics models relates to the aggregation of discrete regeneration steps (such as seed production, dispersal and germination and early seedlings stages) into a single sapling

establishment step (Price et al., 2001). The discrete stages until successful sapling establishment could play an important role, especially under climate change conditions and/or enhanced disturbance regimes. In the current version of the model we paid special attention to two of those stages, namely seed germination as a function of chilling and early stages of seedlings development as controlled by light availability. The parameterization of the above steps was made using lab experiments (development of species-specific germination curves—Fig. A.1, Supplementary Data), and field data (recruitment density across light-availability gradients—Fig. A.2, Supplementary Data), respectively. Similar data and additional studies could relatively easily be designed in order to realistically parameterize other important recruitment steps and obtain a more mechanistic representation of this key ecosystem process.

The parameterization of the growth submodel was based on a tree-ring dataset obtained from individuals in the areas of study. Tree-rings have been extensively used to empirically parameterize individual-based models of vegetation dynamics (Liu and Ashton, 1995; Rickebusch et al., 2007). The limitation of this approach is that such a parameterization is in general considered to have only a



**Fig. 5.** Regeneration dynamics under baseline climate simulations for forest on Lesbos dominated by *P. brutia* at 400 m a.s.l. (a), mixed *P. brutia* (b) and *P. nigra* (c) stands at 650 m a.s.l. and *P. nigra* (d) stands at 750 m a.s.l. Light grey dots illustrate model outputs for *P. brutia* seedlings pool size, light grey triangles *P. brutia* seedlings density field observations, dark grey dots model outputs for *P. nigra* seedlings pool size and dark grey triangles *P. nigra* seedlings density observations. Leaf area index (LAI) was estimated through hemispherical pictures in the field (one sided), while model estimations of LAI were made through the permutation method described in the text. Model outputs from 50 iterations.

limited geographic scope, as it expresses the growing environment and the phenotypic diversity of local tree populations. Additionally such tree-rings analyses can illustrate growth patterns under only current climatic profiles and thus cannot be used to directly extrapolate shifts in growth under future changing climates. In this study we only cored well-developed, “isolated” individuals in order to exclude potential growth limitations due to light extinction by the canopy or belowground competitive interactions with other neighbouring trees. Furthermore, taking a population-level view on the “optimal growth”  $G_{max} = f(dbh)$  was parameterized using the whole species sample, thus regressing the maximum radial growth recorded against the *dbh* of the tree at that time (Fig. A.3). This implementation aims at avoiding the inclusion of non-optimal data points due to the unknown individual-level growth history of the trees in the  $G_{max}$  regression line, and should yield the potential radial growth curve of free growing trees (Canham et al., 2004).

Simulations in both sites illustrated a unimodal relationship between stand biomass (expressed as standing basal area) and age (Figs. 1 and 3). An initial period of forest growth is followed by a decline in productivity, a phenomenon extensively recorded and discussed in both field and modelling studies (Berger et al., 2004; Gower et al., 1996; Weiner and Thomas, 2001). Berger et al. (2004) showed that these stages of stand development can be predicted regardless of the growth curve type that individual trees follow, at least for constant, linearly increasing and non-linear growth rates. This was also the case in this study although the species of inter-

est illustrated discrete functional expressions of the growth rate vs. size relationship (Fig. A.3). The two pine species showed a monotonically declining growth rate with increasing size. *P. brutia* and *P. nigra* are considered relatively shade intolerant species and the nature of  $G_{max}$  relationship is similar to the one followed by the shade intolerant species in the study of Coates et al. (2009). The shape of pines growth rate curves remained the same when the log-normal function of Canham et al. (2004) was fitted to our data (Fyllas, unpublished data). On the other hand, *A. cephalonica* followed a sigmoid growth function, similar to shade tolerant species of Coates et al. (2009). Further exploring the nature of the potential growth rate curve among contrasting life strategy species could provide interesting theoretical and modelling insights.

