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Process-based simulation of seasonality and drought stress in monoterpene emission models

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Abstract

Canopy emissions of volatile hydrocarbons such as isoprene and monoterpenes play an important role in air chemistry. They depend on various environmental conditions, are highly species-specific and are expected to be affected by global change. In order to estimate future emissions of these isoprenoids, differently complex models are available. However, seasonal dynamics driven by phenology, enzymatic activity, or drought stress strongly modify annual ecosystem emissions. Although these impacts depend themselves on environmental conditions, they have yet received little attention in mechanistic modelling.

In this paper we propose the application of a mechanistic method for considering the seasonal dynamics of emission potential using the “Seasonal Isoprenoid synthase Model” (Lehning et al., 2001). We test this approach with three different models (GUENTHER, Guenther et al., 1993; NIINEMETS, Niinemets et al., 2002a; BIM2, Grote et al., 2006) that are developed for simulating light-dependent monoterpene emission. We also suggest specific drought stress representations for each model. Additionally, the proposed model developments are compared with the approach realized in the MEGAN (Guenther et al., 2006) emission model. Models are applied to a Mediterranean Holm oak (*Quercus ilex*) site with measured weather data.

The simulation results demonstrate that the consideration of a dynamic emission potential has a strong effect on annual monoterpene emission estimates. The investigated models, however, show different sensitivities to the procedure for determining this seasonality impact. Considering a drought impact reduced the differences between the applied models and decreased emissions at the investigation site by approximately 33% on average over a 10 year period. Although this overall reduction was similar in all models, the sensitivity to weather conditions in specific years was different. We conclude that the proposed implementations of drought stress and internal seasonality strongly reduce estimated emissions and indicate measurements are needed to further evaluate the models.

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1 Introduction

Isoprenoids represent a heterogeneous compound class made up of a wide range of reactive volatile hydrocarbons (i.e. isoprene, monoterpene, sesquiterpene) which are emitted by most plant species. These emissions are highly important for air chemistry and air pollution (e.g. Fuentes et al., 2000; Kanakidou et al., 2005; Szidat et al., 2006; Gelencser et al., 2007), and are likely to indirectly affect the concentration of greenhouse gases (e.g. Pierce et al., 1998; Olofsson et al., 2005). Air pollution impacts depend on the availability of reaction partners, i.e. reactive nitrogen compounds, which have a regionally specific seasonal pattern that is driven by anthropogenic as well as biological activities (e.g. Pierce et al., 1998; Fiore et al., 2005; Tie et al., 2006). Thus, it is not only the total amount but also the timing of emissions that is important.

Plant physiological processes are largely affected by seasonal cycles of environmental conditions such as temperature, radiation, and water availability. It has been recognized that climate change already affects seasonal cycles in terrestrial ecosystems, most notably in phenology (e.g. Walther et al., 2002; Menzel et al., 2006), and will continue to do so in the future (Gitay et al., 2001). Temperature is expected to increase while water availability will probably decrease in many regions, one of them being the Mediterranean basin (Giorgi et al., 2004; Giorgi, 2006; Beniston et al., 2007; IPCC, 2007). It is thus expected that temperature is affecting short-term isoprenoid emission directly by enhancing biosynthesis and evaporation, but also indirectly by changing boundary conditions on medium and longer time scales. These are particularly the dynamics of foliage development and enzymatic activities that are related to cumulative temperature (and others) and are known to affect emission (Mayerhofer et al., 2005; Pio et al., 2005). Seasonal changes in emissions due to these two factors are termed as seasonality throughout the following text. Seasonality effects are reported for deciduous as well as coniferous. Additionally, environmental stresses, which also often follow a seasonal dynamic, such as drought, can alter the physiological pre-conditions for plant emission (Monson et al., 2007; Grote et al., 2009a). A better understanding

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of these seasonal dynamics is therefore also necessary to consider for reliable projections of both current and projected future isoprenoid emissions.

The short-term emission of isoprenoids is a function of temperature and radiation and has been described as such by several models (see reviews in Arneth et al., 2007; Grote and Niinemets, 2008), which have been applied on local, regional and global scales. These models, however, have a developmental bias towards short term responses – partly due to a lack of long term seasonal measurement data. Other processes, operating over longer time scales, such as the effect of seasonality, the effect of seasonal cycles of water availability, and potential effects of CO₂ fertilisation have received little attention. Projected future atmospheric CO₂ concentration changes have been suggested to modify the emission response on the decadal or longer time scale (Possell et al., 2005; Arneth et al., 2007, 2008a). The determination of seasonality and drought effects, however, has not as yet been systematically investigated, and still represents a major uncertainty of biogenic emission simulations (Funk et al., 2005; Monson et al., 2007; Arneth et al., 2008b).

The potential (or basal) emission is a species specific factor that describes emission rates under standard conditions (e.g. 30°C, 1000 μmol PAR m⁻² s⁻¹). The isoprenoid emissions from most models scale linearly with this factor which is however known to change considerably during the year (e.g. Monson et al., 1994; Hanson and Sharkey, 2001; Hakola et al., 2006; Holzinger et al., 2006). The change in potential emission throughout the year is either neglected (particularly when only short periods are investigated) or empirically derived correction factors/equations are introduced (e.g. Staudt et al., 2000, 2002; Schaab et al., 2003). Although it is known that emission potential depends on prevailing temperature and light conditions (e.g. Staudt et al., 2003), only few approaches have been developed to derive seasonality dynamically from environmental influences:

Fuentes and Wang (1999) used a function fitted to cumulated temperature or growing degree days, respectively, He et al. (2000) correlated emission potential to the number of monthly sunshine hours, and Geron et al. (2000) applied the integrated temperature

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of the previous 18 h instead of instantaneous temperature. However, there are only two models known to the authors that explicitly account for the cumulative effect of both impacts temperature and radiation, throughout longer time periods. One is the respective routine of the MEGAN model (Guenther et al., 2006; Müller et al., 2008), which applies an empirical adjustment based on the past 10 d of light and temperature to calculate emissions, and the other is the SIM model that derives the seasonal course of the isoprenoid forming enzyme activity, which is closely related to potential emission, explicitly from the previous days climatic conditions (Lehning et al., 2001). Only the latter model reflects the finding that seasonal changes in enzyme activity result from physiological production and destruction processes (Lehning et al., 1999; Loreto et al., 2001; Fischbach et al., 2002; Mayrhofer et al., 2005).

The second seasonal emissions driver is drought stress. Mild drought stress does not affect the light dependent emission of isoprene and monoterpenes or reduces it only moderately (e.g. Bertin and Staudt, 1996; Brilli et al., 2007; Staudt et al., 2008). Strong, long-lasting drought, however, decreases isoprenoid emissions considerably (Hansen et al., 1999; Pegoraro et al., 2004; Lavoit et al., 2009). Overall, an impact of summer drought on annual isoprenoid emission has frequently been observed (Geron et al., 1997; Staudt et al., 2002; Plaza et al., 2005). A mechanistic understanding of isoprenoid responses to drought stress, however, has not yet been established. Due to this limited understanding as well as the strong dependence on species and site, drought effects have not been consistently represented in emission modelling yet.

In this paper, we investigate the sensitivity to drought stress and seasonality of three isoprenoid models commonly used in regional/global applications (GUENTHER, Guenther et al., 1993; MEGAN, Guenther et al., 2006, and NIINEMETS, Niinemets et al., 2002a), and one model of higher detail that has only been applied to specific sites and species (BIM2, Grote et al., 2006). We are concentrating on the investigation of light-dependent monoterpene emissions, whose emission behaviour is generally similar to that of isoprene (Ciccioli et al., 1997). Emissions from storages are assumed not to be relevant in the investigated ecosystem and are thus not accounted for. We propose the

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implementation of the SIM model as the seasonal driver of changes in emission potentials for all models except MEGAN, which comes with its own seasonality procedure. Additionally, we suggest relations between monoterpene emission and relative soil water availability that are adapted to the different ways of modelling isoprenoid emission as represented by the emission models.

The models are compared on the basis of the same canopy model which had been constrained through FLUXNET carbon flux data (Baldocchi et al., 2001; Misson et al., 2007) and of the boundary conditions of a Mediterranean Holm oak stand (*Quercus ilex*). Field emission data, gathered at the site are used to calibrate the models.

