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Journal

Canadian Journal of Forest Research-Revue Canadienne de Recherche Forestiere, 34(4)

ISSN

0045-5067

Authors

Misson, Laurent
Rathgeber, C
Guiot, J

Publication Date

2004-04-01

Peer reviewed

Dendroecological analysis of climatic effects on *Quercus petraea* and *Pinus halepensis* radial growth using the process-based MAIDEN model

Laurent Misson, Cyrille Rathgeber, and Joël Guiot

Abstract: A process-based model (MAIDEN, modeling and analysis in dendroecology) is compared with statistical response functions to analyze the climate–growth relationship for two different species (sessile oak (*Quercus petraea* (Matt.) Liebl.) and Aleppo pine (*Pinus halepensis* Mill.)) growing in contrasting climates (temperate and Mediterranean). Growth data were obtained using dendroecological sampling procedures. Results obtained with both methods are consistent, but the MAIDEN model provides a more explanatory analysis than classical statistical tools. Analyses with MAIDEN indicate that oak stomatal conductance is sensitive to atmospheric vapor deficit, whereas precipitation and soil water deficit are not limiting factors in the study area. In contrast, the soil water regime is the major controlling factor of bole growth variability for Aleppo pine. The model shows that remobilization of the carbohydrate reserves in spring is of major importance for leaf and root expansion, and it affects the subsequent bole increment of oak. Because the amount of carbon that can be mobilized in spring is linked to carbon stored the previous year, these processes explain how the growth of oak trees is linked in this way from one year to the next. In contrast, the MAIDEN model shows that carbohydrate-reserve dynamics, phenology, and bole growth are less connected for Aleppo pine trees.

Résumé : Un modèle basé sur les processus (MAIDEN, modélisation et analyse en dendrochronologie) est comparé à des fonctions de réponse statistiques dans le but d'analyser la relation entre la croissance et le climat pour deux espèces différentes (chêne sessile (*Quercus petraea* (Matt.) Liebl.) et pin d'Alep (*Pinus halepensis* Mill.)) croissant dans des climats contrastés (tempéré et méditerranéen). Des données de croissance ont été obtenues à partir de procédures d'échantillonnage propres à la dendroécologie. Les résultats obtenus avec les deux méthodes sont consistants, même si le modèle MAIDEN offre une analyse plus explicative comparativement à celle des outils statistiques traditionnels. Les analyses faites avec MAIDEN indiquent que la conductance stomatique du chêne est sensible au déficit de pression de vapeur atmosphérique alors que la précipitation et le déficit en eau du sol ne sont pas des facteurs limitants dans l'aire d'étude. Par contre, le régime hydrique du sol est le principal facteur régissant la variabilité de la croissance du tronc pour le pin d'Alep. Le modèle montre que la remobilisation des réserves en hydrates de carbone au printemps est d'une importance majeure pour l'expansion du feuillage et des racines et qu'elle affecte subséquemment la croissance du tronc du chêne. Puisque la quantité de carbone qui peut être mobilisée au printemps est liée au carbone emmagasiné l'année précédente, ces processus expliquent pourquoi la croissance du chêne est corrélée de cette façon d'une année à l'autre. À l'opposé, le modèle MAIDEN montre que la dynamique des réserves en hydrates de carbone, la phénologie et la croissance du tronc sont moins connectées dans le cas du pin d'Alep.

[Traduit par la Rédaction]

Introduction

While micrometeorological studies have allowed us to analyze the effects of short-term climatic variations on energy, carbon, and water fluxes at stand level (e.g., Williams et al. 1996; Baldocchi and Meyers 1998; Law et al. 2000), dendroecological methods have been developed for several decades to answer various ecological questions at larger time and spatial scales (Fritts and Swetnam 1989). Both ap-

proaches are complementary and should be connected by combining data collection, analysis, and modeling at various time and spatial scales (e.g., Hunt et al. 1991; Granier et al. 1999; Baldocchi and Wilson 2001; Rasse et al. 2001). So far, such methodology has not been extensively used.

In dendroecology, the control of annual tree growth by climatic factors is generally studied using multiple linear regressions between tree-ring indices and monthly climatic variables (Fritts and Swetnam 1989). This statistical method

Received 14 February 2003. Accepted 14 October 2003. Published on the NRC Research Press Web site at <http://cjfr.nrc.ca> on 20 April 2004.

L. Misson^{1,2} and J. Guiot. Centre Européen de Recherche et d'Enseignement des Géosciences de l'Environnement (Centre National de la Recherche Scientifique, Unité Mixte de Recherche 6635), Europôle Méditerranéen de l'Arbois, B.P. 80, 13545 Aix-en-Provence CEDEX 4, France.

C. Rathgeber. Climatic Research Unit, School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, UK.

¹Corresponding author (e-mail: lmisson@nature.berkeley.edu).