Overall, the model performed well for monospecific tree stands (Figs. 1b and 3b and d), but had a poorer performance in mixed stands (Fig. 4b, d and f). This behaviour could arise as a result of not including a drought regulated performance of seedling at their initial life stages. Empirical drought indices have been important predictors of the overall establishment probability for both pines in the Lesbos study site (Fyllas et al., 2008), with *P. nigra* being more (negatively) affected by increase in drought conditions. Here, drought conditions have not been explicitly taken into account due to data availability issues. However, experimental studies aiming to derive seedlings drought performance curves are relative straightforward and should be included in future versions of the simulator.

Experimental studies on seed germination of dwarf shrubs and/or annual herbaceous species from alpine and arctic environments have not reached to a single conclusion in respect to the effect of either interruption or decrease of winter cold stratification period, showing thus the variability of species response. Graae et al. (2008) found no difference in germination percentage between seeds of *Empetrum hermafroditum* L. and *Vaccinium uliginosum* (both dwarf shrubs) stratified at 0.5°C in incubators and seeds experiencing colder temperatures outdoors at boreal (−0.5 to −2°C) and arctic sites. Similarly, Baskin et al. (2002) could not detect any difference between full- and half-snow-cover treatments on the germination of *E. hermafroditum*. However, it was found that colder winter temperatures delayed the germination in ten species and decreased the germination percentage in other four. Results from Baskin et al. (2004), suggest that the interruption of winter cold stratification period for seeds of annual weeds from high northern latitudes is not constant. Seeds showed either no response or they were not completely induced into dormancy. Milbau et al. (2009) demonstrated that the projected reductions in snow depth and duration in sub-arctic and alpine regions may have important implications for seed germination, both by affecting the number of germination seeds and the timing of germination.

Although Mediterranean climate is thought to prevail over the Mediterranean region, not all areas are governed by extended dry-hot summers and mildly cold rainy winters (Nahal, 1981). Plants growing at altitudes higher than 800 m are definitely facing low winter temperatures, while snow and frost are quite frequent. It is well established that even seeds of warm climate may require cold stratification when they are becoming old in order to break their

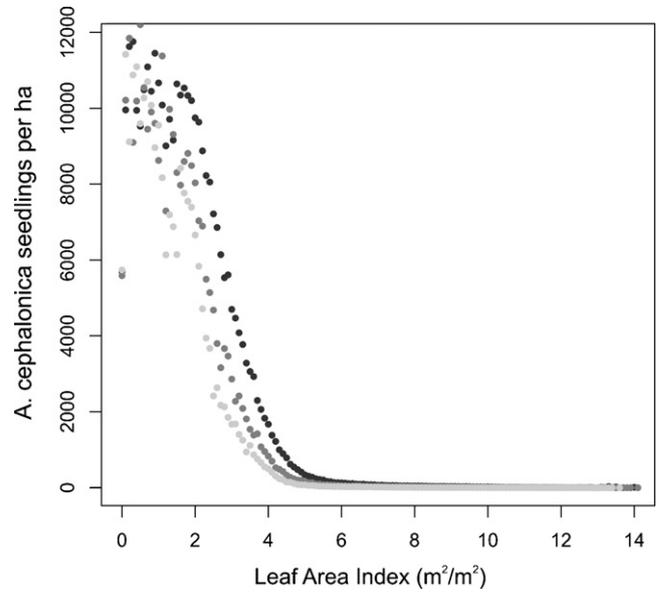


Fig. 6. Regeneration dynamics under baseline and climate change simulations for forest stands on Cephalonia at 950 m a.s.l. Black dots indicate mean values under baseline climatic conditions while dark grey and light grey indicate seedling densities under a B2 and an A1 warming scenario, respectively.