2 Materials and methods

2.1 Site description and data availability

Data and simulations refer to a study site located 35 km NW of Montpellier (Southern France) in the Puéchabon State Forest (3°35'45" E, 43°44'29" N, 270 m a.s.l.). Vegetation is largely dominated by a dense over-storey of Holm oak (*Quercus ilex*) trees (mean canopy height: 5.5 m, rooting depth down to 4.5 m). The climate is typical Mediterranean with cool and wet winters and warm and dry summers. The mean annual temperature is 13.5°C and the mean annual precipitation is 872 mm. Soil texture is homogeneous down to 0.5 m depth and can be denoted as silty clay loam (referring to the textural triangle, United States Department of Agriculture), with a limestone rock base. For more details on the site see <http://www.cefe.cnrs.fr/fe/puechabon/>.

Due to the Mediterranean-type climate and the low water holding capacity, the water content in summer falls regularly below the value at which drought stress limitations to photosynthesis are expected (Rambal et al., 2003; Keenan et al., 2009b). The timing and extent of drought conditions varies from year to year, but water content values close to the wilting point are observed in almost every year. From the years of measurements, 2005 was slightly cooler (annual average temperature 13.0°C) and

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2006 warmer and dryer than the long-term average (total precipitation 773 mm, annual average temperature of 14.1°C, see Allard et al., 2008). The period 1998 to 2007 that we used to compare the different emission models was slightly warmer and wetter than the long-term average (13.7°C, 913 mm). The standard deviations in this period are 0.6°C and 228 mm, respectively.

The investigation of well-watered trees has been carried out at a 10-year old Holm oak plantation which was irrigated regularly during 2006. This plantation is located in Montpellier close to the CEFE-CNRS institute in southern France (43°36' N, 5°53' E) on a deep clay soil with good water availability. Genetic similarity of the trees to those of the eddy-covariance measurement site is ensured because the trees originate from acorn samples from the same site (Puéchabon State Forest). Since only measurements of new leaves are used for fitting the emission potential of the models, stand structural aspects are not important. Due to the close vicinity of both sites that are only app. 30 km apart, we assume no difference with respect to their atmospheric climate conditions.

Measurements of leaf scale emissions are taken from Grote et al. (2009a) and Lavoit et al. (2009). They were conducted from May to October (12 occasions in 2005, 9 occasions in 2006) on the field site Puéchabon at current year leaves of adult trees about every second week under sunlit conditions (mostly between 10 and 12 a.m.). Identical measurements were carried out in 2006 at the irrigated plot in Montpellier during the weeks in between (9 occasions).

Enzyme activity has been determined in 2006 according to standard protocols described in Fischbach et al. (2000) using the same leaves as used for emission measurements. Enzymatic data provided calibration information for the seasonal dynamics model SIM. The emission measurements from the irrigated plot (only 2006) are used to calibrate the combined SIM/emission models (without drought stress). The emission data from the natural field site (2005 and 2006) are then used to evaluate the results from simulations that included drought stress (=relative soil water depletion). Although drought stress acts differently on GUENTHER and NIINEMETS models, no model spe-

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cific fitting has been carried out. BIM2 relies on previous calibration based on a smaller data set (Grote et al., 2009a). For both years half-hourly weather input data was available. Long term comparisons are based on hourly weather data from 1998 to 2007. In order to investigate the sensitivity of the models to drought and seasonality, we ran different simulation experiments which considered: A) a fixed emission factor with no drought stress, B) a fixed emission factor with drought stress, C) a seasonally dynamic emission factor with no drought stress and, D) a seasonally dynamic emission factor including drought stress. For all long term simulations, the initial set of forest structural boundary conditions was re-set in the model framework at the beginning of each year to avoid confounding effects of shifts in structural components such as leaf area, etc.

2.2 Model description

2.2.1 Modelling framework

For all simulations, a modelling framework has been used which is designed to couple one-dimensional biosphere models to describe different processes within the ecosystem. The framework provides climate data and initial variables for every (below- and aboveground) layer of the ecosystem from available site information or estimates. This ensures the same initial conditions and dynamic boundary conditions for all emissions models in the investigation. Short time step model results are aggregated in order to be used as input for models with larger time steps. The models implemented can be applied alternatively or in addition to each other (for more information see Grote, 2007; Grote et al., 2009a, b; Holst et al., 2009).

In the current context the short-term isoprenoid emission models MEGAN (Guenther et al., 2006), GUENTHER (Guenther et al., 1993), NIINEMETS (Niinemets et al., 2002a), and BIM2 (Grote et al., 2006) are coupled with models describing the canopy micro-climate within the canopy (ECM, Grote et al., 2009a) and the soil (DNDC, Li et al., 1992), photosynthesis (FARQUHAR, Farquhar and Von Caemmerer, 1982), seasonal development of enzyme activity and basal emission factors (SIM, Lehning et al., 2001),

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phenology (PSIM, Grote, 2007), and soil hydrological conditions (QUERCUS, Rambal et al., 1993, 2003) (see Fig. 1 and model descriptions below). The photosynthesis and emission models are run on a half hourly time step, corresponding to the available weather data. The boundary conditions for emissions, i.e. enzyme activities or basal emission factors, leaf development states, and the state of relative water supply are updated daily.

2.2.2 Biosphere models

ECM (empirical canopy model) calculates radiation, temperature, vapour pressure, and wind profiles for a given canopy. The radiation regime is determined using a simple one-dimensional light extinction scheme based on canopy layers with fixed extension and empirical foliage distribution (Grote, 2007). The sunlit and shaded fractions of the foliage are differentiated for each layer (Spitters et al., 1986). Temperature development in the canopy is given by an empirical function for each layer between the canopy upper boundary and at the soil surface. Soil surface temperature is calculated by the DNDC (DeNitrification-DeComposition) module (Li et al., 1992) on the basis of heat capacity and conductance of the soil components in each soil layer.

FARQUHAR: the common Farquhar approach (Farquhar and Von Caemmerer, 1982) is used along with the parameterization provided by Long et al. (1991). Stomata conductance is calculated with the approach suggested by Ball et al. (1987). Photosynthesis is calculated separately for sunlit and shaded foliage but pooled over each layer for emission input. This is in accordance with the determination of emission activity which is also layer specific.

Drought stress is accounted for by the stomata conductance calculations inherent in the model and additionally by means of a reduction in the rate of electron transport and maximum carboxylation capacity (Vc_{max}) (Keenan et al., 2009b). Here we apply a simple linear relation to relative soil water content (RWC), parameterised from

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measurements of stomata conductance (Rambal et al., 2003):

$$DS = \text{Min} \left(1.0, \frac{RWC}{RWC_{lim}} \right) \quad (1)$$

with DS denoting the drought stress scaling factor. The limit value of relative soil water content at which drought stress starts to affect a process (RWC_{lim}) has been set to 0.7 (Rambal et al., 2003; Keenan et al., 2009b).

QUERCUS (Rambal et al., 1993, 2003) uses a lumped approach on soil water conditions considering the whole soil as one layer. Water exceeding the infiltration capacity of the soil is treated as deep drainage that is released over time using an empirical exponential equation. Potential evapotranspiration is estimated with a modified Priestley-Taylor approach (Priestley and Taylor, 1972; with parameter alpha fixed to a value of 1.1) that accounts for a variable proportion of ground heat flux in dependence on leaf area index (LAI) and vegetation density. Transpiration is determined from potential evapotranspiration and foliage conductance in half hourly time steps using air temperature and solar irradiation as input. The model has already accurately represented the soil water content throughout the years 1993 to 2006 at the Puéchabon site (see Grote et al., 2009a) and is able to reproduce gross primary production for the site reasonably well (see Fig. 2).

2.2.3 Emission models

Three commonly used emissions models of varying complexity were coupled to the biosphere modelling framework.

