

Adaptation of a modelling strategy to predict the NPP of even-aged forest stands

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Received: 21 April 2011 / Revised: 14 October 2011 / Accepted: 2 November 2011 / Published online: 21 December 2011
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Abstract The assessment of net forest production is important for both scientific and practical purposes. The current paper presents the application of a recently developed strategy to estimate the net primary productivity of an even-aged Mediterranean pine forest (Natural Park of San Rossore, Central Italy). The strategy is based on the use of two models, C-Fix and BIOME-BGC, whose outputs are combined with forest volume data in order to describe the actual status of the ecosystems examined. The accuracy of the simulation is tested against measurements of current annual increment (CAI) derived from a recent forest inventory of the Park. The results of this test indicate that the methodology must be modified to account for the even-aged nature of the study stands. The modification is performed by the analysis of dendrochronological and tree density data, which characterize the temporal volume and CAI evolution of representative forest stands. The modified methodology is capable of taking into account the effect of stand ageing and yielding nearly unbiased estimates of forest CAI.

Keywords Even-aged forest · NPP modelling · C-Fix · BIOME-BGC · Dendrochronology

Introduction

Forest ecosystems cover about one-third of the Earth's ice-free land surface and represent a fundamental natural and economic resource and a significant part of the global carbon stock (FAO 2005). The assessment of forest ecosystem production is therefore a central issue in applied ecology and is becoming increasingly important for evaluating the role of forests as possible carbon sink. Net primary production (NPP), which represents the rate at which biomass is accumulated in the ecosystems, is one of the main parameters used to characterize forest carbon sink (Chapin et al. 2006; Waring and Running 2007).

Commonly, forest NPP is evaluated through user-driven national or regional inventories (Rodeghiero et al. 2010). More precisely, current annual increment (CAI) data collected during these inventories are converted into estimates of dry matter or carbon NPP through the use of species-specific biomass expansion factors (BEFs) (Federici et al. 2008). Conventional procedures used for CAI estimation, however, are much more complex, expensive and prone to possible data sampling and elaboration errors than those applied for assessing more basic forest attributes (tree density and height, basal area, stem volume, etc.) (Federici et al. 2008; Chirici et al. 2007; Miehle et al. 2010).

An alternative method which has been recently developed by our research group is based on the combination of the outputs from a parametric, remote-sensing-driven model (C-Fix), and a model of ecosystem processes (BIOME-BGC). All main issues implied in the use of these models for forest production assessment have been extensively treated in a number of investigations (Chiesi et al. 2007, 2011; Maselli et al. 2006, 2009a, 2010). These studies have shown that the conversion of forest gross primary production (GPP) into NPP is a non-trivial process

Communicated by R. Matyssek.

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which requires the consideration of the different compartments which are actually present in each ecosystem. Forest woody NPP derived from tree-growth increments, in fact, is completely based on the accumulation of tree wood biomass, which is obviously limited where tree density is low and other ecosystem components (grasses, shrubs) are prevalent. This phenomenon can cause a substantial uncoupling between ecosystem GPP (which includes non-tree components) and wood NPP (which is mostly determined by standing trees) (Maselli et al. 2009a). This uncoupling can be further complicated by the influence of variable tree ageing and stand development phases on ecosystem respiration and allocation patterns. Such complications are quite common in most areas of the globe, where several forms of human-induced disturbances (deforestation and forestation processes, tree loggings and thinnings, wildfires, etc.) concur to limit the natural growth of tree biomass (Thornton et al. 2002).

The method proposed by Maselli et al. (2009a) addresses this issue by introducing the concept of ecosystem distance from equilibrium condition (*sensu* Odum (1971)) to characterize the actual status of forests depending on the occurred disturbances. The equilibrium condition is simulated by the use of BIOME-BGC and is then converted into the condition of real ecosystems through the use of a proxy variable given by the ratio of real over potential tree volumes. The approach is based on the assumption that the examined ecosystems are composed of a mixture of trees in heterogeneous development stages which mimics the structure and functions of forests under quasi-equilibrium condition. The application of the strategy to even-aged forests may therefore present additional problems. The current work investigates this issue concerning a protected pine wood area in Central Italy (Natural Park of San Rossore), where intensive measurement campaigns have been carried out in the last few years. The study ultimately aims at adapting the original modelling strategy to simulate the NPP of even-aged forest stands using commonly available data.

The paper is organized as follows. First, the original modelling strategy to estimate forest CAI is briefly introduced. The main features of the San Rossore test site are then described together with the data utilized. Next, the application of the strategy and the results obtained are presented. In particular, the possible causes of inaccurate CAI estimation are investigated by the analysis of dendrochronological measurements and tree density information. This enables the development of a methodological modification capable of accounting for the effect of even-aged forest management. The paper is concluded by “Discussion” and “Conclusion” sections which highlight the potential and limits of the methodology applied for forest NPP assessment on various spatial and temporal scales.

CAI modelling strategy

The current strategy to model forest NPP and CAI has been presented and tested in a number of publications, to which the reader can refer for specific details. The strategy is schematized in the upper part of Fig. 1 and will be concisely described in the following sections. Its first steps consist in applying the parametric model C-Fix to produce forest GPP estimates which are used to both calibrate and stabilize the outputs of the bio-geochemical model BIOME-BGC (Maselli et al. 2009a).

C-Fix estimates forest GPP as function of photosynthetically active radiation (PAR) absorbed by vegetation (Veroustraete et al. 2002). More specifically, annual GPP ($\text{g C m}^{-2} \text{ year}^{-1}$) can be computed by the general equation:

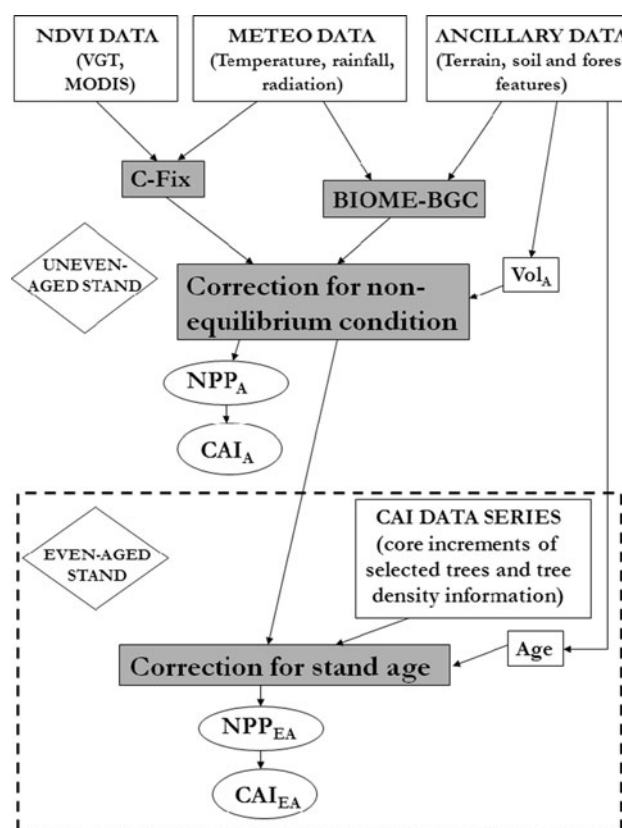


Fig. 1 Scheme of the CAI modelling approach applied. The upper part (uneven-aged stand diamond) represents the original methodology proposed by Maselli et al. (2009a). The GPP and respiration estimates of two models, C-Fix and BIOME-BGC, are combined with normalized volume to take into account ecosystem departure from equilibrium condition. In this way, the actual NPP of uneven-aged stands can be simulated (NPP_A), which is convertible into relevant CAI (CAI_A) by the use of BEFs. The dotted box (even-aged stand diamond) contains the modification which is currently added to account for the effect of stand ageing. The GPP and respiration estimates of the two models are combined considering also age-dependent variations in the ratios between leaf and stem carbon pools. In this way, the NPP and CAI of even-aged stands can be simulated (NPP_{EA} and CAI_{EA} , respectively)

$$\text{GPP} = \varepsilon \sum_{i=1}^{12} T_{\text{cor}_i} \text{FAPAR}_i \text{Rad}_i \quad (1)$$

where ε is the maximum radiation use efficiency (set equal to 1.2 g C MJ^{-1} APAR, according to Chiesi et al. 2011), T_{cor} is a factor accounting for the dependence of photosynthesis on air temperature T_i , FAPAR is the Fraction of Absorbed Photosynthetically Active Radiation, and Rad is the solar incident PAR, all referred to month i . FAPAR can be estimated as a function of top of canopy normalized difference vegetation index (NDVI) according to the expression proposed by Myneni and Williams (1994).

Maselli et al. (2009b) have recently proposed a modification of C-Fix aimed at improving its performance in Mediterranean areas, which are characterized by a long summer dry season during which vegetation growth is limited by water availability. This was done by introducing a water stress index which limits photosynthesis in case of short-term water stress.

BIOME-BGC is a bio-geochemical model which estimates the storage and fluxes of water, carbon and nitrogen within terrestrial ecosystems (Running and Hunt 1993; White et al. 2000). It requires daily climate data, information on the general environment (i.e. soil, vegetation and site conditions) and parameters describing the ecophysiological characteristics of vegetation. The model works by finding a quasi-equilibrium with local eco-climatic conditions through the spin-up phase, whose aim is to quantify the initial amount of all carbon and nitrogen pools. After this phase, BIOME-BGC simulates all respiration and allocation processes corresponding to the requested simulation years (White et al. 2000; Churkina et al. 2003).

BIOME-BGC is not a growth model, as it does not explicitly take into account age and age structure within a forest (Tatarinov and Cienciala 2006). In particular, the model uses the so-called big leaf approach, which means that vegetation canopy is treated as a unique transpiring and photosynthesizing entity that is characterized by its leaf area index (LAI) (Running and Hunt 1993). LAI is considered to be linearly related to the simulated leaf carbon, which in turn is nearly proportional to the existing stem carbon. This implies the existence of an approximately constant ratio between the model estimates of stem volume and LAI, which is typical for each biome type at quasi-equilibrium condition.

BIOME-BGC modelling of this condition has also important consequences on the simulated carbon budget: the sum of all simulated respirations becomes in fact nearly equivalent to GPP, which makes annual NPP approach heterotrophic respiration (Rhet) and net ecosystem exchange (NEE) tend to zero. Moreover, such modelling renders the obtained GPP estimates similar to those produced by C-Fix,

which are descriptive of all ecosystem components (Maselli et al. 2009a). This functional equivalence renders the outputs from the two models combinable by multiplying BIOME-BGC respiration estimates for a ratio between C-Fix and BIOME-BGC GPP (Maselli et al. 2008).

The combination of the outputs from the two models enables to estimate forest carbon fluxes descriptive of a full tree density, quasi-equilibrium situation. This situation, however, does not correspond to that of most European forests, where stand biomass is kept well below potential levels due to the occurred disturbances. The final step of the modelling strategy corrects the carbon flux estimates obtained by using the ratio between actual and potential tree volumes (NV_A) as an indicator of ecosystem proximity to equilibrium (Maselli et al. 2009a). According to this theory, actual forest NPP (NPP_A , $\text{g C m}^{-2} \text{ year}^{-1}$) can be approximated as:

$$NPP_A = \text{GPP} * FC_A - Rgr * FC_A - Rmn * NV_A \quad (2)$$

where GPP, Rgr and Rmn correspond to the GPP, growth and maintenance respirations estimated by BIOME-BGC ($\text{g C m}^{-2} \text{ year}^{-1}$), and the two dimensionless terms FC_A (actual forest cover) and NV_A (actual normalized standing volume) are derived from tree volume estimates. More specifically, NV_A is computed as the ratio between actual (measured) standing volume and potential tree volume simulated by BIOME-BGC. Actual LAI, (LAI_A), is then calculated assuming a constant stem C/leaf C ratio:

$$LAI_A = NV_A * LAI_{\text{MAX}} \quad (3)$$

where LAI_{MAX} is again predicted by BIOME-BGC. Finally, FC_A is estimated through Beer's law as:

$$FC_A = 1 - \exp(-LAI_A) \quad (4)$$

From NPP_A , actual CAI, CAI_A ($\text{m}^3 \text{ ha}^{-1} \text{ year}^{-1}$) can be computed through the formula (Maselli et al. 2010):

$$CAI_A = NPP_A * \text{SCA}/\text{BEF}/\text{BWD} * 2 * 100 \quad (5)$$

where SCA is the stem C allocation ratio, BEF is the biomass expansion factor corresponding to the volume of above ground biomass/standing volume (both dimensionless), and BWD is the basic wood density (Mg m^{-3}). The SCA of pine forest is taken from BIOME-BGC default value (White et al. 2000), while BEF and BWD are taken from Federici et al. (2008). The multiplication by 2 accounts for the transformation from carbon to dry matter and that by 100 for the change in magnitude from g m^{-2} to Mg ha^{-1} .

