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The process-based SIM–BIM model: towards more realistic prediction of isoprene emissions from adult *Quercus petraea* forest trees

W. Zimmer[a,1], R. Steinbrecher[a], C. Körner[b], J.-P. Schnitzler[a,*]

[a] *Institut für Meteorologie und Klimaforschung, Atmosphärische Umweltforschung (IMK-IFU), Forschungszentrum Karlsruhe GmbH, Kreuzeckbahnstr. 19, Garmisch-Partenkirchen D-82467, Germany*

[b] *Botanisches Institut Universität Basel, Schönbeinstr. 6, Basel CH-4056, Switzerland*

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Abstract

The seasonal isoprene synthase model–biochemical isoprenoid biosynthesis model (SIM–BIM) is a recently developed process-based model to simulate isoprene emissions from vegetation. This model was validated using isoprene emission measurements from adult *Quercus petraea* (Mattuschka) Liebl. trees growing in a natural forest. Temperature and photosynthetic photon flux density (PPFD) data from a 120-year-old forest stand at Hofstetten in NW Switzerland were used to run SIM–BIM. Experimental isoprene synthase activity and isoprene emission rates from adult *Q. petraea* trees were compared to the model outputs for the years 2000 and 2001. High correlation (16.5% average deviation for isoprene synthase activity and 28% average deviation for isoprene emission factors) was observed between modelled and experimental data. In addition, a comparison was performed of the modelled values of SIM–BIM to values calculated using the algorithm ISOG97 of Guenther (Ecol. Appl. 7 (1997) 34). On the basis of the temperature and PPFD data from Hofstetten, this comparison clearly displayed the capability of SIM–BIM to simulate dynamic isoprene emission capacities during warm and sunny periods, and thus to model isoprene emission rates in a realistic manner for these conditions.

Keywords: Isoprene emission rate; Seasonality; SIM–BIM; ISOG97; Isoprene synthase; Model validation; *Quercus petraea*

1. Introduction

The volatile organic compound (VOC) isoprene is mainly emitted by trees. At high light intensities and temperatures, and in the presence of NO_x, it contributes to ozone production during summer smog periods (Biesenthal et al., 1997; Derwent et al., 1998). To be able to forecast ozone formation in summer, there is a high interest in precisely predicting isoprene emissions by trees. Emission algorithms such as ISOG97 (Guenther, 1997) are able to predict the average of isoprene emissions in an adequate manner for many plant species but do not consider the ability of plants to adapt (i.e. either increase or decrease) their isoprene biosynthesis capacity dynamically during sunshine and bad weather periods (Pétron et al., 2001). Therefore, the development of a model was necessary to take into account the physiological state of the leaves and the biochemical processes in the leaf leading to isoprene formation. Deciduous oaks (*Quercus* sp.) belong to the main isoprene emitting tree species in Central Europe.

*Corresponding author. Tel.: +49-8821-183131; fax: +49-8821-73573.

E-mail address: joerg-peter.schnitzler@imk.fzk.de (J.-P. Schnitzler).

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The mechanistic seasonal isoprene synthase model (SIM)–biochemical isoprenoid biosynthesis model (BIM) (Fig. 1) has been constructed recently to calculate isoprene emission rates of *Quercus robur* L. in middle Europe (Zimmer et al., 2000; Lehning et al., 2001) and contains all the specific parameters for this species. The module SIM calculates the bud break and senescence of the leaf in dependence of the seasonal temperature. It also calculates the day-to-day increase and decay of isoprene synthase activity in leaves in dependence of light and temperature history during the growing period and delivers these data to BIM. In contrast to other process-based isoprene emission models, which use either the ATP content or the plastidic redox charge for their calculations (Martin et al., 2000; Niinemets et al., 1999), BIM (Zimmer et al., 2000) uses the photosynthetic carbon input delivered by a light fleck photosynthetic module (LFPM) (Kirschbaum et al., 1998) to calculate the enzymatic conversions and the pool sizes of isoprenoid precursors necessary for isoprene formation in dependence of actual light intensity and temperature (Fig. 1). The model SIM–BIM was previously validated by seasonal isoprene synthase activity data and diurnal leaf isoprene emission data derived from 2 to 4 year old *Q. robur* saplings in nursery and green house experiments (Lehning et al., 2001). The average deviation of the modelled emission and the measured values was 50% closer to the experimental data than the values calculated by Guenther algorithms (Zimmer et al., 2000; Lehning et al., 2001). Whereas these validations were performed with young saplings the aim of the current work was to run SIM–BIM with available temperature and light intensity data from the sunlit canopy of adult *Q. petraea* and to validate it by the isoprene emission rates of leaves at the same place during the same time period.