GUENTHER/MEGAN: by far the most widely used model for simulation of natural isoprenoid emissions is developed by Guenther et al. (1991, 1993). This approach describes the emission rates using potential emission factors for isoprene (E_I) and monoterpenes (E_M), and adjusting these potentials by two empirical factors, one describing the response to light intensity and the other to leaf temperature. The correlation between short term fluctuations, light intensity and leaf temperature is widely

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studied and much work has gone into validating the GUENTHER model under different environmental conditions (Monson et al., 1994; Petron et al., 2001). The emission factors used in the model are emission rates normalized to a leaf temperature (T) of 30°C and quantum flux density (Q) of 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic active radiation (PAR) (Guenther, 1991; Guenther et al., 1993, 1995, 1997). For more information, we refer to the detailed descriptions in these papers.

In the original Guenther model, several coefficients that describe the dependency to light and temperature are fixed parameters. In the MEGAN emission model, these values are dynamic in time and depend on short term (24 h) and long term (10 d) fluctuations in temperature and light intensity (see Guenther et al., 2006). Additionally, the sunlit and shaded parts of the foliage within one canopy layer are parameterised differently, representing their sensitivity to light. These algorithms are applied for all simulations indicated as the MEGAN model, whereas SIM is not used. Other specifications of the MEGAN model are not considered which is possible particularly because we apply the model to an evergreen canopy (in this case no leaf age factor is considered in MEGAN).

NIINEMETS: this model (Niinemets et al., 2002a) for isoprene and monoterpene emissions takes a more process-based approach. It links the emission rates to synthase enzyme activity (S_S) to predict the capacity of isoprenoid synthesis as well as to foliar photosynthetic metabolism via the photosynthetic electron transport rate, J , to predict substrate (Niinemets et al., 1999, 2002a). The supply of dimethylallylpyrophosphate (DMADP) and nicotinamid-dinucleotid-phosphate (NADPH), which both depend on the rate of photosynthetic electron transport, are considered to be the main controlling factors.

Emission rates are calculated from the fraction of total electron flow that is used for isoprenoid synthesis, the rate of photosynthetic electron transport, and the cost of isoprenoid synthesis in terms of electrons. Thus, emissions are closely linked to photosynthetic activity of leaves using only one single leaf dependent parameter ε , the fractional allocation of electron transport to synthase activity. Emission rates are given

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by the equation (Niinemets et al., 1999, 2002a):

$$E = \varepsilon J_T \frac{C_i - \Gamma^*}{\zeta (4C_i + 8\Gamma^*) + 2(C_i - \Gamma^*)(\vartheta - 2\zeta)} \quad (2)$$

where J_T is the total rate of photosynthetic electron transport, C_i is the internal CO_2 concentration, and Γ^* is the hypothetical CO_2 compensation point of photosynthesis that depends on photorespiration (Farquhar and Von Caemmerer, 1982). ζ is the carbon cost of specific isoprenoid (6 mol mol^{-1} for isoprene and 12 mol mol^{-1} for monoterpenes) and ϑ is the NADPH cost of specific isoprenoids (mol mol^{-1}). For monoterpenes, ϑ is found as a weighted average of the costs of all terpene species emitted. In practice, $\vartheta \cong 28 \text{ mol mol}^{-1}$, with small variability because the contribution of oxygenated monoterpenes that may have lower electron cost or reduced monoterpenes that may have higher electron cost is generally small (Niinemets et al., 2002a, 2004). ε , the fractional allocation of electron transport to isoprenoid synthesis, is given by:

$$\varepsilon = F_d \frac{S_S}{J_{\max}} \quad (3)$$

where S_S is the specific activity of isoprenoid synthase (either isoprene or monoterpene synthase) in $\text{mol isoprenoid (g isoprenoid synthase)}^{-1} \text{ s}^{-1}$ that depends on temperature according to an Arrhenius type equation that has a temperature optimum, and J_{\max} is the light saturated rate of total electron transport that scales with temperature in a similar manner (Niinemets and Tenhunen, 1997). F_d ($\text{g m}^{-2} \text{ mol electrons mol isoprenoid}^{-1}$) is the scaling constant that depends on isoprenoid synthase content (g m^{-2}) and also converts from isoprenoid units to electron transport units ($\text{mol isoprenoids mol electrons}^{-1}$) (Niinemets et al., 1999, 2002a). Thus, light dependence of isoprenoid emission entirely results from the light effects on photosynthetic electron transport, while temperature dependence is a combined temperature response of isoprenoid synthase and electron transport activities.

BIM2: the BIM2 model (Grote et al., 2006, 2009a) calculates pool changes of isoprene, monoterpene, and a number of precursors representing the methylerythritol-

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phosphate (MEP) pathway (Rohmer, 1999). The model basically consists of a sequence of first-order Michaelis-Menten equations that depend on instantaneous temperature. Assuming the absence of specific storage structures and neglecting the effect of unspecific storages, the isoprene and monoterpene production is set equal to the emission of these substances. Potential production rates are determined by activities of isoprenoid biosynthesis-related enzymes (i.e. isoprene and monoterpene synthases). Primary substrates for the emission model are provided by photosynthesis (Grote et al., 2009a). The emission model uses a fixed internal time step of seven seconds. To mitigate the impact of the different time steps between photosynthetic supply and usage, the supply rate is adjusted to continuously increase or decrease between two consecutively following assimilation rates.

The immediate substrates for isoprenoid formation PEP (phosphoenolpyruvat) and PGA (phosphoglycerate) are assumed to be smaller than the photosynthetic production of triose phosphates (tp), considering exchange equilibrium caused by import and export from the plastids and transformation of triose-phosphate into larger molecules such as starch. The integrated effect is seen as an equilibrium relation to photosynthetic production:

$$\text{PGA} = \text{FPGA} \cdot \frac{\text{tp}^2}{\text{KM}_{\text{tp}} + \text{tp}} \quad (4a)$$

$$\text{PEP} = (1 - \text{FPGA}) \cdot \frac{\text{tp}^2}{\text{KM}_{\text{tp}} + \text{tp}} \quad (4b)$$

KM_{tp} (Michaelis-Menten constant for triose-phosphate removal) and FPGA (fraction pga of whole available triose-phosphates) are empirical determined parameters. While FPGA is a priori set to 0.375 (Grote et al., 2006), KM_{tp} is estimated to be 100 (Grote et al., 2009a).

It should be considered that the concentration of photosynthetic products and inter-

mediates is exponentially declining with time. This is simply described by:

$$c'_i = c_i - LR_i \cdot ts \cdot c_i \quad (5)$$

where ts denotes the time step (7 s) and c is substrate concentration ($\mu\text{mol L}^{-1}$). Subscript i denote the substrates (PGA, PEP, NADPH, and adenosine-triphosphate [ATP]) as well as the intermediates of the MEP pathway to isoprene and monoterpene production. LR is the loss rate set to the same value for PGA, PEP, and all intermediates. Loss rate has been derived iteratively by fitting BIM2 to the measured emissions of the well watered plants (Grote et al., 2009a; see Fig. 3). The value is $0.0035 \mu\text{mol} \mu\text{mol}^{-1} \text{s}^{-1}$. The loss rates of ATP and NADPH molecules are set 10-fold the value of other molecules to obtain realistic concentrations (Loreto and Sharkey, 1993; Nogues et al., 2006).

2.2.4 Drought impacts in emission models

Drought impacts on emissions are realized either directly by reducing the emission process itself, or indirectly by the effect of a reduced photosynthesis. Further indirect impacts, e.g. due to changes in leaf temperature when transpiration is reduced are currently not considered.

The MEGAN model includes a direct effect of limiting soil water availability that has originally been applied for isoprene emissions only (Guenther et al., 2006). In the current approach, both the GUENTHER and MEGAN emission calculations are reduced by drought stress directly in parallel with photosynthesis, by applying Eq. (1). We admit that this direct consideration can hardly be termed “process-based” as stated in the title of the manuscript. It serves however as a comparison to the more mechanistic approaches described below.

The same drought stress formulation determines the response of the NIINEMETS model, but the effect is indirect because not emission itself but the rate of electron transport (J_T) is reduced in addition to $V_{c_{\max}}$. Since both photosynthetic variables are used to determine the emission capacity, drought stress leads to reduced emissions.

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In the BIM2 model, the effect is also indirect because none of the variables used to describe the emission process itself are affected by soil water availability. The impact is solely due to a lack of precursor availability, which is controlled by photosynthetic production and depletion of emission precursors by various processes.