Study area

The test pine forest (43.73° N , 10.28° E) is placed within the Natural Park of San Rossore (Pisa, Italy) (Fig. 2). This

is a protected area bounded by the Tyrrhenian Sea on the West and by the Arno and Serchio rivers on the South and North, respectively. The climate is Mediterranean sub-humid; the average annual temperature is 14.8°C, and the average rainfall is 900 mm (Rapetti and Vittorini 1995). The annual rainfall minimum coincides with the temperature summer maximum, usually originating a water stress period of about 2 months. The soils of the area are prevalently sandy and are vulnerable to the infiltration of saline water particularly during the dry period (D.R.E.Am. 2003).

The coastal area is mostly covered by a large and homogeneous forest dominated by two Mediterranean pine species, that is *Pinus pinaster* Ait. and *Pinus pinea* L. (Chiesi et al. 2005). All pine stands are even-aged, and most of them are relatively old (mean age greater than 70 years).

Study data

San Rossore forest inventory (SRFI)

The reference information to test the described methodology is derived from the San Rossore forest inventory (SRFI) which was recently carried out in the Park. During

SRFI, a series of parameters were measured and elaborated for all stands of the Park; the sampling and measurement procedures applied are fully described in a technical report produced by D.R.E.Am. (2003). Regarding *P. pinea*, which covers about 1,115 ha, two sampling methods were applied. Part of the stands were characterized by examining 170 circular sampling plots (20 m radius). From one to four plots were selected for each stand following structural criteria and considering the foreseen thinning and cutting operations. Within each plot, diameter at breast height (DBH) was measured for all trees having DBH greater than 1.5 cm, together with height for some sample trees. In the remaining stands, which mainly corresponded to the oldest and less uniform forest areas, all pine trees were callipered using a minimum DBH of 10 cm. Tree height was then estimated using locally tuned allometric models. Regarding *P. pinaster*, which extends over 320 ha, only circular plots were sampled. No additional detail is provided on the sampling and processing methods applied for CAI assessment.

The information collected was organized within a geodatabase, which reports the main features of all forest stands (species, age, volume, CAI, etc.). This information has an intrinsic uncertainty due to the data measurement and elaboration protocols applied (D.R.E.Am. 2003). In particular, stand ages are aggregated for classes of 10 years up to

Fig. 2 Spot-VGT NDVI image of August 2003, with indication of the San Rossore study area. The Park extends over about 12 km North–South and 8 km East–West. The land cover map in the enlarged rectangle is taken from D.R.E.Am. (2003)

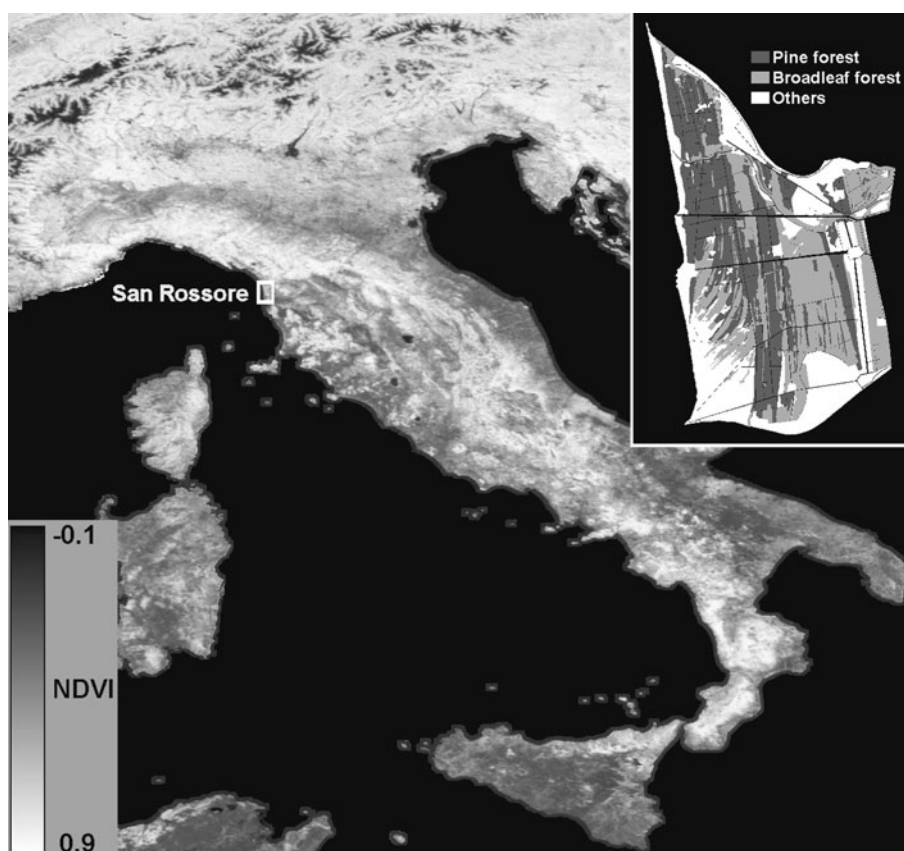


Table 1 Number of stands sampled in the San Rossore Natural Park, with mean volume for each age class and for both species

Age class	<i>P. pinaster</i>		<i>P. pinea</i>	
	Number of stands	Mean volume ($\text{m}^3 \text{ha}^{-1}$)	Number of stands	Mean volume ($\text{m}^3 \text{ha}^{-1}$)
10–20			5	172
20–30			1	460
30–40	9	295	13	475
40–50	1	395	18	439
50–60	45	392	39	422
60–80			48	443
80–100			57	425
100–120			52	449
Total	55	376	233	432

The size of the stands ranges from 0.3 to 25 ha

60 years and of 20 years for older ages. Table 1 reports the main average parameters of the study stands (number of samples and volume) for each pine species and age class.

Other ancillary and satellite data

Daily meteorological data were collected from ground weather stations for the years 1999–2008 and extrapolated to the Park area through the DAYMET and MT-CLIM algorithms (Thornton et al. 1997, 2000). Soil information (i.e. depth and percentage of sand, silt and clay) was derived from D.R.E.Am. (2003).