²Present address: Department of Environmental Science, Policy and Management, 151 Hilgard Hall, University of California Berkeley, Berkeley, CA 94720-3110, USA.

is empirical and does not allow an in-depth process-oriented data analysis. With the use of physiologically based dendroecological models, several attempts have been made to gain insight into causal biological relationships (Federer et al. 1989; Fritts et al. 1991; LeBlanc and Foster 1992; Foster and LeBlanc 1993; Granier et al. 1999; LeBlanc and Terrel 2001). These approaches still assume that the relationship between climate and tree rings is stable over time. This hypothesis is very much questioned in the context of global changes (Briffa et al. 1998; Rathgeber 2002). Furthermore, these approaches do not allow researchers to include the physiological effect of change in the concentration of atmospheric CO_2 on tree growth.

To overcome these problems, Rathgeber et al. (2000a) used dendroecological data with a biogeochemistry model (BIOME3, Haxeltine and Prentice 1996) to provide a realistic evaluation of the impact of global change on the productivity of forest stands (see also Rathgeber et al. 2003). By using BIOME3, they applied a global model at a local scale. In such an approach, the spatial and temporal scales at which some vegetative processes were mathematically described did not correspond to the scales at which the data were acquired. Several other carbon-based models exist that take into account tree-growth processes with various details (Ceulemans 1996; Leroux et al. 2001). In their review Leroux et al. (2001) raised two critical issues for tree-growth models that call for the development and testing of original modeling schemes: (1) the representation of carbon allocation and (2) carbon storage and remobilization. These linked processes possibly explained why the stem growth of trees is often linked from one year to the next, producing autocorrelation in tree-ring series (e.g., LeBlanc et al. 1987; Larsen and MacDonald 1995; Kahle and Spiecker 1996; Desplanque et al. 1998). At this level as well, dendroecologists and modelers could find a common basis for studying tree-growth responses to the environment.

The aim of this study is to develop, calibrate, and test an exploratory model that allows an in-depth process-oriented analysis of the relationship between climate and tree growth represented by dendroecological data (MAIDEN model, modeling and analysis in dendroecology). Then, we aim to mathematically describe the ecophysiological processes involved at the time and the spatial scales of dendroecological studies. The main characteristics of the MAIDEN model are described in Misson (2004). In that paper, the model is tested against high-resolution ecophysiological data and larger timescale dendroecological series in a temperate ecosystem dominated by sessile oak (*Quercus petraea* (Matt.) Liebl.). For this paper we used dendroecological data to test the same model on a very different species, Aleppo pine (*Pinus halepensis* Mill.), in a different climate (Mediterranean climate of southeast France). In addition, the paper focuses on testing an original modeling procedure of carbon storage and remobilization to reproduce the autocorrelation structure of tree-ring series.

Material and methods

Experimental *Quercus petraea* stand in Belgium

This site (50°06'N, 04°16'E) provided detailed ecophysiological and dendroecological data. Data collection has been

extensively described in Misson (2004) and will be summarized here. The experimental stand is located at an altitude of 260 m, in the temperate climate of the medio-European phytosociological domain. The mean annual temperature is 8.5 °C, and annual precipitation is around 1000 mm. The stand is a coppice with standards, with 116-year-old sessile oak as the dominant species. The soil is classified as a Dystric Cambisol (FAO class).

From May to December 2001, throughfall was estimated using stemflow collectors and automatic rain gauges installed in the understorey. Volumetric soil water content was measured using time domain reflectometry probes (CS615, Campbell Scientific Ltd., Loughborough, UK) installed at different depths inside pedological pits. Sap flux density was monitored using the Granier thermal method (Granier 1987). With the use of direct and indirect leaf area index (LAI) measurements, maximum LAI was estimated to be 5.75. During the winter 1999–2000, 20 oaks were harvested, and a stem disk was sampled on each tree at a height of 1.3 m. Ring widths were measured along four radii on each stem disk. Individual (for one tree) chronologies of ring-width ($RW(t)$, where t is time in years) were not standardized because no significant time trend was detected. Long-term climatic data (maximum temperature, minimum temperature, and precipitation at daily time steps from 1954 to 2000) were obtained from a meteorological station in an open field (Rance meteorological station, IRM, Brussels, Belgium) located 3 km from the experimental stand.

Dendroecological *Pinus halepensis* stands in France

Data were obtained from 21 Aleppo pine stands located on calcareous soil in Provence, southeast France. These stands were selected to represent the distribution of Aleppo pine in this Mediterranean region. Botanical, ecological, and topographical details were recorded at each site (Nicault 1999). Tree age at the time of sampling ranged from 80 to 180 years. The altitude ranged from 150 to 600 m. At least 12 dominant trees were cored at each site, with three cores taken from each tree at a height of 1.3 m. Annual earlywood width (E_W), latewood width (L_W), earlywood density (E_D), and latewood density (L_D) were used to calculate an index of annual wood increment that takes into account not only stem radial growth but also wood density (Rathgeber et al. 2000b).