5 2.2.5 Emission activity and emissions potentials

All other factors being equal, simulated emissions scale linearly with the species specific emission potential, E_M . This emission potential has been found to exhibit strong seasonal variation, though this variation has not yet been explained in a process based manner. The SIM model provides a mechanistic description of this seasonal variation, relating the emission potential to temperature and radiation driven enzyme dynamics.

The SIM model is a simple algorithm that derives daily enzyme activity from the previous day's value, an increasing and a decreasing term. The increase is defined by the daily radiation sum I (J cm^{-2}), an Arrhenius term based on daily average temperature, T (K), and the relative development state of the leaves, $pstat$, whilst the decrease is a constant fraction of the previous days enzyme activity. Thus the change in enzyme activity for a particular day and canopy layer can be written as:

$$\frac{\Delta act}{dt} = \alpha_0 \cdot pstat \cdot I \cdot arrh - \mu \cdot act$$

$$arrh = A \cdot e^{\left(\frac{-E_{act}}{R \cdot T}\right)}, \quad (6)$$

where act is the enzyme activity of the previous day ($\mu\text{mol L}^{-1} \text{s}^{-1}$), R the general gas constant ($8.3143 \text{ J mol}^{-1}$), α_0 the enzyme formation term (s^{-1}), μ the enzyme decay term (0.175 s^{-1}) (Lehning et al., 2001), A a unitless factor for normalizing the Arrhenius term to 1 at 30°C (660.1×10^6), and E_{act} , the activation energy for a doubling of the reaction velocity ($51164.8 \text{ J mol}^{-1}$). Emission activity is calculated for each canopy layer separately ($\text{nmol m}^{-2} \text{ foliage s}^{-1}$). The leaf development term $pstat$ indicates the phenological state of the leaf according to Lehning et al. (2001) and Grote (2007). It increases from 0 to 1 during the period of flushing and decreases with age after

senescence has started. The monoterpene synthase formation term, α_0 , is adjusted to measurements taken on site (see Fig. 4).

Enzyme activity is transformed to the emission factor using the specific leaf weight (LSW), which changes linearly with canopy depth from 233 g m^{-2} at the upper canopy boundary to 100 g m^{-2} at the bottom of the canopy (Niinemets et al., 2002b). For the GUENTHER approach, EF ($\mu\text{g g}^{-1} \text{ dry weight h}^{-1}$) is given by:

$$EF = \frac{\text{act} \cdot \Theta}{\text{LSW} \cdot F_{SC}} \quad (7)$$

The transformation term Θ is 120×3.6 , which is the molar mass of carbon atoms within one monoterpene molecule times the transformation from nmol s^{-1} into $\mu\text{mol h}^{-1}$. F_{SC} is a factor that accounts for the fact that the enzyme activity reflects a state that is substrate saturated which is never the case and thus has to be reduced to reflect the emission factor. It is adjusted based on the measurements from well watered plants (see below). Similarly, Eq. (7) is also used to derive the basal emission factor for the NIINEMETS approach, E_{act} ($\mu\text{mol g}^{-1} \text{ dry weight s}^{-1}$). The value of Θ here is 0.01, corresponding to the unit conversion from nmol to $\mu\text{mol C}$ considering 10 carbon atoms in one monoterpene molecule.

For the GUENTHER and NIINEMETS models we calibrated the scaling factor (F_{SC}) to the same data (obtained under well watered conditions) in order to approach the 1:1 line for each model separately (see Fig. 3). This resulted in an F_{SC} value of 5.2 for the GUENTHER and 7.7 for the NIINEMETS model (regression r^2 values are 0.74 for BIM2 and GUENTHER, and 0.62 for NIINEMETS; standard errors are 2.08, 2.86, and 2.26 for BIM2, GUENTHER and NIINEMETS, respectively).

In order to compare the effect of the seasonality in the three model approaches, simulations are additionally run with a fixed emission factor of $28 \mu\text{g g DW}^{-1} \text{ h}^{-1}$ (Seufert et al., 1997) which is in good accordance with the measured maximum factor at the site in Puéchabon reported by Staudt et al. (2002) and Lavoit et al. (2009). The value has been transformed into enzyme activity using the reciprocal of Eq. (7). Additionally, the

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MEGAN model is run for comparison using the fixed emission factor and the internal modification of variables (see above). The representation of seasonality in the MEGAN model is derived from emission result-comparisons of MEGAN and GUENTHER models. This is demonstrated in Fig. 4 showing the relation of MEGAN and SIM algorithm output.

2.2.6 Simulated boundary conditions and other model constraints

For scaling from leaf to canopy we used assumptions on foliage distribution as outlined in Grote (2007). These are based on measurements of Sala et al. (1994) that show a highly skewed foliage distribution with more than 90% of the total leaf weight concentrated in the upper 30% of the canopy. Also, phenological development has been accounted for as described in Grote (2007) considering a variation of leaf area index between 2 and 3.5 with the minimum in spring and the maximum in early summer.

The ECM model calculations of microclimate are discussed in Grote et al. (2009a). They show distinct radiation absorption averaging to 80% light reduction within the upper half of the canopy but only small variation in temperature (app. ± 1 degree between upper and lower canopy layers during typical summer days).

To evaluate simulated photosynthesis at the canopy scale we used data of a continuously measuring flux tower at the Puéchabon site that also provided climatic boundary data (averages 1998–2006 are presented in Allard et al., 2008). This tower is part of the EUROFLUX network (see Baldocchi et al., 2001; Baldocchi, 2003). The correlation between simulations and measurements is reasonably well despite occasional mismatches that are caused by mechanisms not covered in the modelling approach, e. a loss of foliage caused by an insect attack occurred during spring 2006 (Fig. 2). The smaller amount of foliage decreased GPP and is a likely reason for an over-estimation of GPP during this time and an over-estimation of drought stress (under-estimation of GPP) during early summer.

The soil water content calculated daily by the QUERCUS model has been successfully evaluated for the Puéchabon site (Rambal et al., 2003; Grote et al., 2009a) for the

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period from 1998 to 2006.

3 Results

3.1 Monoterpene emission at leaf scale

First, we compared the measured leaf scale emissions from the drought stressed
5 Puéchabon site with simulation results from the same time periods (Fig. 5). This was
done similarly as described for calibrating the F_{SC} factor of the NIINEMETS and GUEN-
THER models, but considering a dynamically calculated drought stress impact (Eq. 1).
High r^2 values (BIM2: 0.82, GUENTHER: 0.69, NIINEMETS: 0.83) and small standard
errors (BIM2: 1.65, GUENTHER: 1.65, NIINEMETS: 1.45) were obtained for simulat-
10 ing monoterpene emission under these natural conditions (Fig. 5). The slope of the
GUENTHER and NIINEMETS models were less than 1% different from one. Only the
BIM2 model slightly overestimated the emissions under drought stress by 16%.

3.2 Stand scale monoterpene emissions

3.2.1 Diurnal effect

15 Seasonal and annual model differences originate at least partly from differences in the
diurnal cycle of simulated emission. It should be noted that evaluation is based only
on measurements taken at midday and early afternoon. The daily dynamics of the
models show that even if emissions are similar during this time, the daily integral could
be different. The reason is the different weighting of environmental drivers that develop
20 differently during the day. This is particularly obvious during the high drought stress
period of 2006, when the BIM2 results are considerably smaller than the ones from
the other two models (6b and 6d). Another example is that the NIINEMETS model
generally simulates a steep increase of emission in the early hours because only small
photosynthetic activities are needed to support monoterpene production. Thus, the

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emissions from this model are usually considerably higher during the first 1–2 h after sunrise (Fig. 6). This does not necessarily lead to higher daily emissions because under unstressed conditions, the GUENTHER and BIM2 models reach higher maximum emissions (Fig. 6a). However, the NIINEMETS model is also relatively insensitive to changes of photosynthetic activity once a threshold is reached. This is the main reason for the higher emissions during stressed conditions and in deeper canopy layers, if compared to results from the other two models (Fig. 6b, c, and d). It should be noted that in very occasional cases (hot, no clouds, no drought stress) emission simulation in NIINEMETS and BIM2 (but not in GUENTHER) can be affected by a photosynthetic decline due to stomata midday depression.