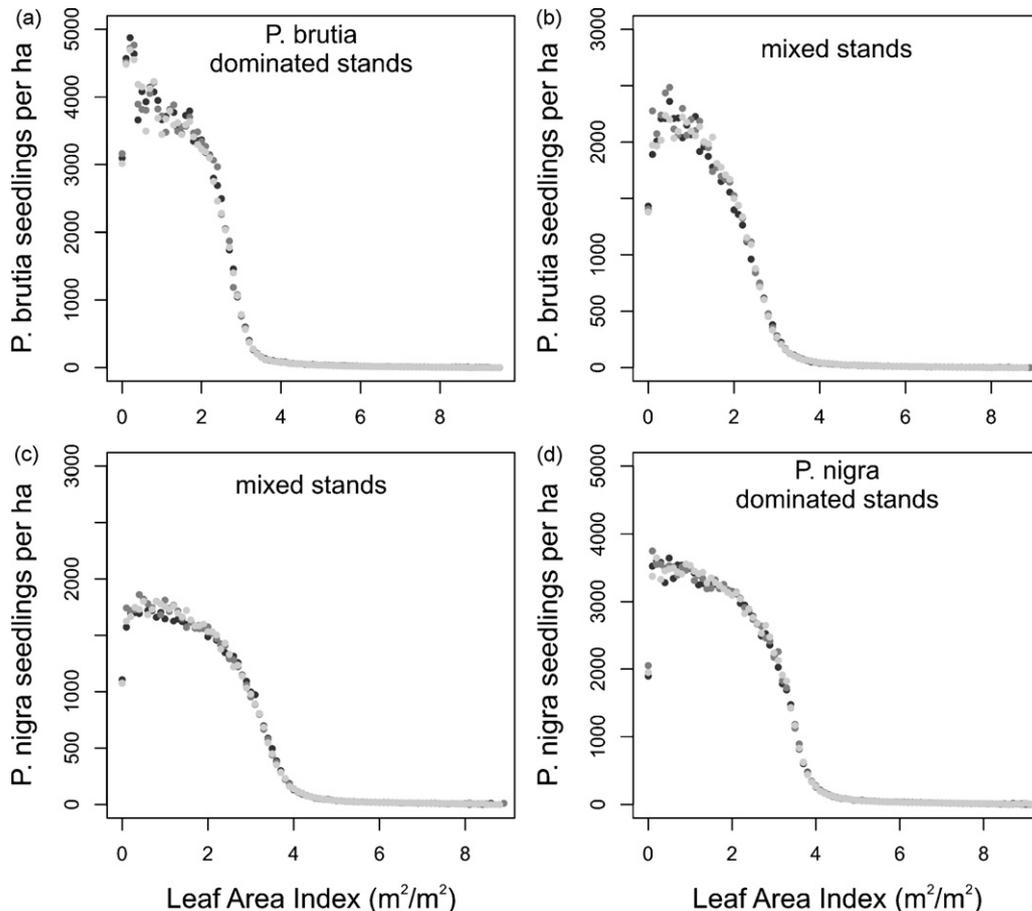


Fig. 7. Regeneration dynamics under baseline and climate change simulations for forest stands on Lesbos. Seedlings density in *P. brutia* stands at 400 m a.s.l. (a), in mixed *P. brutia*–*P. nigra* stands at 650 m a.s.l. (b and c, respectively) and in *P. nigra* stands at 750 m a.s.l. (d). Black dots indicate mean values under baseline climatic conditions while dark grey and light grey indicate seedling densities under a B2 and an A1 warming scenario, respectively.