Low-resolution normalized difference vegetation index (NDVI) imagery taken by the Spot-VEGETATION sensor was downloaded from the VITO website for the years 1999–2008 and processed as described in Maselli et al. (2006).

Dendrochronological data

Dendrochronological measurements were collected and processed to get an estimate of stand CAI evolution independent of SRFI data. In March 2003, eight trees within each of eight forest stands spread over the San Rossore pine wood area were randomly selected and measured (DBH and height). Trees were cored at 1.3 m height with an increment borer 0.5 cm in diameter. Tree cores were then processed by standard methodologies in order to reconstruct annual tree-ring widths up to 2001 (Cook et al. 1990).

Data analysis and results

Application of the original CAI modelling strategy

Modified C-Fix and BIOME-BGC were fed with the ground and satellite data previously described (see Maselli et al.

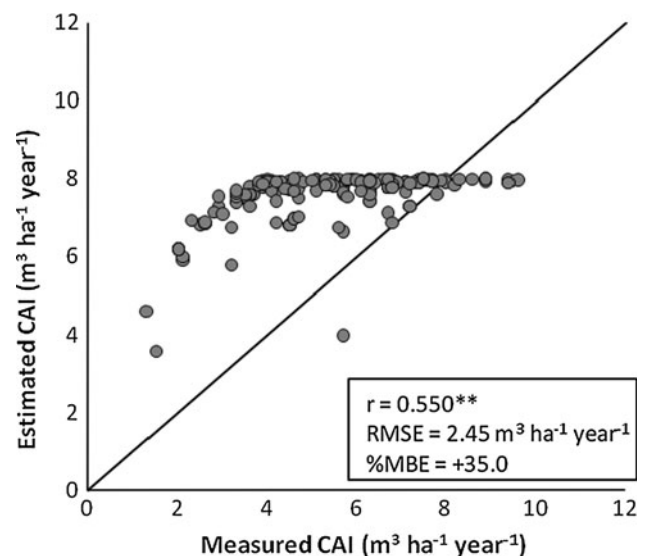


Fig. 3 Comparison of stand CAIs measured and simulated by the original modelling approach ($N = 249$; **highly significant correlation, $P < 0.01$)

2009a, for details). The BIOME-BGC version used was that calibrated for Mediterranean pines in Chiesi et al. (2007, 2011). C-Fix and BIOME-BGC yielded very similar annual GPP estimates (around 1,590 and 1,530 $\text{g C m}^{-2} \text{year}^{-1}$, respectively), which corresponded to a predicted autotrophic respiration of about 1,040 $\text{g C m}^{-2} \text{year}^{-1}$. These model outputs were combined with the standing volumes of SRFI by the methodology described. More precisely, the SRFI volume of each pine forest stand was used to compute FC_A and NV_A , which were integrated with the model outputs through Eqs. 1–5 to produce relevant estimates of NPP_A and CAI_A . The comparison of estimated versus measured stand CAIs gives the results shown in Fig. 3. A marked overestimation is visible, which is particularly evident for low-medium CAIs.

To investigate the origin of this overestimation, the main characteristics of the San Rossore pine stands were analysed. Table 1 shows that most *P. pinaster* stands are older than 50 years, while the majority of *P. pinea* stands fall in the 60–120 years age classes. This implies that all trees within each stand grew for several decades in similar and competing conditions, which affected the accumulation of wood tissues in an age-dependent way. Since BIOME-BGC simulates the functions of ecosystems showing heterogeneous tree ages and development phases, this pattern would likely result in CAI estimation errors dependent on stand age.

The plausibility of this expectation was assessed by analysing the CAI residuals of the modelling process (i.e. measured minus estimated stand CAIs). The scatter plot between these residuals and SRFI ages is shown in Fig. 4. Age accounts for almost 50% of the CAI variance not explained by the applied modelling. The significant

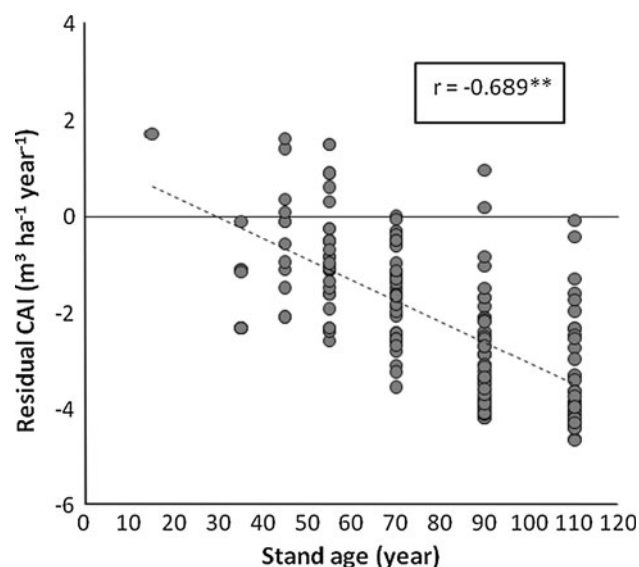


Fig. 4 Linear regression between stand CAI residuals from the original modelling approach and San Rossore forest inventory (SRFI) ages ($N = 249$; **highly significant correlation, $P < 0.01$)

negative correlation provides a clear indication that the residual CAI variability is mostly due to stand ageing.

Development and application of a modified CAI modelling strategy

The data shown in Fig. 4 could be statistically analysed to characterize and model the effect of stand age on CAI. Such an approach, however, requires the availability of ground CAI measurements representative for a large number of stands in all development phases and site quality conditions. Even though a similar data set is partly available for the San Rossore pine forest, its collection in other cases would be costly and time-expensive, which would limit the portability of the entire methodology.

This led to the search for an alternative, more generally applicable approach which could be driven by the analysis of a smaller data sample independent of SRFI. This alternative was provided by the elaboration of the annual tree-ring widths obtained by dendrochronological analysis. Table 2 summarizes the main features of the eight study stands (volume and CAI) at the time of core collection (2003). The ring widths of these eight study stands were treated as described in Chiesi et al. (2005) to reconstruct the variability of forest volume and CAI as a function of age from 0 to 100 years.