3.2.2 Seasonality effect

Throughout a simulation period of 10 y (1998 to 2007) emissions using a fixed emissions factor and no drought stress were highest with the NIINEMETS model, which produced annual total emissions 1.6 times higher than BIM2 and 1.3 times higher than the GUENTHER model (Table 1). The differences in model results are caused by the different sensitivity to environmental variables in winter, spring and autumn (Table 2): while the substrate limitation in BIM2 strongly restricts emissions in winter, the NIINEMETS model scales much closer to temperature and allows for considerable emissions even in the Mediterranean winter (Fig. 7a and b). The stronger light dependence in the GUENTHER model renders this model's sensitivity to be in between that of the two other models (Fig. 8a and b). Accordingly, the NIINEMETS model is most strongly affected when an external seasonal driver is introduced. The effect of the application of SIM is so strong that no difference in seasonality between the models can be detected (Fig. 7c and d) and that the annual emission drops to a level in between the other models in most years included in this study (Fig. 8c and d).

The NIINEMETS model is also the least sensitive to annual environmental conditions with a difference of 30 mmol m^{-2} ground between the year with the highest (2003) and the lowest (2000) total emissions. With the GUENTHER and BIM2 models, emissions

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differ by approximately 40 mmol m^{-2} ground. Correlation of annual emission is better to annual maximum than to annual mean temperatures. It is also slightly negative to GPP (data not shown) which indicates that temperatures in summer are unfavourable for production even if drought stress is not considered.

3.2.3 Drought stress effect

In 2006, in which the most intense drought of all investigated years occurred, photosynthesis as well as simulated emission started to decline around day 150 (Fig. 7b and d) and recovered in late summer (app. day 260). Scaled across the whole canopy, annual emission in 2006 was only between 24% (BIM2) and 45% (NIINEMETS) of that calculated for unstressed conditions. On average over the 10 y period, simulated annual emissions were reduced between 28 and 36% (Table 1). Monoterpene emissions under Mediterranean conditions were more closely correlated to water availability than to primary production or average temperature in all models. The sensitivity, however, is largest in BIM2, leading to particular low simulated emissions in 2006 despite producing otherwise similar results as those of the NIINEMETS model (-5%) and moderately smaller values than the GUENTHER model (-29%). The MEGAN model produced higher emission estimates than the other models ($+34\%$). This reflects the fact that MEGAN contains an empirical measure of seasonality that is not as strong as that given by the SIM calculations (see Fig. 4) and thus leads to higher emissions particularly outside the dry period in spring and autumn (Fig. 7c and d).

Overall, the application of both, a seasonally dynamic emission factor and drought stress, dramatically reduced emissions for all models when compared to the original model formulations with fixed potential emission factors and no drought stress. The combined effect of a seasonally dynamic emission factor and drought stress reduces the total emissions budget of the GUENTHER and NIINEMETS models by an average of 74%.

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4 Discussion

4.1 Temporal and spatial variations

The results demonstrate the potential importance of considering the seasonality of emission dynamics. This corroborates the findings of many authors before (e.g. Monson et al., 1994; Tarvainen et al., 2005; Holzinger et al., 2006; Hakola et al., 2006; Dominguez-Taylor et al., 2007). We have presented a general process-based solution that computes this seasonality from temperature and light conditions which is applicable to at least the most common emission models used today in regional to global applications, be they empirical or more process-based. However, it remains to be investigated to which degree the approach can be applied with regard to species-dependent or plant-functional type related parameters.

The different models showed different sensitivity to the temperature and light driven seasonal dynamic impact factor due to the fact that their primary emission algorithms respond differently to these two environmental factors. The NIINEMETS model already has a strong relation to light regime and energy production (see description above and Eq. 2). Thus, with a uniform emission factor, emission can be sustained even in winter because light availability is still sufficient to supply photosynthesis and electron transport at the study site. In the GUENTHER model, the strong and direct response of emissions to both temperature and light results in a stronger seasonality by itself and thus gives a slightly smaller effect of dynamic basal emission. Surprisingly, the smallest effect of an explicitly calculated seasonality is obtained with the BIM2 model although the instantaneous emission response has a similarly strong link to temperature development as the GUENTHER model. This is attributed to the fact that emissions additionally depend on photosynthetic substrate supply which is sometimes limiting even under non-stressed conditions, particularly in deeper canopy layers.

The comparison with the MEGAN model shows that seasonality is less expressed than with the SIM approach. Due to limited evaluation data, we cannot judge which model is “better”. Also the absolute emission values obtained have to be taken with

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care because the leaf-scale emission factor used in this study is determined on sunlit leaves and is not the same as the “canopy emission factor” used in MEGAN that already takes into account a variation throughout the canopy. It is however assumed that introducing a leaf age factor also to evergreen canopies would bring the MEGAN approach closer to the one applied in SIM. In any case, the finding should encourage further investigations into the matter and indicates that seasonality settings may not easily be transferred between species and regions.

Overall, the application of the SIM algorithm for the calculation of emissions potentials provides an algorithm through which seasonal variation of the basal emission factor or activity can be accounted for. Higher temperatures in the future could alter the seasonal cycle of enzyme activity, which may increase the emissions potential, in particular during spring and autumn, where temperature is currently a limiting factor. Increased enzyme activity could lead to increased emissions in the future, a fact that is currently not included with mechanistic detail in any large scale emissions model estimates. The advantage of an activity-based description in comparison to an empirical one is in particular that it can be more easily evaluated. Our example simulations indicate that the SIM mechanism results in smaller and less variable spring and autumn emissions than the standard-MEGAN procedure in the Mediterranean area. This dependence of enzyme activity on the temperature and radiation regime also implies a differentiation of species emission potentials over a climatic gradient, which may explain the reported regional variation in emissions potentials (Guenther et al., 2006) and the generally large variability in reported emission potentials in the literature. The implication of the SIM model may thus provide a mechanistic means of describing regional changes in emissions potentials, but more data is required to reach a conclusive decision.

Due to the dependence of enzyme activity on the temperature and radiation regime, long-term dynamics in dependence on environment also leads to a spatial differentiation of emission factors within the canopy. This corresponds to results from Geron et al. (1994) and Harley et al. (1996) which indicate that the emission capacity varies

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with canopy depth. In Western Hemlock emission potentials in different canopy heights were significantly different although this was not found in Douglas fir forests (Pressley et al., 2004).

4.2 Drought stress effect

5 Strong and long-lasting drought stress has been observed to significantly reduce BVOC emissions (Bertin and Staudt, 1996; Brüggemann and Schnitzler, 2002; Pegoraro et al., 2004, 2006; Grote et al., 2009a). The quick recovery of the emissions after re-watering suggests that this reduction is due to either the reduction of synthase activity, or due to reduced substrate availability (Grote and Niinemets, 2008; Grote et al., 2009a). Given
10 the high uncertainty about the role of different processes involved, the resulting magnitude of the reduction of emissions due to drought, and interspecific differences in responses to this stress, modelling emissions during dry periods is still largely a hypothetical exercise (Arneith et al., 2008b; Monson et al., 2007). Here we apply a simple linear reduction function (Eq. 1), but more work is necessary to understand drought stress responses of emissions mechanistically.

15 No major difference was observed in the ability of each model to represent the measurements of monoterpene emissions on the leaf scale. The overestimation of 16% with the BIM2 model indicates that the resource limitation is possibly not the only mechanism responsible for the emission decrease under drought. This is in accordance with the discussion results in Grote et al. (2009a). However, the uncertainties
20 in the measurements are relatively large and need corroboration with additional data, particularly at the stand scale. We thus cannot yet conclude that the models do reproduce the decline in emissions under a natural seasonal drought cycle. The stand scale calculations showed considerable differences despite very similar results obtained at
25 the leaf scale, which highlights the uncertainty related to temporal and spatial scaling. The BIM2 model shows the largest sensitivity to drought. It is demonstrated that this effect originates from the resource limitation due to drought stress and is increased by the fact that less favourable photosynthetic conditions occur in deeper canopy layers.