Individual chronologies for each variable (E_D , E_W , L_D , L_W) were first standardized using a stand-specific productivity index to eliminate productivity differences among sites (Becker and Le Goff 1988; Rathgeber et al. 2000b). Then, a second standardization was applied to reduce the age effect within the individual chronologies to focus on short-term fluctuations that are mainly influenced by climate (Becker 1989; Rathgeber et al. 1999). The methodology is fully described in Rathgeber et al. (2000b) and will be summarized here. The stand-specific productivity index was defined as the mean of the first 50 years of each variable so that it was independent of stand age. The corresponding standardized variable is then defined as the ratio between its annual increment and the productivity index. A regional age-related growth trend for the four variables was then calculated using a polynomial fitting for density variables and an exponential growth function for ring-width variables. These growth

Table 1. Model parameters and calibrated value obtained by maximizing the coefficient of determination (r^2) with observations.

Model parameters	Symbol	Units	<i>Quercus petraea</i>	<i>Pinus halepensis</i>
Growing degree-days	G_{DD}	°C	500	200
Daily proportion of A_n limited by W_c	p	Fraction	0.28	0.5
Coefficient linking g_s to A_n^a	a_1	—	7.9	6.0
Coefficient linking g_s to D_s^a	D_0	Pa	375	600
Soil water stress parameter	θ_c	mm	314	95.8
Canopy water storage coefficient	C_{ws}	—	0.34	0.30
Temperature function coefficient for $f_{gpp \rightarrow npp}$	c_1	—	30	40
Temperature function coefficient for $f_{npp \rightarrow store}$	c_2	—	30	44.7
Root to leaf fraction (phase 1)	λ	—	0.25	0.68
Carbon stored to leaf and root fraction (phase 2)	$f_{store \rightarrow leaf/root}$	Fraction	0.05	0.001
NPP to bole fraction (phase 3)	$f_{npp \rightarrow bole}$	Fraction	0.61	≈ 1.0
Carbon stored to bole fraction (phase 3)	$f_{store \rightarrow bole}$	Fraction	9.0×10^{-5}	1.0×10^{-6}

Note: W_c , rate of carboxylation when ribulose biphosphate is saturated; A_n , net photosynthesis; g_s , stomatal conductance; D_s , humidity deficit at leaf surface; $f_{gpp \rightarrow npp}$, fraction of gross primary production (GPP) to net primary production (NPP); $f_{npp \rightarrow store}$, fraction of NPP to store carbon.

^aFrom Leuning (1995).

trends were used to standardize the individual chronologies a second time, by dividing the productivity indexed increment of each tree-ring variable by its regional age-related function. Basing our calculations on the twice standardized individual chronologies, we established an index of annual wood increment for each tree, by taking into account not only ring width but also wood density. This index was computed by combining the four previously standardized tree-ring variables:

$$[1] \quad W(t) = E_{Wss}(t) \times E_{Dss}(t) + L_{Wss}(t) \times L_{Dss}(t)$$

where $W(t)$ is the annual wood increment index for date t , and the subscript ss denotes the double standardization of the tree-ring variables. Based on individual chronologies of $W(t)$ (for trees), arithmetic means were computed for each year to generate a series of $W(t)$ covering the entire region. The Aix-en-Provence meteorological station (Météo France) provided maximum temperature, minimum temperature, and precipitation data at daily time steps. The distance between this station and the pine study sites varies between 5 and 65 km (Rathgeber et al. 2003).

The MAIDEN model

General description

MAIDEN is extensively described in Misson (2004). The model needs site and species parameters such as altitude, latitude, maximum absolute LAI, specific leaf area (SLA), initial bole biomass, soil thickness, and soil textural classes. In addition, the model has 12 calibration parameters that can be tuned to adjust the outputs of the model to ecophysiological and stand growth data (Table 1). Climatic driving variables are daily minimum and maximum temperature and precipitation. We coupled MAIDEN to the MT-CLIM model (Running et al. 1987) to estimate daily solar radiation and vapor pressure deficit from daily temperature and precipitation data.

The model calculates processes such as photosynthesis production (gross primary production), stomatal regulation, and respiration. The model computes the water balance at ecosystem level, including canopy water interception, transpiration, soil evaporation, soil water transfer, drainage, and runoff. Then MAIDEN partitions daily net primary production between carbon reservoirs (leaf, bole, root, and store) according to phenological phase-dependent ratios. These phases are (1) winter: no activity, (2) spring: leaf and root expansion, (3) summer: bolewood production, (4) early fall: carbohydrate-reserve accumulation, (5) late fall: leaf and root senescence. An original modeling procedure of carbon storage and mobilization was developed to reproduce the autocorrelation structure of tree-ring series. The annual increment of bole carbon reservoir at stand level, $B_{ci}(t)$, is the modeled variable that will be compared with the dendro-chronological tree-ring series.

Parameterization

In many dendroecological studies, there are few measurements of site and (or) species parameters. Some of these parameters could possibly be estimated statistically by adjusting the outputs of the model to ecophysiological and (or) tree-ring data. When developing the MAIDEN model, we tried to limit the number of calibration parameters to avoid problems such as over-parameterization, which lead to nonunique solutions and (or) nonsensical estimates (i.e., estimates that are inconsistent with the observed data) (Sievänen and Burk 1994). To achieve this objective, we tried, as much as possible, to link the properties of the model to biochemical and ecophysiological principles and then to constrain model parameters to each other (Baldocchi and Meyers 1998).