This operation obviously considered only trees which were standing at the time of core collection and did not take into account tree density decreases with time due to natural mortality and management practices (thinnings and cuttings). These decreases were additionally modelled by

Table 2 Main characteristics of the eight study stands where dendrochronological data were collected

ID	Species	Forest age (years)	Volume ($\text{m}^3 \text{ha}^{-1}$)	CAI ($\text{m}^3 \text{ha}^{-1} \text{year}^{-1}$)
2	<i>Pinus pinaster</i>	59	489	3.35
3	<i>Pinus pinaster</i>	57	567	5.14
5	<i>Pinus pinaster</i>	54	512	4.53
7	<i>Pinus pinaster</i>	51	505	4.02
8	<i>Pinus pinaster</i>	53	618	5.53
11	<i>Pinus pinea</i>	103	192	2.42
12	<i>Pinus pinea</i>	102	288	4.07
13	<i>Pinus pinea</i>	70	359	5.98

Volume corresponds to the value of the last reconstructed year (2001), while CAI is computed as an average of the last 5 years

the use of a logarithmic relationship between stand age (Age, in years) and number of trees per hectare (Nt). As suggested by La Marca (1999), this relationship is bounded by the maximum number of trees ($N_{t\text{MAX}}$) when Age is 1 and tends to 0 as Age approaches maximum stand age (Age_{MAX}):

$$Nt = -N_{t\text{MAX}} / \ln(\text{Age}_{\text{MAX}}) \ln(\text{Age}) + N_{t\text{MAX}} \quad (6)$$

Age_{MAX} and $N_{t\text{MAX}}$ were separately derived for *P. pinaster* and *P. pinea* from various references (Bussotti 1997; D.R.E.Am. 2003; Castellani 1970). Maximum ages of 200 and 250 years and maximum densities of 1,050 and 750 trees/ha were thus identified for the two species, respectively. The accuracy of the defined age/density relationship could be verified using the SRFI data only for *P. pinea*, since *P. pinaster* does not show a sufficiently diversified age class distribution (see Table 1). For the former species, taking into consideration only age classes comprising at least 10 stands, a high accordance is obtained between measured and predicted number of trees (Fig. 5).

The correction of the dendrochronological data for the tree density of each age class computed by Eq. 6 allowed the estimation of mean volumes and CAIs representative of all forest ages. These values were computed in a weighted way, that is, considering the different numbers of *P. pinaster* and *P. pinea* stands reported by SRFI. The stand volumes obtained were then used to feed the modelling strategy (i.e. to compute NV_A and FC_A estimates) and simulate stand CAIs through Eqs. 1–5. The simulation was performed by using the same C-Fix and BIOME-BGC outputs obtained previously.

The mean CAIs obtained from the analysis of the dendrochronological data for all available SRFI age classes are contrasted with simulated CAIs in Fig. 6. Measured increments show an increasing trend up to about 30 years and are then notably reduced. This behaviour is not

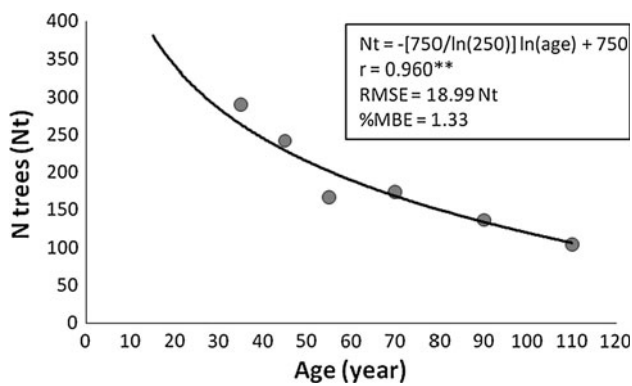


Fig. 5 Comparison between number of *P. pinea* trees (Nt) measured by SRFI and modelled by the logarithmic equation tuned as described in the text ($N = 6$; **highly significant correlation, $P < 0.01$)

simulated well by the applied modelling strategy. More particularly, simulated CAIs are lower than reference CAIs for young stands (age below 30–40 years), while become higher than these for oldest stands. This means that young stands (<30 year old) invested in new tissue accumulation more than expected by the model simulations based on volume levels, while in older stands wood biomass accumulation was inhibited more than expected.

This pattern can be mostly attributed to the inherent incapability of BIOME-BGC to take into account some major factors which determine age-related changes in forest NPP (see “Discussion”). In particular, the model assumes constant ratios among the various carbon pools, which is not valid to simulate even-aged stand development (Running and Hunt 1993). In this case, in fact, these pools show different accumulation and turnover rates (i.e. over the whole plant life for stem and coarse root C and

over only a few years for leaf and fine root C), which results in age-dependent carbon pool ratios.

Based on this consideration, a modification of the original modelling strategy was tested to correct the effect of even-aged forest management (Fig. 1, dotted box). The modification concerns the ratio between leaf and stem carbon pools, which decreases asymptotically during even-aged stand growth. This increases simulated NPP during early stand development due to increased photosynthesis/respiration ratio and has an opposite effect for older ages.

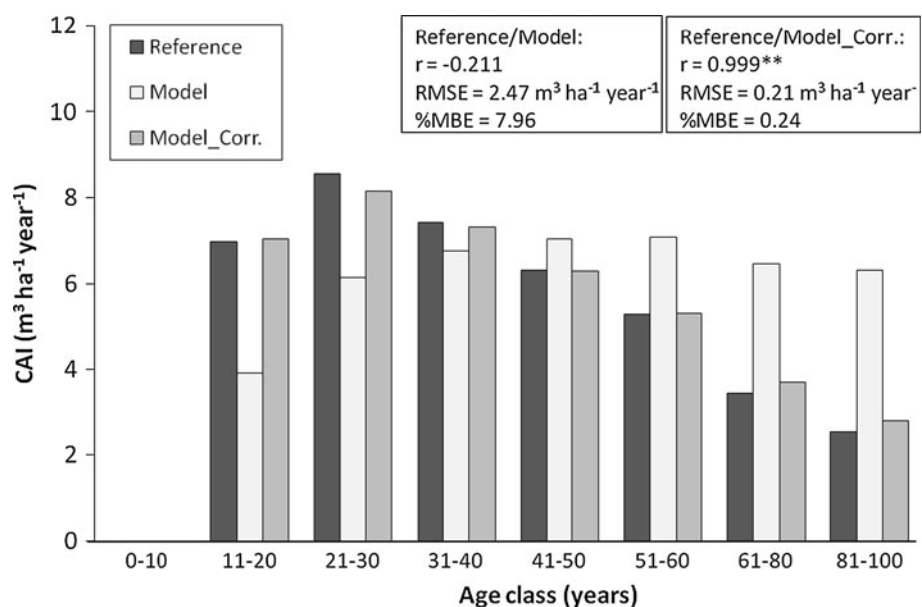
The modification was implemented by modifying the relationship between stem and leaf C used in Eq. 3. The temporally variable relationship was fitted on the same CAI values of Fig. 6, obtaining the following equation:

$$LAI_{EA} = \left[0.4 + 2.7 \exp^{(-age/26)} \right] LAI_A \quad (7)$$

where LAI_{EA} is the new estimated even-aged LAI which depends not only on actual stand volume but also on stand age. The use of LAI_{EA} in place of LAI_A within Eqs. 3–5 allows the prediction of NPP_{EA} and CAI_{EA} . In this way, the modelling strategy corrects almost all model errors for both young and old ages (still Fig. 6).