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Despite its relation to photosynthesis the NIINEMETS model was shown to be the least sensitive of the studied models.

5 Conclusions

The presented results that show the effect of seasonality are expected to be generally applicable, for both monoterpenes and isoprene. This is likely to have large ramifications for regional and global emissions estimates, potentially reducing previous emission inventories considerably, in particular in regions characterised by a strong seasonal changes in water availability. The importance for drought exposed systems is due to the fact that dry periods generally converge with times when basal emission activity is high. In such cases the reduction of emission occurs particularly in the potentially most “productive” times whereas in other periods the basal emission potential is limiting. Such regions commonly have a large coverage of isoprenoid-emitting species either due to natural (Kellomäki et al., 2001) or anthropogenic (Vizueté et al., 2002; Lathiere et al., 2006; Geron et al., 2006) reasons (e.g. plantation of crops and fast growing trees to produce bio-energy).

It should however be noted that the estimation of absolute emission amounts is subject to a number of uncertainties related to measurements, model structure, and initialization conditions. With the inclusion of SIM calculated seasonality, we have reduced one of the major sources of differences between emission model estimates, though large differences, particularly in model temperature responses, remain (Arneth et al., 2007; Keenan et al., 2009a). With respect to emission measurements it will be necessary to increase the temporal and spatial density in future studies. It has been shown that variation of annual simulated emissions particularly results from 1) early and late hours of the day, 2) periods in spring and autumn and 3) deeper canopy layers. However, measurements for model evaluation at these times and places are scarce. It has also been demonstrated that the variation between years is considerable which underlines the importance of long-term investigations (Lavoit et al., 2009). Finally, for

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evaluating the upscaling procedure, stand scale emission measurements are urgently needed.

We conclude that the consideration of seasonality and drought impacts are highly important elements for climate change scenario analyses of isoprenoid emission for many regions, in particular in areas that exhibit seasonal drought stress today or in the future and host isoprenoid emitting plants (e.g. Lathiere et al., 2005; Wang et al., 2007). Our results suggest that many studies involving modelled BVOC emissions (e.g. regional inventories, effects of emissions on tropospheric ozone concentrations and air quality, etc.) may need to be revised to take into account the effect of seasonal cycles on emission estimates.

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Table 1. Average and standard deviation (shown in brackets) of annual emissions ($\text{mmol m}^{-2} \text{y}^{-1}$) for each model for the four experimental setups at the Puechabon site over the period 1998–2007. “Average emissions ($\text{mmol m}^{-2} \text{y}^{-1}$)” refers to the average annual emissions from all models for a particular experimental setup. Values correspond to Fig. 8.

Period 1998–2007	Fixed EF, no drought (Fig. 8a)	Fixed EF, drought (Fig. 8b)	Dynamic EF, no drought (Fig. 8c)	Dynamic EF, drought (Fig. 8d)
NIIN	140.01 (8.83)	110.29 (11.11)	54.01 (10.72)	37.75 (4.90)
BIM2	85.83 (12.03)	56.45 (10.49)	58.13 (12.57)	35.77 (7.42)
GUEN	107.95 (13.58)	74.19 (9.90)	45.50 (12.01)	27.62 (4.50)
MEGAN	–	–	67.19 (12.84)	44.35 (6.35)
Average emissions ($\text{mmol m}^{-2} \text{y}^{-1}$)	111.26	80.31	56.21	36.37

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Table 2. Emissions totals (mmol m^{-2}) for the periods JFM (January, February, March), AMJ (April, May, June), JAS (July, August, September), and OND (October, November, December) for the four experimental set ups, for each model, at the Puechabon site in 2006. “Average emissions ($\text{mmol m}^{-2} \text{y}^{-1}$)” refers to the average annual emissions from the three models for a particular experimental setup. Values correspond to Fig. 7.

Period	Fixed EF, No Drought (Fig. 7a)				Fixed EF, Drought (Fig. 7b)				Dynamic EF, No Drought (Fig. 7c)				Dynamic EF, Drought (Fig. 7d)					
	NIIN	BIM2	GUEN	Average	NIIN	BIM2	GUEN	Average	NIIN	BIM2	GUEN	MEGAN	Average	NIIN	BIM2	GUEN	MEGAN	Average
JFM	8.5	1.2	3.3	4.3	8.5	0.9	3.3	4.2	0.6	0.1	0.3	1.1	0.5	0.6	0.1	0.3	1.1	0.5
AMJ	48.7	32.8	42.4	41.3	37.6	15.6	24.9	26.0	16.6	19.9	15.9	26.3	19.7	11.5	8.7	8.1	14.4	10.7
JAS	64.1	59.4	69.4	64.3	29.2	9.2	16.6	18.3	34.2	49.5	40.7	50.5	43.7	14.6	6.8	9.5	11.9	10.7
OND	15.4	5.4	6.6	9.1	14.8	5.2	6.4	8.8	2.0	1.7	1.0	2.4	1.8	2.0	1.6	1.0	2.3	1.7
Total:	136.8	98.8	121.7		90.1	31.0	51.1		53.5	71.2	57.9	80.2		28.7	17.3	18.9	29.7	
Average emissions ($\text{mmol m}^{-2} \text{y}^{-1}$)	119.1				57.4				65.7				23.7					

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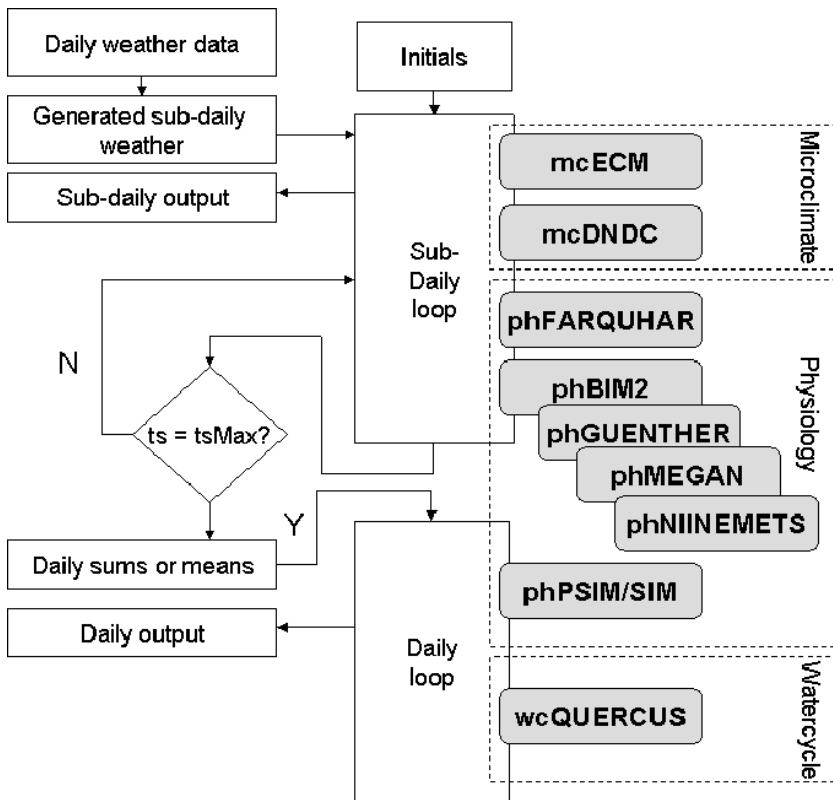


Fig. 1. Model framework. The three modules BIM2, GUENTHER, and NIINEMETS are alternatively called together with the other modules that describe the boundary conditions for isoprenoid emission, i.e. microclimate, physiology (photosynthesis and foliage development), and soil water content. The MEGAN model is in the same module as the GUENTHER model but with additional options to account for the integrated temperature and radiation effects.