At present the MAIDEN model has 12 calibration parameters (Table 1). We used a simple optimization algorithm that does not involve a validation on independent data, but allowed us to test the realism of the modeling schemes used at this first stage of the model development. The parameteri-

zation consists of successively testing all values of each parameter separated by a constant interval inside a preselected range. Each parameter is optimized sequentially one after the other, with all other parameters being kept constant at their previous optimized values. The parametric values that were retained gave the best coefficient of determination (r^2) between an observed and a simulated variable. For the oak stand, extensive data allowed us to calibrate these parameters using measurements of phenology, throughfall ($r^2 = 0.95$ between observations and simulations), soil water content ($r^2 = 0.81$), transpiration ($r^2 = 0.80$), and RW(t) series from 1960 to 1999 ($r^2 = 0.44$) (see Misson 2004). For Aleppo pine, the 12 parameters were calibrated together using the $W(t)$ index from 1963 to 1994. After parameterization, we performed a one-at-a-time sensitivity analysis, which consisted in varying the values of the calibration parameters one after the other (with all other parameters being kept constant at their nominal values) and observing the influence on the relative change of model predictions (Hamby 1994). This analysis should give useful information about over-parameterization and (or) about misspecifications of the model's components.

The MAIDEN model was compared with bootstrap response functions (Guiot 1991, 3PBASE software), a standard method used in dendroecology. For each experimental site, three response functions were calculated, each with one set of 16 climatic regressors. These sets of regressors were, successively, the mean maximum temperatures ($T_{\max}$, °C), minimum temperatures ($T_{\min}$, °C), and total precipitation (P , mm) for the first 9 months of the current year (from January to September of the ring formation year t) and 7 months of the previous year (from June to December of year $t - 1$). The principal components of the regressors were used to avoid problems of collinearity (Guiot et al. 1982). For each site, the significant climatic variables were selected, and a new response function was calibrated for these variables.

Results

Response function analyses indicate that none of the $T_{\min}$ variables are significant for sessile oak and Aleppo pine (data not shown). For both species, response functions show that several $T_{\max}$ monthly variables are significant (Fig. 1). For both species, one $T_{\max}$ variable during spring is significant and has a positive influence on growth: May for oak and March for Aleppo pine. Other significant $T_{\max}$ variables for oak are during the midseason of the previous year (July, negative influence) and the current year (August, negative influence). For pine, they are from the end of the season (September, negative influence) of the previous year and midseason of the current year (June, negative influence) (Fig. 1). For Aleppo pine, some of the precipitation variables are also significant (Fig. 1), and they follow the same monthly pattern as significant $T_{\max}$ variables, but with the opposite influence.

A final response function was calculated for each species with only the significant monthly variables for P and $T_{\max}$ (see Fig. 1). The fit between observations and simulations is not the same for oak and pine (Figs. 2 and 3). For oak, r^2 is not very high (0.37), and major discrepancies between mea-

Fig. 1. Ratios of regression coefficients to standard errors for monthly precipitation variables (grey bars) and monthly maximum temperature variables (black bars) for (a) *Quercus petraea*, and (b) *Pinus halepensis*. Vertical lines indicate significant statistical level at $\alpha = 0.05$.

surements and simulations occur from 1975 to 1976, where the dendroecological model seems unable to predict the observed growth decrease (Fig. 2). Furthermore, model simulations are much less variable than measurements. For pine, r^2 is relatively high (0.61), and some minor discrepancies occur between 1985 and 1989, where the model systematically overestimates the observed growth (Fig. 3). For Aleppo pine as well, simulations are somewhat less variable than measurements.

When calibrated, the MAIDEN model produces annual simulations of bole increment, $B_{ci}(t)$, that match quite well the interannual variations of tree-ring data measured for oak and pine (Figs. 2 and 3). For both species, r^2 is slightly higher with the MAIDEN model than with the response function (Figs. 2 and 3). The variability of the simulations performed with MAIDEN is greater than the variability obtained with the response function. For oak, the 1975 to 1976 growth decrease is well reproduced with MAIDEN, but not with the response function (Fig. 2). The climatic data at the oak site revealed that very high temperatures leading to drought stress occurred in August 1975 and from June to July 1976. The response function cannot reproduce the effect of these climatic events because it statistically links annual ring width with maximum temperature from July of the previous year (1975) and August of the current year

Fig. 2. Measured and modeled bole increment series for *Quercus petraea*. The left y axis gives measured and response function ring-width series. The right y axis gives modeled bole increment, $B_{ci}(t)$, with MAIDEN.

Fig. 3. Measured and modeled bole increment series for *Pinus halepensis*. The left y axis gives measured and response function wood increment index, $W(t)$, series. The right y axis gives modeled bole increment, $B_{ci}(t)$, with MAIDEN.