dormancy (Baskin and Baskin, 1998). Many Mediterranean plant species require cold stratification for seed germination (Skordilis and Thanos, 1995; Gimenez-Benavides et al., 2005), providing some similarities in the mechanisms of seed germination between Mediterranean and temperate and/or arctic-alpine environments. The potential effects of climate change on species regeneration in this study were explored through shifts in the chilling period available for seed germination. Simulations here showed no significant effects in the overall stand dynamics under the two climatic scenarios. In particular, for the fir stands, although a decrease in the seedlings density was projected (Fig. 5), the overall dynamics expressed in terms of achieved basal area and size class distribution, did not change. Changes in simulated seedlings recruitment densities are even less identifiable in the case of the Mediterranean pine forests (Fig. 6). Based on the developed germination curves, an explanation for such results could lie in the ability of Mediterranean taxa for adequate seed germination at low chilling duration (above 20% for both pine species at no chilling). On the other hand, more temperate tree species, *A. cephalonica* in our case, seem to require a distinguishable cold period for effective seed germination, with a decrease of the germination coefficient near to 0 for no chilling (Fig. A.1). It should be noted though, that these simulations could underestimate the potential effects of climate change over regeneration dynamics, as important processes, such as seed dispersal and drought, are not explicitly taken into account.

## 5. Conclusions

Overall, the model developed was capable of adequately simulating the forest dynamics in the two study areas under current climatic conditions. Following scenarios of climate change, simulations of regeneration and overall stand dynamics did not show significant shifts, when solely light availability and chilling were considered. Additional experimental and field data are required to further constrain other important recruitment steps. For example, data on regeneration sensitivity to drought could be used to develop seedlings mortality curves along drought gradients (Engelbrecht et al., 2005), while the inclusion of seed dispersal kernels would provide a more mechanistic representation of the seedling distribution patterns along the landscape (Nathan and Muller-Landau, 2000). A well-informed parameterization of the regeneration submodels used in forest dynamics simulators could increase our ability to project the impacts of combined shifts in the main climate drivers controlling these ecosystems.

## Acknowledgments

We would like to thank Dr. Ted Feldpausch for his suggestions and comments on an earlier version of the manuscript and Prof. K. Kalabokidis for providing the climate record for Lesbos. Comments from two anonymous referees greatly improved this study.

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2010.03.003.