2. Material and methods

2.1. Model input parameters, values and sources

Data and material for the validation of the model were collected at the Swiss Canopy Crane (SCC) site (Körner, 2002; Pepin et al., 2002). A section of a typical Central European forest of adult conifers and deciduous trees at Hofstetten (Switzerland, 550 m a.s.l.) accessible by a crane enabled direct emission measurements and leaf collection in the canopy of the chosen *Quercus petraea* (Mattuschka) Liebl. trees. The forest was 120 years old and the dominant trees varied between 32 and 36 m in height.

Photosynthetic photon flux density (PPFD) and air temperature measured in the canopy are the only driving variables of the model SIM–BIM. Ten minutes means of PPFD and temperature were averaged to give daily means of PPFD (during the light phase) and air temperature. These daily averages of temperature and PPFD starting from the 1st January 2000 to 1st January 2001, respectively, were used as input parameters for the calculation of the physiological development of leaves and isoprene synthase activity. In SIM, biosynthesis of

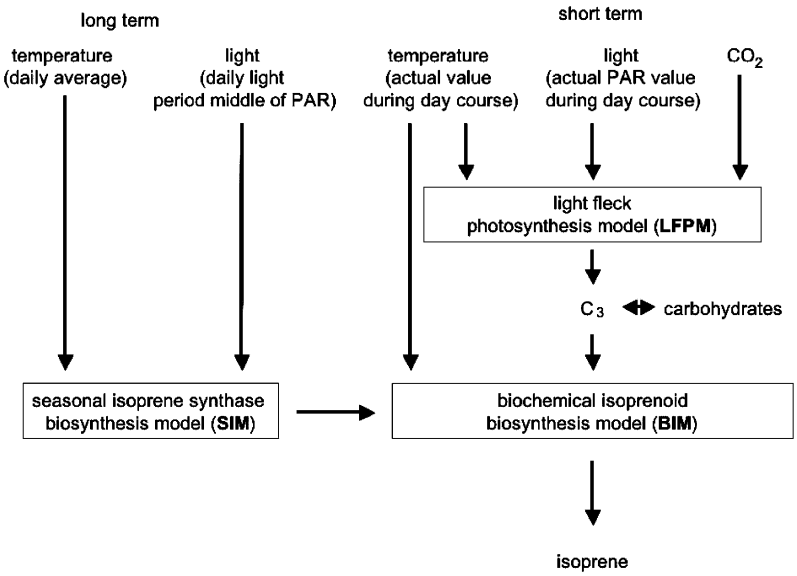

Fig. 1. Scheme of the coupling of the seasonal isoprene synthase biosynthesis model (SIM), the biochemical isoprenoid emission model (BIM) and the light fleck photosynthesis model (LFPM) and their external driving parameters. The structure of the three models is described in detail at the given references (Kirschbaum et al., 1998; Zimmer et al., 2000; Lehning et al., 2001).

isoprene synthase formation is calculated by taking into account the product of PPFD during the light phase and the temperature dependence of the enzyme formation according to an Arrhenius equation (with a doubling of the formation speed in the interval from 20°C to 30°C). For the decay of isoprene synthase activity an exponential function is used. Taking both processes together, the day-to-day differences in isoprene synthase activity were calculated (for details see Lehning et al., 2001) by SIM for the respective day of the year (DOY) and used in BIM as default data to calculate the diurnal isoprene emission rates in relation to the 10-min means of air temperature and PPFD. Model parameters of BIM were similar as described in Zimmer et al. (2000).

2.2. Protein extraction and isoprene synthase activity measurement

For the measurement of isoprene synthase activity leaf samples from different sun-exposed branches of four *Q. petraea* trees at Hofstetten were taken around noon on several days in August 2000 and 2001 (see Fig. 2). These leaves were shock frozen in liquid nitrogen and stored at −80°C until use. In addition, the oak leaves used for cuvette measurements were stored in the same way. Crude extract of the leaves was prepared as described previously (Lehning et al., 1999). Isoprene synthase activity was assayed according to Brüggemann and Schnitzler, 2001. Dimethylallyl diphosphate (DMADP) for the enzyme measurement was synthesised according to Keller and Thompson (1993).