(1976) (Fig. 1). Nevertheless, some discrepancies between MAIDEN simulations and observations are still noticeable, particularly in 1978 and 1979 (Fig. 2). This lack of fit may be due to a natural thinning effect that is not simulated in the model (Misson 2004).

Discrepancies between MAIDEN simulations and observations and also in the response function (Fig. 3) occurred for Aleppo pine during the mid-1980s. Analysis of the climatic variables revealed that this period was characterized by very low winter temperatures. The mean monthly value of minimum temperature from January to February for the period 1985–1987 was $-0.11\text{ }^{\circ}\text{C}$, while the mean over the entire simulation period (1963–1994) was $0.91\text{ }^{\circ}\text{C}$. A winter

temperature constraint on annual bole growth is not included in either the response function or the MAIDEN model, which could explain the differences between observations and simulations.

Results of the calibration process for the MAIDEN model give contrasting values for the parameters when comparing oak and pine (Table 1). The growing degree-days (G_{DD}) value is higher for oak than for pine and, when combined with climate data, provides a mean bud-burst date over the simulation period of 15 March for Aleppo pine and 20 May for sessile oak. These results are in accordance with the response function analyses, which indicate that spring temperatures during the month of March for pine and May for oak

Fig. 4. Percent change of mean bole increment over the simulation period while calibration parameter values were varied sequentially and independently by +20% for (a) *Quercus petraea* and (b) *Pinus halepensis*. Vertical lines are drawn at +20% and -20%.

positively influence annual bole increment. Contrasting values for parameterization of atmospheric (D_0) and soil (θ_c) water stress functions (Misson 2004, eqs. 6, 7, and 8) also reflect dissimilar water economy processes between these ecosystems. Results indicate a high sensitivity of stomatal conductance (g_s) to vapor pressure deficit in oak (D_0 oak = 375 Pa), and a high sensitivity of g_s to soil water deficit in pine (θ_c pine $\approx$ 96 mm) (Table 1). Levels of soil water stress (θ_s) (Misson 2004, eqs. 6 and 7) never fall below 0.9 for oak, while for pine it drops to 0.6 almost each year of the simulation period. Carbon partitioning parameters suggest that the carbon flux through the store reservoir is less important for pine than for oak (Table 1).

Analyses were performed to test the sensitivity of the simulated bole increment, $B_{ci}(t)$, to the model parameters (Fig. 4). Figure 4 shows that G_{DD} is a key parameter for oak: a change of +20% in the G_{DD} calibrated value affects $B_{ci}(t)$ by -23.4% for oak and by only -7.7% for pine. Both pine and oak growth simulations are sensitive to the proportion of photosynthesis when ribulose biphosphate is saturated (p) (Misson 2004, eq. 3). While stomatal conductance parameters related to photosynthesis (a_1) and atmospheric water deficit (D_0) are only important for oak, the soil water stress parameter (θ_c) that influences stomatal conductance is only critical for pine (Misson 2004, eq. 6). Simulations for both pine and oak are insensitive to the parameter that controls the canopy interception of rain in the model (C_{ws}) (Misson 2004, eq. 10), whereas simulations for both species are very sensitive to the parameter regulating respiration temperature sensitivity (c_1) (Misson 2004, eq. 12). $B_{ci}(t)$ does not seem to be sensitive to the leaf carbon reservoir to root carbon reservoir ratio (λ) for oak and pine (Misson 2004, eq. 14). For both species, when the allocation parameters related to carbon storage and mobilization are taken individually (c_2 , $f_{store \rightarrow leaf/root}$, $f_{npp \rightarrow bole}$, $f_{store \rightarrow bole}$) (Misson 2004, Appendix A), they do not seem to affect $B_{ci}(t)$ significantly; however, the sum of absolute values of percent change of $B_{ci}(t)$ for all these parameters reaches 23.6% for oak, while it reaches only 1.1% for pine (Fig. 4).

Other analyses were conducted with the MAIDEN model to test the sensitivity of bole growth to the different climatic

Table 2. Coefficient of determination (r^2) computed between measured ring-width series and bole increment series modeled with different climatic data sets.

Input data set	<i>Quercus petraea</i> ^a	<i>Pinus halepensis</i> ^b
Normal input data set	0.44	0.67
With constant temperature	0.04	0.07
With constant precipitation and θ_s	0.44	0.08
With constant radiation	0.30	0.65
With constant vapor pressure deficit	0.12	0.12
With constant bud-burst date	0.12	0.52
Test without carbon storing	0.09	0.56

^aValues of constant meteorological variables: maximum temperature, 12 °C; minimum temperature, 5 °C; precipitation, 2.7 mm; radiation, 220 W·m⁻²; vapor pressure deficit, 450 Pa; bud-burst date, 1 May.