## References

- Arianoutsou, M., 2004. Predicting the post fire regeneration and resilience of Mediterranean plant communities. In: Arianoutsou, M., Papanastasis, V.P. (Eds.), Ecology, Conservation and Management of Mediterranean Climate Ecosystems. Millpress, Rotterdam, electronic edition.
- Arianoutsou, M., Christopoulou, A., Ganou, E., Kokkoris, I., Kazanis, D., 2009. Post-fire Response of the Greek Endemic *Abies cephalonica* Forests in Greece: An Example of a Natura 2000 Site in Mt Parnitha National Park. ECCB, Prague.
- Baskin, C.C., Baskin, J.M., 1998. Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination. Academic Press, San Diego, CA.
- Baskin, C.C., Milberg, P., Anderson, L., Baskin, J.M., 2004. Germination ecology of seeds of the annual weeds *Capsella bursa-pastoris* and *Descurainia sophia* from high latitudes. Weeds Res. 44, 60–88.
- Baskin, C.C., Zackrisson, O., Baskin, J.M., 2002. Role of warm stratification in promoting germination of seeds of *Empetrum hermaphroditum* (Empetraceae), a circumboreal species with a stone endocarp. Am. J. Bot. 89, 486–493.
- Berger, U., Hildenbrandt, H., 2000. A new approach to spatially explicit modelling of forest dynamics: spacing, ageing and neighbourhood competition of mangrove trees. Ecol. Model. 132, 287–302.
- Berger, U., Hildenbrandt, H., Grimm, V., 2004. Age-related decline in forest production: modelling the effects of growth limitation, neighbourhood competition and self-thinning. Ecology 92, 846–853.
- Berger, U., Piou, C., Schiffers, K., Grimm, V., 2008. Competition among plants: concepts, individual-based modelling approaches, and a proposal for a future research strategy. Perspect. Plant Ecol. 9, 121–135.
- Botkin, D.B., Janak, J.F., Wallis, J.R., 1972. Some ecological consequences of a computer model of forest growth. J. Ecol. 60, 849–872.
- Botkin, D.B., 1993. Forest Dynamics: An Ecological Model. Oxford University Press, New York, USA, 309 p.
- Brown, P., Wu, R., 2005. Climate and disturbance forcing of episodic tree recruitment in a southwestern ponderosa pine landscape. Ecology 86, 3030–3038.
- Bugmann, H.K.M., 1996. A simplified forest model to study species composition along climate gradients. Ecology 77, 2055–2074.
- Bugmann, H., 2001. A review of forest gap models. Climatic Change 51, 259–305.
- Bugmann, H., Lindner, M., Lasch, P., Flechsig, M., Ebert, B., Cramer, W., 2000. Scaling issues in forest succession modelling. Climatic Change 44, 265–289.
- Burton, P.J., Cumming, S.G., 1995. Potential effects of climatic change on some western Canadian forests, based on phenological enhancements to a patch model of forest succession. Water Air Soil Pollut. 82, 401–414.
- Canham, C.D., LePage, P.T., Coates, K.D., 2004. A neighborhood analysis of canopy tree competition: effects of shading versus crowding. Can. J. Forest Res. 34, 778–787.
- Catovsky, S., Bazzaz, F.A., 2000. The role of resource interactions and seedling regeneration in maintaining a positive feedback in hemlock stands. J. Ecol. 88, 100–112.
- Clark, D.A., Clark, D.B., 1992. Life history diversity of canopy and emergent trees in a neotropical rain forest. Ecol. Monogr. 62, 315–344.