2.3. Isoprene emission measurement

Isoprene emission rates were measured on three *Q. petraea* trees at three different dates (18th July, 22nd August, and 30th August) in 2000 with a LiCor-LI-6400 (LiCor, Walz, Effeltrich, Germany) gas exchange measurement system equipped with an air sample enrichment system. The system was operated from a crane gondola and the leaf cuvette was mounted on the respective leaf before the measurement. At each tree two independent leaves were measured. After mounting of the cuvette the photosynthetic gas exchange of the leaves was allowed to stabilise for 30–60 min prior the onset of air sampling. The air sampling was performed for 1 h. Inlet and outlet air of the cuvette was collected on a three-bed-absorbent tube (90 mg Carbotrap C, 60 mg Carbotrap, 60 mg Carbopack X, Supelco Bellafonte PA). A coupled thermo-desorption gas chromatograph with flame ionisation and mass-selective detectors (ATD400, Autosystem XL gas chromatograph, Turbo-Mass, Perkin Elmer, Weiterstadt, Germany) was used for isoprenoid analysis in air samples. The samples were desorpted at 280°C from the sampling tube and injected using the ATD 400. Five minutes after injection when all

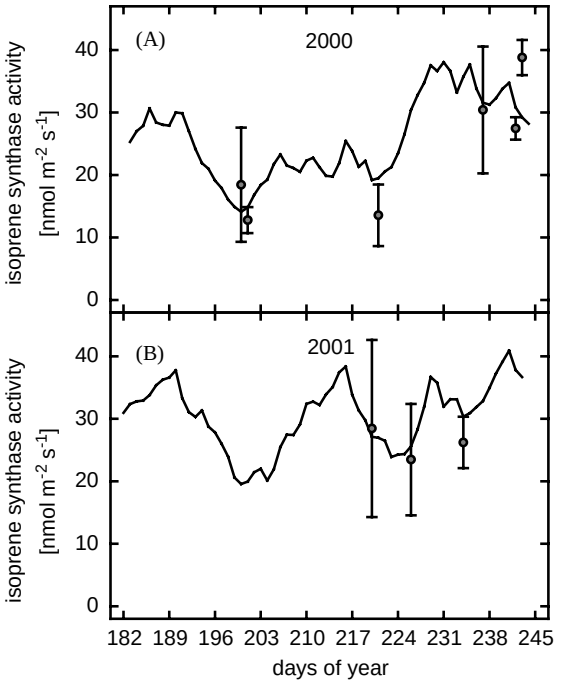

Fig. 2. Comparison of modelled and measured isoprene synthase activity (nmol m^{-2} total leaf area s^{-1}). In the period July–August 2000 (A) and 2001 (B) enzyme activity measurements were performed (•). For each date three leaf samples from different sun-exposed branches of individual trees ($n = 4$) were taken at Hofstetten (near Basel, Switzerland) at the given day and the isoprene synthase activity was measured as described (Brüggemann and Schnitzler, 2001). Light and temperature data of the vegetation period in Hofstetten were used as input data to calculate isoprene synthase activity by SIM (—).

compounds $< C_6$ and water have reached column C2 (aluminium oxide/potassium chloride, film thickness 10 μm, inner diameter 0.53 mm, length 30 m) a four-port valve was switched connecting column C1 (RTX-1701, film thickness 1 μm, inner diameter 0.25 mm, length 30 m) with the MS. This way all compounds $> C_5$ were analysed by MS. The low boiling fraction was separated on column C2 and detected by FID. The separation was achieved by starting the temperature program at 15°C with heating rate of 10°C min^{-1}. After 3.5 min the heating rate was reduced to 5°C min^{-1} until 200°C was reached. Calibration was performed with a gas standard of isoprene (Messer, Griesheim, Germany). The emission rates were calculated by multiplying the mixing ratio difference of the compounds in the air between chamber inlet and outlet with the airflow through the enclosure divided by the total leaf enclosed. After gas exchange analysis the leaf from inside the cuvette was shock frozen in liquid nitrogen and stored at −80°C until protein extraction.