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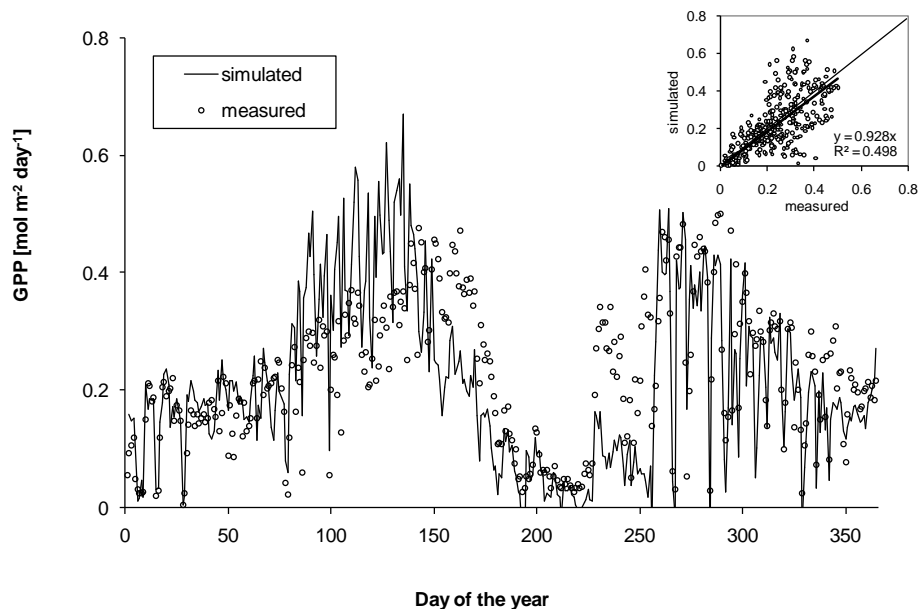
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**Fig. 2.** Simulated and measured gross primary production (GPP) during the year 2006.

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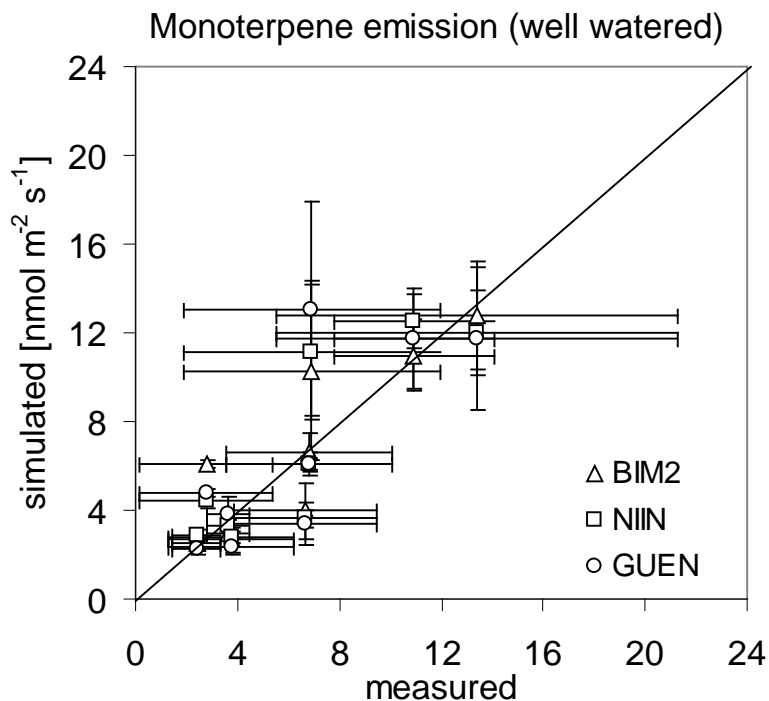


Fig. 3. Simulated and measured leaf scale monoterpene emissions at selected dates in 2006 from sunlit leaves of the well watered Holm oak site. Three models (BIM2, NIINEMETS, GUENTHER) are applied using SIM based seasonality. Each data point represents three leaf-measurements from a separate tree each. The error bars represent the standard deviation of measurements and the simulations for the three measurement times.

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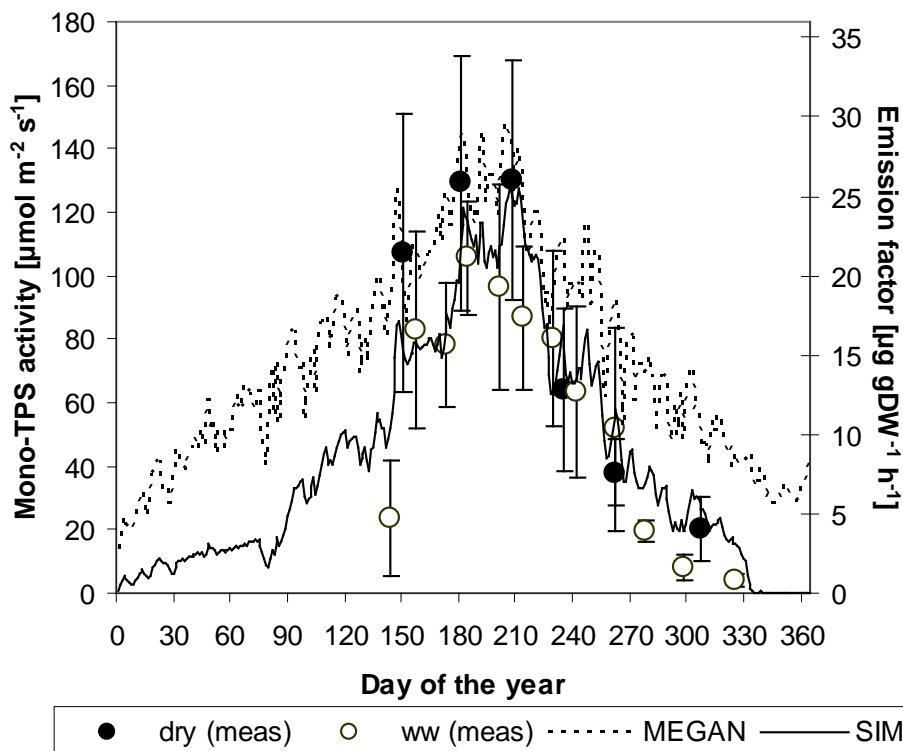


Fig. 4. Seasonal development of monoterpene activity and estimated emission factors for the year 2006 (reproduced from Grote et al., 2009a) together with the effective emission factor for the MEGAN model presented on the left y-axis (see text for further information).

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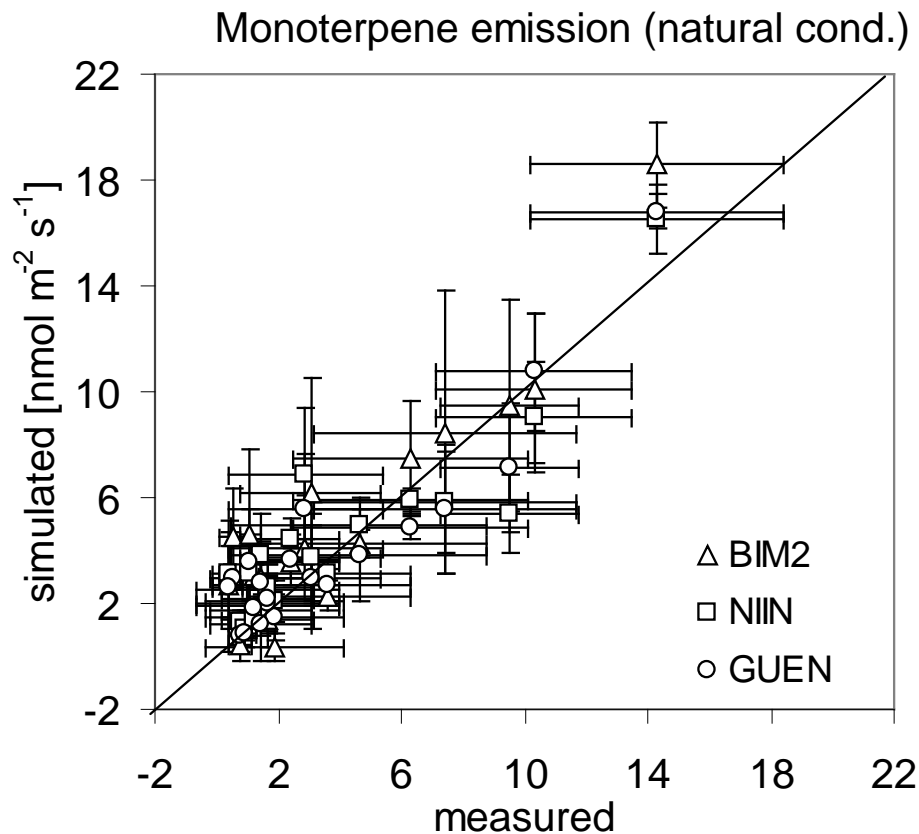


Fig. 5. See Fig. 3 but for drought stressed site and including measurement occasions in 2005 and 2006.