- Coates, K.D., 2002. Tree recruitment in gaps of various size, clearcuts and undisturbed mixed forest of interior British Columbia, Canada. Forest Ecol. Manage. 155, 387–398.
- Coates, K.D., Canham, C.D., LePage, P.T., 2009. Above- versus below-ground competitive effects and responses of a guild of temperate tree species. J. Ecol. 97, 118–130.
- Connell, J.H., 1989. Some processes affecting the species composition in forest gaps. Ecology 70, 560–562.
- Ehman, J.L., Fan, W., Randolph, J.C., Southworth, J., Welch, N.T., 2002. An integrated GIS and modeling approach for assessing the transient response of forests of the southern Great Lakes region to a doubled CO<sub>2</sub> climate. Forest Ecol. Manage. 155, 237–255.
- Engelbrecht, B.M.J., Kursar, T.A., Tyree, M.T., 2005. Drought effects on seedling survival in a tropical moist forest. Trees—Struct. Funct. 19, 312–321.
- Figuerola, J., 2003. Seed germination in temperate rain forest species of southern Chile: chilling and gap-dependency germination. Plant Ecol. 166, 227–240.
- Frich, P., Alexander, L.V., Della-Marta, P., Gleason, B., Haylock, M., Klein Tank, A.M., Peterson, T., 2002. Observed coherent changes in climatic extremes during the second half of the twentieth century. Climate Res. 19, 193–212.
- Fyllas, N.M., Phillips, O.L., Kunin, W.E., Matsinos, Y.G., Troumbis, A.Y., 2007. Development and parameterization of a general forest gap dynamics simulator for the North-eastern Mediterranean Basin (GREek Forest Species). Ecol. Model. 204, 439–456.
- Fyllas, N.M., Dimitrakopoulos, P.G., Troumbis, A.Y., 2008. Regeneration dynamics of a mixed Mediterranean pine forest in the absence of fire. Forest Ecol. Manage. 256, 1552–1559.
- Fyllas, N.M., Troumbis, A.Y., 2009. Simulating vegetation shifts in north-eastern Mediterranean mountain forests under climatic change scenarios. Global Ecol. Biogeogr. 18, 64–77.
- Gimenez-Benavides, L., Escudero, A., Perez-Garcia, F., 2005. Seed germination of high mountain Mediterranean species: altitudinal, interpopulation and interannual variability. Ecol. Res. 20, 433–444.
- Good, N.F., Good, R.E., 1972. Population dynamics of tree seedlings and saplings in a mature eastern hardwood forest. B. Torrey Bot. Club 1972, 172–178.
- Gower, S.T., McMurtrie, R.E., Murty, D., 1996. Aboveground net primary production decline with stand age: potential causes. Trends Ecol. Evol. 11, 378–382.
- Graae, N.J., Alsos, I.G., Ejrnaes, R., 2008. The impact of temperature regimes on development, dormancy breaking and germination of dwarf shrubs from arctic, alpine, and boreal sites. Plant Ecol. 198, 275–284.
- Grime, J.P., Mason, G., Curtis, A.V., Rodman, J., Band, S.R., 1981. A comparative study of germination characteristics in a local flora. J. Ecol. 69, 1017–1059.
- Grove, A.T., Rackham, O., 2001. The Nature of Mediterranean Europe. An Ecological History. Yale University Press, New Haven/London.
- Goubanova, K., Li, L., 2007. Extremes in temperature and precipitation around the Mediterranean basin in an ensemble of future climate scenario simulations. Global Planet. Change 57, 27–42.
- Grubb, P.J., 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biol. Rev. 52, 107–145.
- Kobe, R.K., Pacala, S.W., Silander, J.A., Canham, C.D., 1995. Juvenile tree survivorship as a component of shade tolerance. Ecol. Appl. 5, 517–532.