3. Results and discussion

3.1. Validation of isoprene synthase activity calculated by SIM with experimental enzyme activity data

For the validation of the enzyme activity data calculated by SIM, at least three leaf samples from different sun-exposed branches of four *Q. petraea* trees were taken at Hofstetten on several days in August 2000 and 2001 (see Fig. 2) and analysed for isoprene synthase activity in the laboratory. In parallel, isoprene synthase activity of oak leaves was modelled by SIM using the daily average temperature and the daily mean PPFD of the light period starting from the 1st January 2000 and 1st January 2001, respectively, as input data for the calculation of the bud break and the physiological development of the leaves. The model calculated isoprene synthase activity for the period from 1st July to 31st August 2000 (days of year 183–244, Fig. 2A) and 2001 (days of year 182–243, Fig. 2B). In both years strong fluctuations of isoprene activity were observed in the modelled and measured data (Fig. 2), which were based on rapid changing weather conditions during these episodes (e.g. see Fig. 3). Nevertheless, in both years isoprene synthase activity calculated by SIM matched almost the range of experimental data (average deviation 16.5%). Taking into account that the measured activities were from individual trees and the modelled values were calculated for an average *Q. petraea* tree the comparison confirmed that the values of isoprene synthase activity modelled by SIM were realistic and well suitable for the calculation of isoprene emission rates by the coupled model SIM–BIM. In SIM light and temperature are the driving forces regulating the isoprene emission potential. However in nature, other additional abiotic and biotic environmental constraints may act as predisposition factors leading to qualitative and quantitative changes in the regulation of isoprene biosynthesis. Additional factors that may affect isoprene emission potential are: (a) influence of powdery mildew (*Microsphaera alphitoides*) on oak leaves (Brüggemann and Schnitzler, 2001), soil water availability (Brüggemann and Schnitzler, 2002) or enhanced atmospheric CO_2 concentrations under a future climate (Sharkey et al., 1991). All these influences have to been included in a future version of SIM by introducing correction factors, which account for the above-mentioned constraints.

3.2. Comparison of experimentally determined isoprene emission factors and isoprene emission rates determined by SIM–BIM

In order to validate the isoprene emission rate calculated by SIM–BIM for the adult *Q. petraea* trees at Hofstetten, emission factors determined experimentally by leaf cuvette measurements for 25°C and a PPFD of 1000 ($\mu mol\,m^{-2}\,s^{-1}$) from the 18th July, 22nd and 30th August 2000 were used (Table 1). To obtain emission factors by SIM–BIM, isoprene synthase activities for the respective days modelled by SIM (as described above) and 24 h spread sine curves with a maximum at 25°C for temperature and with a maximum of 1000 ($\mu mol\,m^{-2}\,s^{-1}$) for PPFD were used as input data for BIM. The emission rates calculated by BIM at the maxima of the sine curves were compared to the emission factors (Table 1). Two experimental determined standard emission rates in August (Qp 3 and Qp 7) were almost identical to the values modelled by SIM–BIM. In case of tree Qp 1 sampled on the 18th July the emission factor was higher than the modelled value. On this day (day of year 200) the calculated and the modelled isoprene synthase activity were at a minimum (Fig. 2A), which led to the assumption that tree Qp 1 reacts as an high isoprene emitter rather than as a mean tree. Reasons responsible for this behaviour can be due to (i) important environmental parameters not described by the model or (ii) due to the high intrinsic genetic variability of basal isoprene emission rates (see also Lehning et al., 2001). However, the average deviation of all three measured isoprene emission factors to the modelled emission rates is less than 28%. Therefore, it can be stated that within the framework of this validation, the isoprene emission rates calculated by SIM–BIM fit well to experimentally determined emission rates or standard emission factors for adult *Q. petraea* trees.

3.3. Comparison of the process-based model SIM–BIM to the empirical model ISOG97

In a sensitivity study run for 6 days we compared SIM–BIM with the classical used empirical model ISOG97 (Guenther, 1997). This algorithm is currently being applied to modelling isoprene emission at specific sites as well as in regional (Simpson et al., 1999) and global emission (Guenther et al., 1995) and its general applicability for estimating short-term variations of isoprene emission have been widely demonstrated for many plant species (e.g. Harley et al., 1996, 1997, 1998; Kesselmeier and Staudt, 1999).