The application of the same method to the data of Fig. 3 using the SRFI stand ages yields the results visible in Fig. 7. This scatter plot shows a dramatic decrease in the errors between measured and estimated CAIs, which corresponds to the correction of the previously seen model overestimation. The correlation between the two data series is only moderate ($r = 0.742$) mainly due to the great spread of the CAI estimates. This last feature is partly attributable to the use of approximated age values (i.e. grouped in classes of 10 or 20 years, see Table 1) for driving the age correction through Eq. 7.

Fig. 6 CAI values estimated by the analysis of the available reference data (cored trees of the 8 stands and tree density information) and simulated by the original modelling approach and by the modelling approach corrected through Eq. 7. The available dendrochronological sequence did not allow the estimation of volume and CAI values for the first age interval (0–10 years) ($N = 7$; **highly significant correlation, $P < 0.01$)



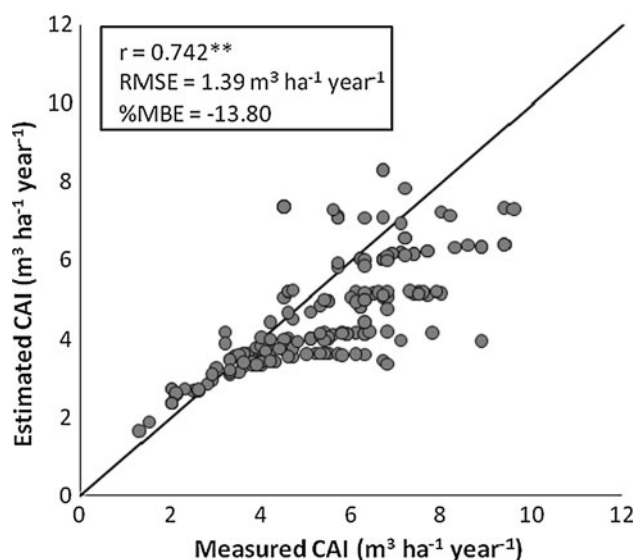


Fig. 7 Comparison of CAIs measured and simulated by the modelling approach corrected for coetaneous stand ageing through Eq. 7 ($N = 249$; **highly significant correlation, $P < 0.01$)

Discussion

Previous investigations demonstrated that a modelling strategy based on the use of C-Fix and BIOME-BGC is capable of predicting gross and net carbon fluxes of Mediterranean forests (Maselli et al. 2008, 2009a). This is confirmed by the current case study, where the ecosystem GPP predicted by both models is very close to that measured by an eddy covariance flux tower placed within the San Rossore pine forest (around $1,600 \text{ g C m}^{-2} \text{ year}^{-1}$, see Chiesi et al. 2011).

The strategy, however, resides on the assumption that the fundamental functions of the examined ecosystems can be simulated by the use of BIOME-BGC. This model was not created to simulate the temporal evolution of even-aged forest ecosystems, whose respirations and allocations are affected by peculiar growth and competition patterns. In contrast, BIOME-BGC reproduces the behaviour of ecosystems in quasi-equilibrium conditions, which are composed of trees in heterogeneous growing phases (Running and Hunt 1993; Waring and Running 2007). The method applied to account for departures from quasi-equilibrium conditions maintains such fundamental property (Maselli et al. 2009a). This implies that the modelling strategy simulates the carbon storage corresponding to a given standing volume within forests composed of nearly natural mixtures of differently aged trees. For this reason, the strategy cannot be accurate in predicting the NPP of even-aged stands.

More specifically, such stands should show carbon accumulation levels higher than expected during juvenile

stages, while they should have an opposite behaviour when the stands become older, due to the well-known phenomenon of age-related decline in forest production (e.g. Berger et al. 2004; Suchanek et al. 2004; Bradford and Kastendick 2010; Gough et al. 2010). Such phenomenon, whose existence is supported by both theoretical and experimental evidences, has been explained by a number of possible causes. For example, it has been related to tree density decrease, to time-varying competition or allocation, to altered balance between respiration and photosynthesis and to reduction of soil nutrients (Gower et al. 1996; Weiner and Thomas 2001; Berger et al. 2004; Binkley et al. 2002). Recent studies suggest that age-related decline in forest production is not due to a unique factor, but to a number of eco-physiological mechanisms which act in combination (Berger et al. 2004). Such decline is therefore variable depending on several environmental or human-induced factors (Zhou et al. 2002).

The findings of the current study support these considerations, since they indicate that the modelling strategy overestimates the CAI of most San Rossore pine stands in a way which is dependent on stand ageing. This issue has been analysed by the use of dendrochronological data, which characterize the temporal evolution of the relationship between measured and expected CAIs. The analysis is based on the reasonable assumptions that the cored trees are representative of the entire study area and that the local climate and management practices have remained approximately constant during stand ageing. The combination of this analysis and of locally tuned age/density relationships has permitted the reconstruction of volume and CAI temporal evolution in the examined stands.

The results obtained indicate that carbon accumulation peaks at 20–30 years, and it is clearly reduced during mature growth phases (see Fig. 6). These patterns, which are consistent with those reported in the literature (see for example Smith and Long 2001) are only partly reproduced by the applied modelling strategy. As expected, the measured CAIs are higher than those simulated for young ages, while the opposite is true for older ages.

In theory, these results could be used to tune a modified version of BIOME-BGC capable of accounting for the effect of stand ageing. This is the approach followed by previous investigators through the forcing and/or modification of some BIOME-BGC functions (Pietsch and Hasenauer 2002; Vetter et al. 2005). In general, implementing such modifications is rather complex and requires specific information on site conditions which is currently not available. Some trials in this direction, carried out by forcing the model to start stand growth with reduced carbon pools, confirmed these problems, as they did not succeed in reproducing the temporal CAI evolution derived from dendrochronological data.