- Lexer, M.J., Hönninger, K., 2001. A modified 3D-patch model for spatially explicit simulation of vegetation composition in heterogeneous landscapes. *Forest Ecol. Manage.* 144, 43–65.
- Liu, J., Ashton, P.S., 1995. Individual-based simulation models for forest succession and management. *Forest Ecol. Manage.* 73, 157–175.
- Luna, B., Pérez, B., Céspedes, B., Moreno, J.M., 2008. Effect of cold exposure on seed germination of 58 plant species comprising several functional groups from a mid-mountain Mediterranean area. *Ecoscience* 15, 478–484.
- van der Meer, P.J., Jorritsma, I.T.M., Kramer, K., 2002. Assessing climate change effects on long-term forest development: adjusting growth, phenology and seed production in a gap model. *Forest Ecol. Manage.* 162, 39–52.
- Milbau, A., Graae, B.J., Shevtsova, A., Nijs, I., 2009. Effects of a warmer climate on seed germination in the subarctic. *Ann. Bot.* 104, 287–296.
- Mitchell, T.D., Carter, T.R., Jones, P.D., Hulme, M., New, M., 2004. A comprehensive set of high-resolution grids of monthly climate for Europe and the globe: the observed records (1901–2000) and 16 scenarios (2001–2100). Tyndall Centre Working Paper 55. Tyndall Centre, Norwich, UK.
- Monsi, M., Saeki, T., 2005. On the factor light in plant communities and its importance for matter production. *Ann. Bot.* 95, 549–567.
- Mouillot, F., Rambal, S., Joffre, R., 2002. Simulating climate change impacts on fire frequency and vegetation dynamics in a Mediterranean-type ecosystem. *Global Change Biol.* 8, 423–437.
- Nahal, 1981. The Mediterranean climate from a biological point of view. *Ecosystems of the world*. In: di Castri, F., Goodall, D.W., Specht, R.L. (Eds.), *Mediterranean Type Shrublands*, vol. 11. Elsevier, pp. 63–86.
- Nathan, R., Muller-Landau, H.C., 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends Ecol. Evol.* 15, 278–285.
- Nitschke, C.R., Innes, J.L., 2008. A tree and climate assessment tool for modelling ecosystem response to climate change. *Ecol. Model.* 210, 263–277.
- Ordoñez, J.L., Retana, J., Espelta, J.M., 2005. Effects of tree size, crown damage, and tree location on post-fire survival and cone production of *Pinus nigra* trees. *Forest Ecol. Manage.* 206, 109–117.
- Pausas, J.G., 1999. Response of plant functional types to changes in the fire regime in Mediterranean ecosystems: a simulation approach. *J. Veg. Sci.* 10, 717–722.
- Peñuelas, J., Boada, M., 2003. A global change-induced biome shift in the Montseny mountains (NE Spain). *Global Change Biol.* 9, 131–140.
- Politi, P.I., Arianoutsou, M., Georghiou, K., 2007. Aspects of the reproductive biology of the Greek fir (*Abies cephalonica* Loud.) in the Mt. Aenos National Park. In: Rokich, D., Wardell-Johnson, G., Yates, C., Stevens, J., Dixon, K., McLellan, R., Moss, G. (Eds.), *Proceedings of the MEDECOS XI 2007 Conference*, Perth, Australia. Kings Park and Botanic Garden, Perth, Australia, pp. 191–192.
- Politi, P.I., Arianoutsou, M., Stamou, G.P., 2009. Patterns of *Abies cephalonica* seedling recruitment in Mount Aenos National Park, Cephalonia, Greece. *Forest Ecol. Manage.* 258, 1120–1136.
- Price, D., Zimmermann, N., van der Meer, P., Lexer, M., Leadley, P., Jorritsma, I., Schaber, J., Clark, D., Lasch, P., McNulty, S., Wu, J., Smith, B., 2001. Regeneration in gap models: priority issues for studying forest responses to climate change. *Climatic Change* 51, 475–508.
- R Development Core Team, 2008. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0, URL <http://www.R-project.org>.
- Rickebusch, S., Lischke, H., Bugmann, H., Guisan, A., Zimmermann, N.E., 2007. Understanding the low-temperature limitations to forest growth through calibration of a forest dynamics model with tree-ring data. *Forest Ecol. Manage.* 246, 251–263.
- Sala, O., Chapin Stuart, F., Armesto, J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L., Jackson, R., Kinzig, A., Leemans, R., Lodge, D., Mooney, H.A., Oesterheld, M., Poff, N., Sykes, M., Walker, B., Walker, M., Wall, D., 2000. Global biodiversity scenarios for the year 2100. *Science* 287, 1770–1774.
- Sánchez-Gómez, D., Valladares, F., Zavala, M.A., 2006. Performance of seedlings of Mediterranean woody species under experimental gradients of irradiance and water availability: trade-offs and evidence for niche differentiation. *New Phytol.* 170, 795–806.
- Shugart, H.H., 1984. *A Theory of Forest Dynamics: The Ecological Implications of Forest Succession Models*. Springer-Verlag, New York, NY, USA.
- Skordilis, A., Thanos, C.A., 1995. Seed stratification and germination strategy in the Mediterranean pines *Pinus brutia* and *P. halepensis*. *Seed Sci. Res.* 5, 151–160.
- Skordilis, A., Thanos, C.A., 1997. Comparative ecophysiology of seed germination strategies in the seven pine species naturally growing in Greece. In: Ellis, R.H., Black, M., Murdoch, A.J., Hong, T.D. (Eds.), *Basic and Applied Aspects of Seed Biology*. Kluwer Academic Publishers, Dordrecht, pp. 623–632.
- Smith, T., Huston, M., 1989. A theory of the spatial and temporal dynamics of plant communities. *Plant Ecol.* 83, 49–69.
- Thanos, C.A., Skordilis, A., 1987. The effects of light, temperature and osmotic stress on the germination of *Pinus halepensis* and *P. brutia* seeds. *Seed Sci. Technol.* 15, 163–174.
- Venable, D.L., Lawlor, L., 1980. Delayed germination and dispersal in desert annuals: escape in space and time. *Oecologia* 46, 272–282.
- Weiner, J., Thomas, S.C., 2001. The nature of tree growth and the “age-related decline in forest productivity”. *Oikos* 94, 374–376.
- Weishampel, J.F., Urban, D.L., 1996. Coupling a spatially-explicit forest gap model with a 3-D solar routine to simulate latitudinal effects. *Ecol. Model.* 86, 101–111.
- Williams, M., 1996. A three-dimensional model of forest development and competition. *Ecol. Model.* 89, 73–98.