^bValues of constant meteorological variables: maximum temperature, 19 °C; minimum temperature, 7 °C; precipitation, 1.5 mm; radiation, 290 W·m⁻²; vapor pressure deficit, 850 Pa; bud-burst date, 1 May.

driving variables. For both sites, we computed the $B_{ci}(t)$ series while each of the successive climatic variables was kept constant at its daily mean over the simulation period. For each run, r^2 coefficients were computed and compared with the r^2 coefficient obtained with the normal input data set to determine which variable, when kept constant, resulted in a decrease of explained variance (Table 2). A constant temperature considerably reduces r^2 for oak and pine (Table 2), thus indicating that temperature is a major controlling factor of annual bole increment variability for both species. These results are consistent with the response function analyses (Fig. 1). To separate the effects of temperature through spring phenological processes and photosynthesis – carbon allocation, we ran the model with the normal temperature data set as input, while keeping the bud-burst date constant (1 May). The value of r^2 is reduced by 0.32 for oak (from 0.44 to 0.12) and by only 0.15 for pine (from 0.67 to 0.52) (Table 2), which suggests that bole growth variability associated with temperature-related bud-burst process is more important for oak. In contrast, precipitation and soil water stress seem to be the most important controlling factors of

Fig. 5. Autocorrelations for (a) observed and (b) simulated bole increment series for *Quercus petraea*. Black bars are significant autocorrelations at the 5% level; grey bars are nonsignificant autocorrelations.

Fig. 6. Autocorrelations for (a) observed and (b) simulated bole increment series for *Pinus halepensis*. All autocorrelations are nonsignificant at the 5% level.

bole increment variability for pine (Table 2). These results are in accordance with the response function analyses. Furthermore, solar radiation is a more limiting factor at the oak site.

The ability of the model to reproduce carbohydrate storage and mobilization processes that link the performance of trees from one year to the next can be tested to some extent by comparing the autocorrelation structure of observation and simulation series (Guiot et al. 1982). Figure 5a indicates that only first-order autocorrelation for the measured ring-width series at the oak site is noticeably significant. For pine, no autocorrelation is significant for the observation series; however, the first-order value is near the 5% significance level (Fig. 6a). The autocorrelation structure of simulated series at both sites reproduces these observations to a certain extent (Figs. 5b and 6b). For oak, the first-order autocorrelation is significant, and the second-order autocorrelation is not far from the 5% level. For pine, none of the autocorrelations are significant (Fig. 6b).

A sensitivity analysis was conducted to test the importance of carbon-reserve dynamics in explaining bole incre-

ment variability over time. For each ecosystem, we made a run of the model with the $f_{\text{hpp} \rightarrow \text{bole}}$ parameter equal 1.0 and the $f_{\text{store} \rightarrow \text{bole}}$ parameter equal zero, with the result that the only source of carbon allocated to the bole was net primary production. The r^2 dropped from 0.44 to 0.09 for oak and from 0.67 to 0.56 for pine (Table 2); these results suggest that the variance explained by processes of reserve dynamics in the model is very important for oak and less important for pine. Outputs from the model indicate that over the simulation period, around 13% of carbon annually enters and leaves the store reservoir for oak, and only 1.5% in the case of pine (Table 3). For both species, the major part of carbon output from the store reservoir is allocated to constructing new leaves and roots during the spring (carbon store to leaves and roots, Table 3), while store carbon allocated directly to the bole is small (carbon stored to bole, Table 3). Nevertheless, the interannual variability of store carbon allocated to the bole is important for oak (coefficient of variation (CV) = 68.2%) but not for pine (CV = 19.2%), which supports the previous finding that the temporal pattern of the bole increment series is more seriously influenced by

Table 3. Mean annual percentage of carbon flux ($\pm$ SE) through the store reservoir during the simulation period (*Quercus petraea*, 1960–1999; *Pinus halepensis*, 1963–1994), with coefficients of variation given in parentheses.

	<i>Quercus petraea</i>	<i>Pinus halepensis</i>
NPP to C stored/annual C	12.8 $\pm$ 1.2 (9.3%)	1.5 $\pm$ 0.26 (17.4%)
C stored to leaf and root/annual C	12.7 $\pm$ 1.6 (2.8%)	1.4 $\pm$ 0.24 (16.4%)
C stored to bole/annual C	1.9 $\times 10^{-2}$ $\pm$ 1.3 $\times 10^{-2}$ (68.2%)	2.3 $\times 10^{-4}$ $\pm$ 4.5 $\times 10^{-5}$ (19.2%)

Note: NPP, net primary production; annual C, annual sum of carbon through the reservoirs.

carbohydrate-reserve dynamics for oak than for pine (Table 3).

Discussion

We have shown that sensitivity analyses of bole increment to climatic variables with the process-based MAIDEN model produce results that are consistent with the response function analyses, which are classically used in dendroecology. The fact that the results obtained from the MAIDEN model correspond with those produced by a different and reliable tool such as the response function supports our new approach. The advantage of using the MAIDEN model is that it gives more insight into the functional processes involved in tree growth such as regulation of stomatal conductance, phenology, or carbon-reserve dynamics. This allows us to interpret the relationship between climate and growth with less ambiguity and, in addition, to clearly identify weaknesses in our understanding of the system and to design new experiments (Baldocchi and Meyers 1998). Furthermore, the MAIDEN model describes the climate–growth relationship in nonlinear terms and uses threshold values at some stages. This explains the greater interannual variability of the simulations performed with MAIDEN compared with the response functions. Moreover, since the MAIDEN model takes into account the climatic conditions during the whole year, it is more able to predict the effect of unusual climatic events than the statistical response functions.