For the sensitivity study light and temperature data from the SCC stand at Hofstetten from the 9th to 15th July and from the 12th to 18th August 2001 were taken (Fig. 3). The model SIM–BIM was able to calculate the isoprene synthase activity and hence the isoprene emission, for these periods based on the history of light and temperature at this stand. In the case of ISOG97, a *Q. petraea* standard emission factor (emission at 30°C and PPFD of 1000 μmol photons $m^{-2}\,s^{-1}$) of 9.55 nmol isoprene m^{-2} total leaf area s^{-1}—corresponding to 76.6 μg (g DW)$^{-1}\,h^{-1}$—(Kesselmeier and Staudt, 1999)

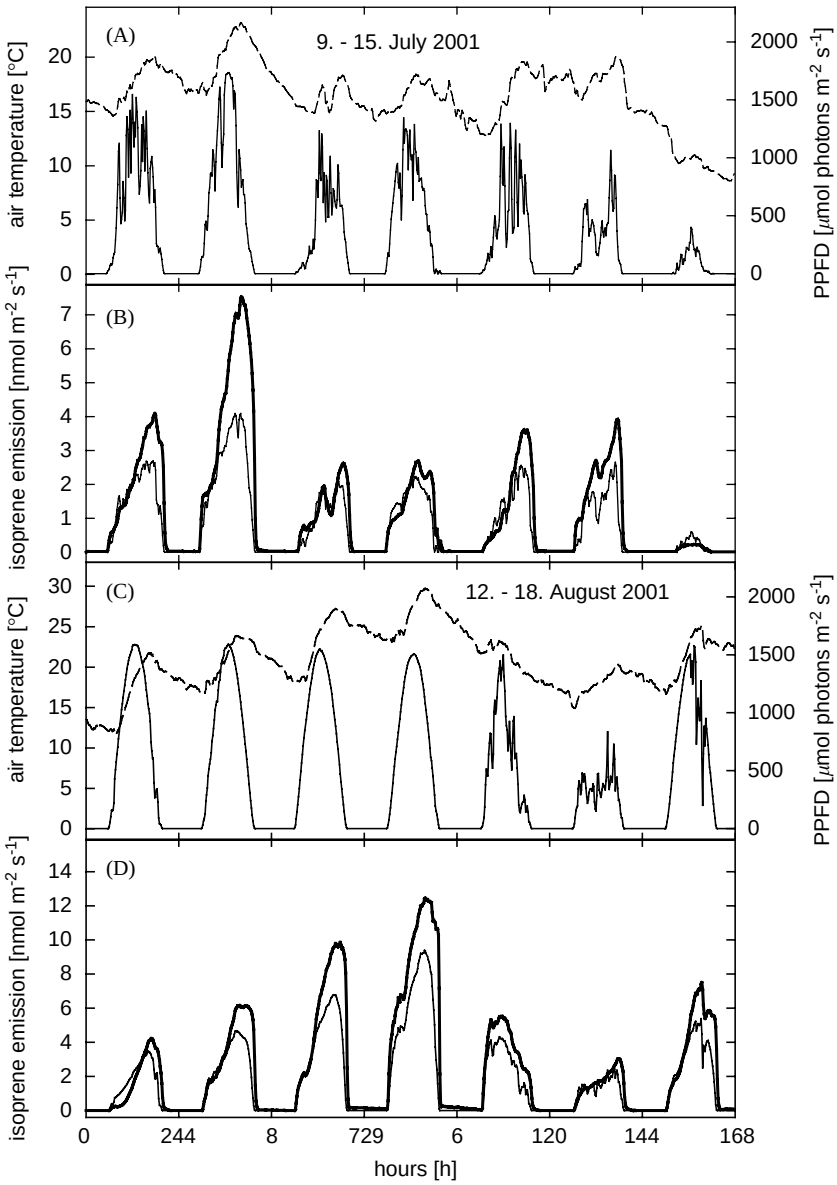

Fig. 3. Comparison of the isoprene emission rate calculated by ISOG97 and SIM–BIM. The isoprene emission rates were calculated by SIM–BIM (——) for *Quercus petraea* for the 9th–15th July (B) and for the 12th–18th August (D) at Hofstetten (near Basel, Switzerland) on the bases of the available temperature (— —) and photosynthetic photon flux density (PPFD, right *y*-axis) (——) in the respective time periods (A) and (C). The standard emission factor 9.55 nmol m^{-2} s^{-1} (for 30°C, 1000 μmol m^{-2} s^{-1} PPFD; Kesselmeier and Staudt, 1999) was used for the calculations by ISOG97 (— —).