A simpler alternative was therefore adopted, which consists of applying an additional modification to the elaboration of BIOME-BGC outputs. This was obtained by rendering the ratios between leaf and stem carbon pools age dependent. This modification alters the relationships between gross production (photosynthesis) and carbon storage in the various compartments, thus implicitly considering most factors which determine age-related decline in forest production (changes in canopy density and inter-tree competition, altered balances between respiration and photosynthesis, time-varying allocations, etc.).

The temporal variation of the stem/leaf carbon ratio was tuned on the same data set used to characterize the CAI evolution during stand growth. The model obtained corresponds to a quasi-asymptotic relationship with stand age which levels off around 0.4. This value corresponds to about 30% of the peak NPP that is found during stand development, which is in line with the figures reported by previous investigations (Gower et al. 1996; Waring and Running 2007).

The application of the correcting equation notably improves the capacity of the modelling strategy to estimate the CAIs of the San Rossore pine stands. The estimation accuracy remains only moderate at stand level, partly due to the numerous approximations which characterize SRFI data. In spite of this, the previously seen overestimation is removed, and, on average, simulated CAIs differ from ground measurements <14%.

Conclusions

The current research has yielded the following main conclusions:

- The modelling strategy based on the use of C-Fix and BIOME-BGC requires proper modification to produce reasonable CAI estimates for even-aged forests. This is due to the basic unsuitability of the strategy to account for even-aged stand development, which shows peculiar time trajectories of ecosystem functions (Mitchell et al. 2009).
- Information on such modification can be obtained from the analysis of representative dendrochronological measurements and of tree density variations in time. This enables a cheap and efficient assessment of the actual effects of stand ageing on woody biomass accumulation in each specific case.
- The results of the previous analysis are usable to modify the modelling strategy by taking into account age-dependent ratios between stem and leaf carbon pools. The modified strategy is capable of producing nearly unbiased estimates of stand CAIs, at least for sufficiently large forest areas (i.e. wider than about 1 ha).

These conclusions confirm the possibility of applying ecosystem modelling approaches to explore and analyse carbon accumulation processes of specific forest stands. As noted by various authors (McRoberts and Tomppo 2007; Corona 2010), this possibility could be now exploited in conjunction with conventional (i.e. ground inventory) and new (i.e. LiDAR remote sensing) techniques for an improved, comprehensive assessment of forest resources and processes. For example, LiDAR techniques, which provide accurate estimates of vertical forest structure (Van Leeuwen and Nieuwenhuis 2010), could be used to obtain information on both stand attributes required by the current modelling strategy (volume and age). This would enable the application of the strategy at high spatial resolution, which could be particularly proficient for the simulation of ecosystem processes in heterogeneous forest areas. This issue should be properly explored together with those related to the possible operational application of the approach in different environmental situations.

Acknowledgments The authors thank Dr. Marco Moriondo (IBI-MET-CNR), Dr. Luca Fibbi (IBIMET-CNR) and Prof. Marco Bindi (DIPSA—University of Florence) for their assistance in the development and application of the modelling approach. Dr. Enrica Arlotta is thanked for her help in the dendrochronological analysis while the administration of the San Rossore Natural Park is thanked for providing the SRFI data. Special thanks are due to Prof. Steven W. Running (NTSG—University of Montana) for his precious suggestions on the subject treated. Finally, three anonymous EJFR reviewers are thanked for their comments which notably improved the quality of the original manuscript.

References

- Berger U, Hildenbrandt H, Grimm V (2004) Age-related decline in forest production: modelling the effects of growth limitation, neighborhood competition and self-thinning. *J Ecol* 92:846–853
- Binkley D, Stape JL, Ryan MG, Barnard HR, Fownes J (2002) Age-related decline in forest ecosystem growth: an individual-tree, stand-structure hypothesis. *Ecosystems* 5:58–67
- Bradford JB, Kastendick DN (2010) Age-related patterns of forest complexity and carbon storage in pine and aspen-birch ecosystems of northern Minnesota, USA. *Can J For Res* 40(3):401–409
- Bussotti F (1997) *Pinus pinea* L. Sherwood—Foreste ed alberi oggi 28:31–34
- Castellani C (1970) Tavole stereometriche ed alsometriche costruite per i boschi italiani. *Annali dell'Istituto Sperimentale per l'Assessmentamento Forestale e per l'Alpicoltura*, vol 1, no 1 (special), Trento
- Chapin FS III, Woodwell GM, Randerson JT, Rastetter EB, Lovett GM, Baldocchi DD, Clark DA, Harmon ME, Schimel DS, Valentini R, Wirth C, Aber JD, Cole JJ, Goulden ML, Harden JW, Heimann M, Howarth RW, Matson PA, McGuire AD, Melillo JM, Mooney HA, Neff JC, Houghton RA, Pace ML, Ryan MG, Running SW, Sala OE, Schlesinger WH, Schulz E-D (2006) Reconciling carbon-cycle concepts, terminology, and methods. *Ecosystems* 9:1041–1050
- Chiesi M, Maselli F, Bindi M, Fibbi L, Cherubini P, Arlotta E, Tirone G, Matteucci G, Seufert G (2005) Modelling carbon budget of