One of the difficulties of the process-based approach is that the model needs additional parameters not required by the statistical approach. At present, parameters concerning the site (altitude, latitude, soil thickness, and soil textural classes) and the species (leaf area index, specific leaf area, and initial bole biomass) are required to run the MAIDEN model. Few dendroecological studies include measurements of many site and (or) species parameters. Furthermore, MAIDEN requires climatic inputs at daily time steps that are rarely available from such studies. The development of new process-based models for use in dendroecology provides an incentive for also estimating critical site and (or) species parameters when sampling tree-ring data. Parameters such as those required by MAIDEN can be easily evaluated from direct or indirect measurements. This is of particular importance for ecophysiological studies based on dendrochronological series, where site and (or) species parameters can also help to interpret the data. Furthermore, the lack of daily climatic data can be overcome by using models such as MT-CLIM, which estimates daily meteorological parameters at one station from observations at another station nearby (Running et al. 1987). MT-CLIM is particularly designed to handle the special problems encountered in mountainous

terrain, but it is applicable in flat terrain as well. If daily data are lacking for any meteorological station, mathematical simulators predicting daily meteorological data from monthly data can be used before MT-CLIM (Hubert et al. 1998). Nevertheless, these approaches should be tested and validated against real data.

Analyses of climate–growth relationship indicate a very considerable contrast between the functioning of the temperate oak and the Mediterranean pine ecosystems we have studied. This contrast is due to species-specific physiological responses as well as environmental variations between these ecosystems. The better fit obtained with the Aleppo pine bole increment data can be explained by the fact that climate is a more limiting factor on vegetation in the Mediterranean area than in the temperate zone. In addition, the oak dendrochronological data are ring-width series, while the pine data are better estimates of whole carbon assimilated by the bole because they take both ring width and wood density into account (Rathgeber 2002). Furthermore, in contrast to oak, the Aleppo pine growth data sampled across multiple sites have allowed us to construct a regional-based dendroecological series that emphasizes the climatic signal at regional level while minimizing the influence of local factors that affect tree growth (such as thinning or insect defoliation).

As shown by the MAIDEN model, solar radiation is not a limiting factor in the Mediterranean area, whereas it explains some interannual variability of carbon assimilation and bole increment in the temperate oak ecosystem. In addition, the model shows that oak stomatal conductance is very sensitive to atmospheric vapor deficit, as also documented in other publications (Beerling et al. 1996; Heath 1998; Misson et al. 2002). Čermák et al. (1980) and Bréda et al. (1993) have shown that *Quercus robur* L. and *Q. petraea* are characterized by a great sensitivity of stomatal conductance (g_s) to leaf water potential variations. In natural conditions, precipitation and soil water deficit are not major controlling factors in the oak ecosystem studied because of high annual precipitation (≈ 1000 mm $\cdot$ year $^{-1}$) and large soil water capacity (≈ 600 mm).

The Mediterranean pine ecosystems studied are characterized by lower soil water capacity (≈ 100 mm) and lower precipitation (≈ 600 mm $\cdot$ year $^{-1}$), which is distributed mainly outside of the vegetative period. These characteristics, combined with an elevated vapor pressure deficit, make the soil water regime the major controlling factor for this type of ecosystem (Schiller and Cohen 1995, 1998; Borghetti et al. 1998; Nicault et al. 2001). In the MAIDEN model, soil water stress expresses its control over assimilation by reducing stomatal conductance (Misson 2004, eq. 6). Nevertheless, drought can limit photosynthesis by stomatal closure or by metabolic impairment (nonstomatal limitation) (Wilson et al.

2000; Flexas and Medrano 2002). When mathematically translated into a model, both processes could finally lead to similar rates of calculated photosynthesis and stomatal conductance (Wilson et al. 2000). Because Aleppo pine is a drought-avoiding species, most of the drought inhibition of photosynthesis should result from stomatal limitation (Martínez-Ferri et al. 2000). Nevertheless, additional physiological data could be collected to test the correctness of the approach used, at least at the species level (Wilson et al. 2000).

The MAIDEN model shows that the bud-burst process triggered by temperature seems to greatly influence the interannual variability of bole increment at the oak site (see also Misson 2004). As shown previously, the importance of phenology in spring is associated with the growing-season length, which greatly controls ecosystem productivity (Goulden et al. 1996; Myneni et al. 1997; White et al. 1999). Results from the MAIDEN model show that the influence of bud-burst date on oak is connected with the carbohydrate-reserve dynamics. Remobilization of the carbohydrate reserves in spring seems to be of major importance for the timing of leaf and root expansion, which affect the growing season length and thus subsequent bole increment. This finding is confirmed by our experimental data, which show that $287.5 \text{ g}\cdot\text{m}^{-2}$ of carbon ($\text{LAI} = 5.75 \text{ m}^2\cdot\text{m}^{-2}$ and $\text{SLA} = 0.02 \text{ m}^2\cdot\text{g}^{-1}$) is needed annually for spring leaf setting at the oak site. This amount of carbon has to come from the carbon store reservoir because it cannot be produced by current photosynthesis in the short time period of bud burst. Because the amount of carbon that can be mobilized in spring is linked to the carbon stored the previous year, these processes explain how the performance of the oak trees is so closely linked from one year to the next.