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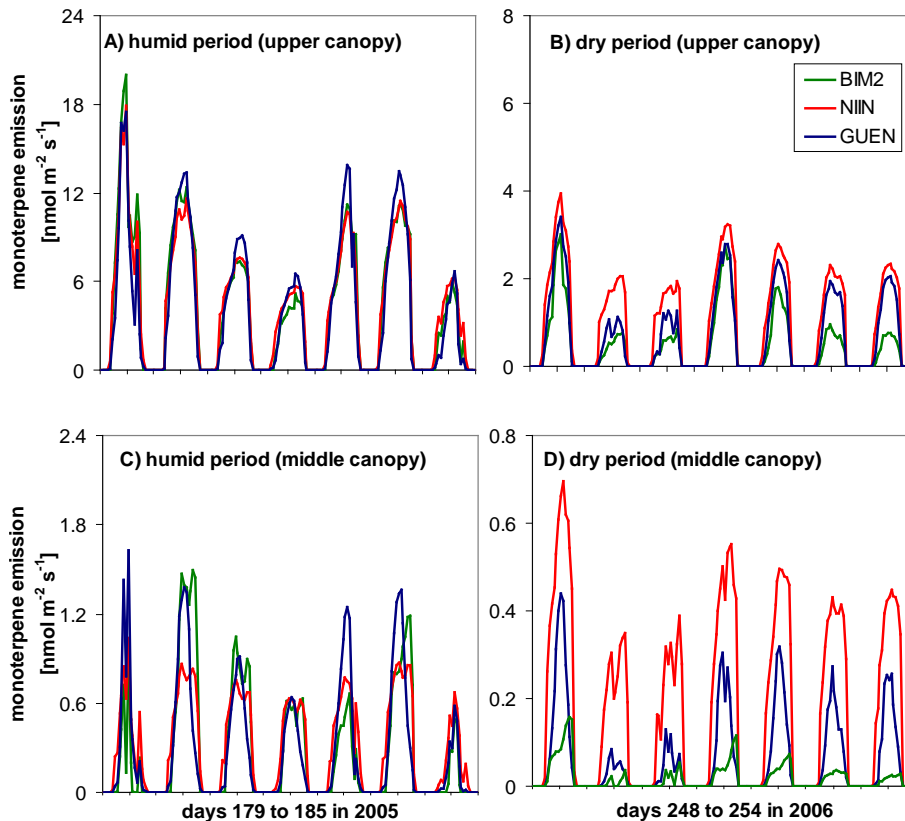


Fig. 6. Diurnal simulated emissions using BIM2, NIINEMETS, and GUENTHER models at selected dates in 2005 (A, C) and 2006 (B, D) for upper and mid canopy locations. Note the different scaling of y-axis.

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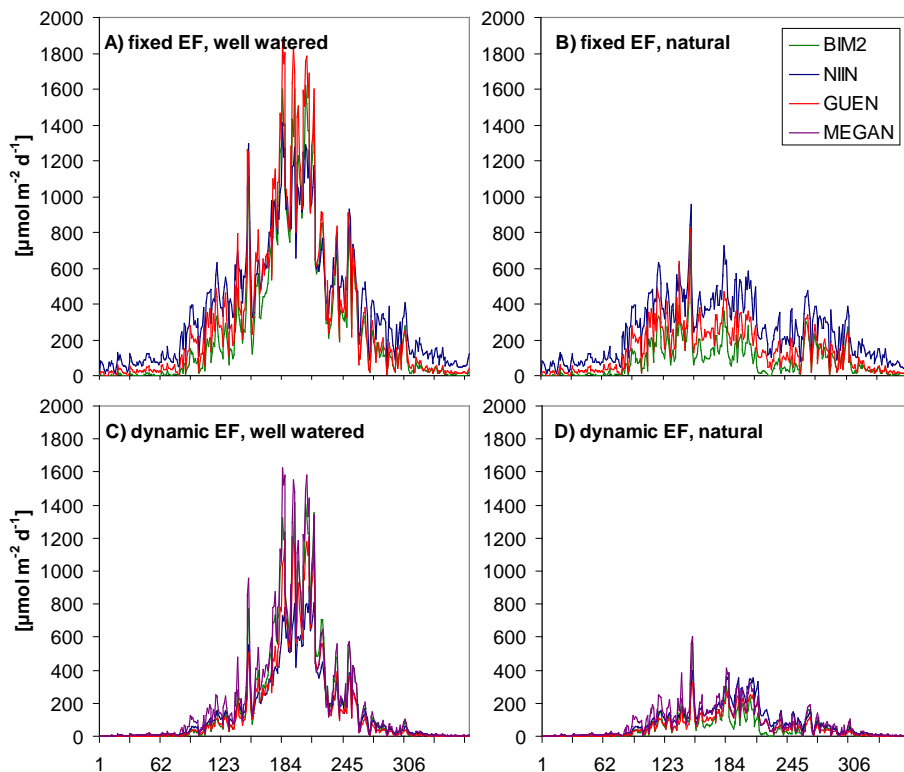


Fig. 7. Simulated daily emissions of the year 2006 based on Puéchabon site information with: **(A)** a fixed emission potential factor and no drought effect; **(B)** a fixed emissions potential factor and drought effects; **(C)** a seasonally dynamic emission potential factor and no drought effects; **(D)** a seasonally dynamic emissions potential factor and drought effects. The seasonally dynamic emission factor with the NIIN, BIM2 and GUEN model is estimated using the SIM enzyme dynamics. The MEGAN model explicitly includes an empirically seasonal emission factor.

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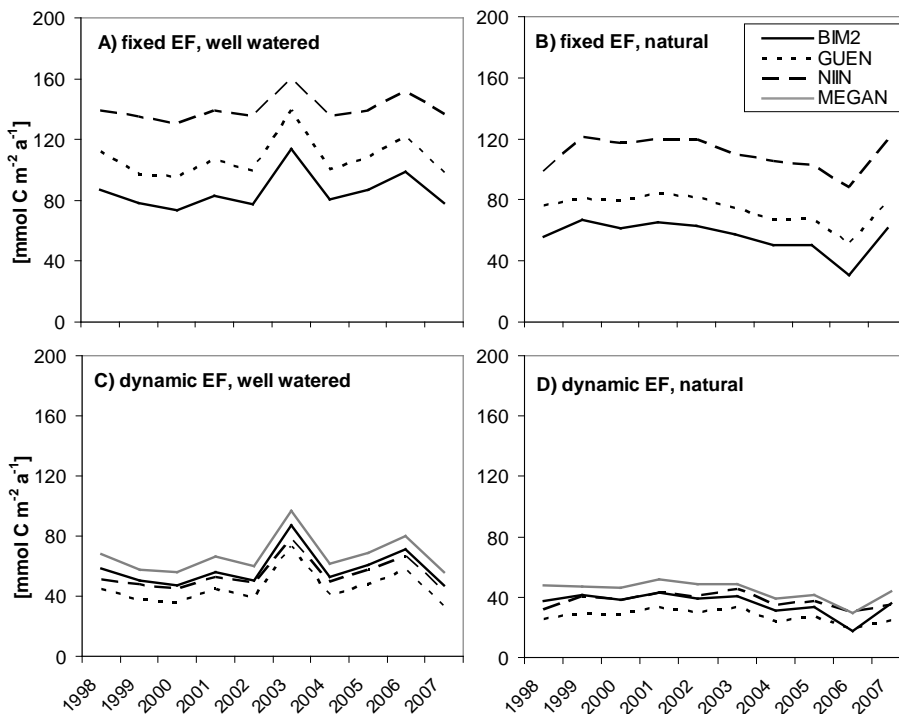


Fig. 8. See Fig. 7 but simulated annual emissions for the period of 1998 to 2007.

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