- Mediterranean forests using ground and remote sensing measurements. *Agric For Meteorol* 135:22–34
- Chiesi M, Maselli F, Moriondo M, Fibbi L, Bindi M, Running S (2007) Application of BIOME-BGC to simulate Mediterranean forest processes. *Ecol Mod* 206:179–190
- Chiesi M, Fibbi L, Genesio L, Gioli B, Magno R, Maselli F, Moriondo M, Vaccari FP (2011) Integration of ground and satellite data to model Mediterranean forest processes. *Int J Appl Earth Obs Geoinf* 13:504–515
- Chirici G, Barbati A, Maselli F (2007) Modelling of Italian forest net primary productivity by the integration of remotely sensed and GIS data. *For Ecol Manag* 246:285–295
- Churkina G, Tenhunen J, Thornton P, Falge EM, Elbers JA, Erhard M, Grunwald T, Kowalski AS, Rannik U, Sprinz D (2003) Analyzing the ecosystem carbon dynamics of four European coniferous forests using a biogeochemistry model. *Ecosystems* 6:168–184
- Cook ER, Shiyatov S, Mazepa V (1990) Estimation of the mean chronology. In: Cook ER, Kairiukstis LA (eds) *Methods of dendrochronology. Applications in the environmental sciences*. Kluwer, Dordrecht, pp 123–132
- Corona P (2010) Integration of forest mapping and inventory to support forest management. *iForest* 3:59–64
- D.R.E.Am (2003) Tenuta di San Rossore. Note illustrative della carta forestale e della fruizione turistica. S.EL.CA., Firenze
- FAO (2005) Global forest resource assessment. Progress towards sustainable forest management. Available on the web page <http://www.fao.org/docrep/008/a0400e/a0400e00.htm>
- Federici S, Vitullo M, Tulipano S, De Lauretis R, Seufert G (2008) An approach to estimate carbon stocks change in forest carbon pools under the UNFCCC: the Italian case. *iForest* 1:86–95
- Gough CM, Vogel CS, Hardiman B, Curtis PS (2010) Wood net primary production resilience in an unmanaged forest transitioning from early to middle succession. *For Ecol Manag*. doi:10.1016/j.foreco.2010.03.027
- Gower ST, McMurtrie RE, Murty D (1996) Aboveground net primary production decline with stand age: potential causes. *Tree* 11:378–382
- La Marca O (1999) *Elementi di dendrometria*. Patron Editore, Bologna
- Maselli F, Barbati A, Chiesi M, Chirici G, Corona P (2006) Use of remotely sensed and ancillary data for estimating forest gross primary productivity in Italy. *Remote Sens Environ* 100:563–575
- Maselli F, Chiesi M, Fibbi L, Moriondo M (2008) Integration of remote sensing and ecosystem modelling techniques to estimate forest net carbon uptake. *Int J Remote Sens* 29(8):2437–2443
- Maselli F, Chiesi M, Moriondo M, Fibbi L, Bindi M, Running SW (2009a) Modelling the forest carbon budget of a Mediterranean region through the integration of ground and satellite data. *Ecol Mod* 220:330–342
- Maselli F, Papale D, Puletti N, Chirici G, Corona P (2009b) Combining remote sensing and ancillary data to monitor the gross productivity of water-limited forest ecosystems. *Remote Sens Environ* 113(3):657–667
- Maselli F, Chiesi M, Barbati A, Corona P (2010) Assessment of forest net primary production through the elaboration of multisource ground and remote sensing data. *J Environ Monit* 12:1082–1091
- McRoberts RE, Tomppo EO (2007) Remote sensing support for national forest inventories. *Remote Sens Environ* 110:412–419
- Miehle P, Grote R, Battaglia M, Feikema PM, Arndt SK (2010) Evaluation of a process-based ecosystem model for long-term biomass and stand development of *Eucalyptus globulus* plantations. *Eur J Forest Res* 129:377–391
- Mitchell S, Beven K, Freer J (2009) Multiple sources of predictive uncertainty in modelled estimates of net ecosystem CO₂ exchange. *Ecol Mod* 220:3259–3270
- Myneni RB, Williams DL (1994) On the relationship between FAPAR and NDVI. *Remote Sens Environ* 49:200–211
- Odum EP (1971) *Fundamentals of ecology*, 3rd edn. W. B. Saunders, Philadelphia
- Pietsch S, Hasenauer H (2002) Using mechanistic modeling within forest ecosystem restoration. *For Ecol Manag* 159:111–131
- Rapetti F, Vittorini S (1995) *Carta climatica della Toscana*. Pacini Editore, Pisa
- Rodeghiero M, Tonolli S, Vescovo L, Gianelle D, Cescatti A, Sottocornola M (2010) INFOCARB: a regional scale forest carbon inventory (Provincia Autonoma di Trento, Southern Italian Alps). *For Ecol Manag* 259:1093–1101
- Running SW, Hunt ER (1993) Generalization of a forest ecosystem process model for other biomes, BIOME-BGC, and an application for global-scale models. In: Ehleringer JR, Field CB (eds) *Scaling physiological processes: leaf to globe*. Academic Press, San Diego, pp 141–158
- Smith FW, Long JN (2001) Age-related decline in forest growth: an emergent property. *For Ecol Manag* 144:175–181
- Suchanek TH, Mooney HA, Franklin JF, Gucinski H, Ustin SL (2004) Carbon dynamics of an old-growth forest. *Ecosystems* 7:421–426
- Tatarinov FA, Cienciala E (2006) Application of BIOME-BGC model to managed forests 1. Sensitivity analysis. *For Ecol Manag* 237:267–279
- Thornton PE, Running SW, White MA (1997) Generating surfaces of daily meteorological variables over large regions of complex terrain. *J Hydrol* 190:214–251
- Thornton PE, Hasenauer H, White MA (2000) Simultaneous estimation of daily solar radiation and humidity from observed temperature and precipitation: an application over complex terrain in Austria. *Agric For Meteorol* 104:255–271
- Thornton PE, Law BE, Gholz HL, Clark KL, Falge E, Ellsworth DS, Goldstein AH, Monson RK, Hollinger D, Falk M, Chen J, Sparks JP (2002) Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needleleaf forests. *Agric For Meteorol* 113:185–222
- Van Leeuwen M, Nieuwenhuis M (2010) Retrieval of forest structural parameters using LiDAR remote sensing. *Eur J Forest Res* 129:749–770
- Veroustraete F, Sabbe H, Eerens H (2002) Estimation of carbon mass fluxes over Europe using the C-Fix model and Euroflux data. *Remote Sens Environ* 83:376–399
- Vetter M, Wirth C, Bottcher H, Churkina G, Schultze E-D, Wutzler T, Weber G (2005) Partitioning direct and indirect human-induced effects on carbon sequestration of managed coniferous forests using model simulations and forest inventories. *Glob Change Biol* 11:810–827
- Waring RH, Running SW (2007) *Forest ecosystems: analysis at multiple scales*, 3rd edn. Academic Press, San Diego, pp 263–291
- Weiner J, Thomas SC (2001) The nature of tree growth and the ‘age-related decline in forest production’. *Oikos* 94:374–376
- White MA, Thornton PE, Running SW, Nemani RR (2000) Parameterisation and sensitivity analysis of the BIOME-BGC terrestrial ecosystem model: net primary production controls. *Earth Interact* 4:1–85
- Zhou G, Wang Y, Jiang Y, Yang Z (2002) Estimating biomass and net primary production from forest inventory data: a case study of China’s *Larix* forests. *For Ecol Manag* 169:149–157