was used to run the model (Fig. 3). The first period (9th–15th July) was cloudy and the temperature was mainly below 20°C. The first 4 days of the second period (12th–15th August) were typical sunshine days without or almost without clouds and rising daily temperatures up to 30°C (Fig. 3). After the 15th August more clouds arose—visible in the fluctuating light intensity (Fig. 3) and the decline of the average temperature—until the 17th. After that date temperature rose again. The behaviour of both models to this weather development differed in two points:

The isoprene emission rate calculated by model ISOG97 reacted very sensitively to fluctuations in light intensity, which is easily visible (Fig. 3) for the first period (Fig. 3A) and the last 3 days of the second period (16th–18th August, Fig. 3B). Model SIM–BIM was able to buffer these fluctuations because it calculates pools of isoprenoid precursors from time step to time step and

Table 1
Comparison of the measured emission factor and the modelled isoprene emission rates

Tree no.	Date of emission measurement	Measured emission factor at 25°C, 1000 PPFD (μmol photons $m^{-2} s^{-1}$)	Modelled isoprene emission rate for 25°C, 1000 PPFD (μmol photons $m^{-2} s^{-1}$)
Qp 1	18th July 2000 (DOY 199)	15.6±1.9	4.2
Qp 3	22th August 2000 (DOY 234)	10.0±3.7	10.1
Qp 7	30th August 2000 (DOY 242)	8.1±5.3	8.9

For the determination of the emission factor isoprene emission rates were measured in leaf cuvettes on three trees at Hofstetten (near Basel, Switzerland) at the given day. At each tree two independent leaves were measured for one hour each ($n = 2$; ±SD). Light and temperature data of the vegetation period in Hofstetten for 2000 were used as input data for SIM. The coupled BIM (Zimmer et al., 2000) was driven by sine curves with maximum of 25°C and a PPFD of 1000 (μmol photons $m^{-2} s^{-1}$) as day course input for temperature and light, respectively.

each reaction has time constants, which led to a smoothed release of isoprene. The ISOG97 algorithm equates the instantaneous leaf emission rate to its basal isoprene emission potential—or standard emission factor—multiplied by terms, which reflect the temperature and light dependency as the primary physiological drivers of the emission rate. It gave similar emission rates in height and shape of the emission curve as SIM–BIM at days with low temperature and low light intensities. However, when temperature and light intensities increased during the next few days SIM–BIM slowly increased the isoprene synthase activity, which led to increased isoprene emission rates. This feature of the model is perfectly demonstrated for the sunshine period from 12th to 15th August. ISOG97 with its constant standard emission factor could not take into account this change in basal isoprene emission potential and therefore underestimated the diurnal isoprene emission in this period. To overcome this disadvantage of ISOG97 initial empirical (Schnitzler et al., 1997) and phenological attempts (Guenther, 1997; Guenther et al., 1999; Geron et al., 2000) have been made to introduce additional emission potential factors which account for leaf age shade-adaptation, and past climate history. However, due to the current limited number of observations it is not clear how these models can be extrapolated to the SCC site for a model comparison.

4. Conclusions

The current work describes the successful validation of the model SIM–BIM by the use of experimental data gathered from adult *Q. petraea* trees at a forest stand in Hofstetten near Basel, Switzerland. The results also display the advantages of SIM–BIM. Its ability to dynamically adapt the isoprene biosynthesis capacity by modulating the enzyme amounts in the leaf in dependence of the historical weather pattern led to a realistic simulation of isoprene emission rates.

The application of SIM–BIM to other deciduous isoprene-emitting trees of temperate regions, however, awaits further species-specific details of the biochemical properties of crucial enzymes as well as of temperature and light-activation of isoprene synthase in these tree species. In particular, the factors describing synthesis and decline of daily isoprene synthase activity (see Lehning et al., 2001) have to be calculated for the model development from experimental data, and species-specific phenological data have to be implemented in the model. With respect to a changing global climate the coupled version of SIM–BIM might be also of considerable predictive value when used for sensitivity studies that simulate isoprene emission rates under elevated temperatures during different annual seasons and atmospheric CO_2 levels. Current ongoing development on SIM and the input parameter database will lead to the development of a detailed emission module to be coupled to chemistry transport models for setting up more realistic BVOC emission inventories.

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