The MAIDEN model, on the other hand, shows that carbohydrate-reserve dynamics, phenology, and bole growth are less intimately connected in Aleppo pine trees. As an evergreen species, pine is not so dependant on stored carbon for spring leaf growth. Furthermore, as shown by previous studies, shoot growth and needle elongation show a marked multiperiodical pattern (Serre-Bachet 1976a, 1976b; Calamassi et al. 1988). The several shoot and stem growth flushes observed during the vegetative period are characteristics of indeterminate free-growth species (Calamassi et al. 1988; Borghetti et al. 1998; Nicault et al. 2001). In the Aleppo pine ecosystems studied, where drought stress is the foremost controlling factor, trees take advantage of short-term water availability periods to fulfill the basic processes of carbon assimilation and structure development (Nicault et al. 2001). Many studies show that bole radial increment is less linked from one year to the next in what dendroecologists have called a "sensitive" site, because the environment is so limiting that trees mostly respond to the current climatic factors (Fritts 1976; Cook and Kairiukstis 1990). While the MAIDEN model tends to reproduce this process for the pine sites, response function analysis indicates a greater link between previous-year climatic conditions and current-year bole increment. The MAIDEN model would need some further development to be able to bring out the finer points of stem growth processes. At this level, results show that a direct winter temperature effect on the bole in-

crement the following season should be investigated for Aleppo pine. Processes may involve control of stomatal conductance (Running and Coughlan 1988) or inhibition of photosynthesis and cambial activity by freezing temperatures (Öquist 1983; Ottander and Öquist 1991; Guehl 1985; Nicault et al. 2001).

Sensitivity analysis of the response of simulated bole increment, $B_{ci}(t)$, to the model parameters shows that calibration parameters such as the canopy water storage coefficient (C_{ws}) and the root to leaf fraction (λ) may not be so important because of the relative insensitivity of $B_{ci}(t)$ in both of these contrasting ecosystems. This result suggests that these calibration parameters would be better fixed at some standard value that could be deduced from the literature, thus reducing the risk of overfitting the model (Sievänen and Burk 1994). Furthermore, discrepancies between the autocorrelation functions calculated on the measured and the simulated series indicate some possible misspecifications in the carbon allocation submodel. Presently, each allocation parameter related to carbon storing and mobilization has a small individual significance, even though in the case of oak they have a significant influence, when taken altogether. Reducing their number to one or two significant parameters should improve the properties of the simulations.

Conclusion

Natural ecosystems are so complex as to be beyond the limits of our intuitive comprehension based on purely empirical analyses. This paper shows that the process-based MAIDEN model allows us to better understand the climate – tree growth relationship compared with standard statistical methods usually applied in dendroecological studies. We have shown that the use of MAIDEN with dendroecological data is an efficient methodology for understanding major climatic controls on tree growth over several decades, but also enables us to gain insight into high-resolution ecophysiological processes. Most parts of the MAIDEN model were adapted from previous models and combined to offer an original tool to analyze the relationship between climate and tree growth. The carbon allocation submodel is innovative and works satisfactorily at reproducing the autocorrelation structure of tree-ring series. Furthermore, the strong link in the model among carbon storage, remobilization, spring leaf and root expansion, and subsequent bole growth effectively suggests that the carbon allocation submodel is well justified from an ecophysiological point of view.

The MAIDEN model is sufficiently generic to be applied across temperate to Mediterranean ecosystems and on different species. A future step towards generality will be to test the model on mountainous ecosystems. For modeling dendrochronological series in such ecosystems, the effect of winter temperature on bole increment in the following season should be implemented in the model. Furthermore, MAIDEN has been designed to be widely applicable at large spatial scale because it needs only a few climatic inputs as well as simple species and site condition parameters. Nevertheless, the model should be tested at the regional scale, with data collected from different sites, to determine if it is sensitive enough to detect functional differences arising from spe-

cies and ecosystem traits that are less contrasting than those tested in this paper. In the future, we plan to improve the calibration-validation procedure of the model based on the inverse modeling technique that will also allow us to better appreciate the model's sensitivity to the parameters (Guiot et al. 2000).

Acknowledgements

This research has been supported by the European Union (FORMAT project ENV4-CT97-0641), the Walloon region (Belgium), and the region Provence – Alpes – Côte d'Azur (France). I thank Benjamin Simon very sincerely for his technical help during this project. I also thank two anonymous referees and Doug Maynard, who helped to significantly improve the first version of this paper.

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