Biogeosciences Discuss., 12, 7783–7814, 2015
www.biogeosciences-discuss.net/12/7783/2015/
doi:10.5194/bgd-12-7783-2015

Biogeosciences
Discussions
Open Access

Tree water relations trigger monoterpene emissions from Scots pine stem during spring recovery

A. Vanhatalo[1], T. Chan[1], J. Aalto[1,2], J. F. Korhonen[1], P. Kolari[3], T. Hölttä[1], E. Nikinmaa[1], and J. Bäck[1]

[1]Department of Forest Sciences, University of Helsinki, Finland
[2]SMEAR II station, University of Helsinki, Finland
[3]Department of Physics, University of Helsinki, Finland

Received: 29 April 2015 – Accepted: 4 May 2015 – Published: 22 May 2015

Correspondence to: A. Vanhatalo (anni.vanhatalo@helsinki.fi)

Published by Copernicus Publications on behalf of the European Geosciences Union.

Title Page
Abstract | Introduction
Conclusions | References
Tables | Figures
◀| | |▶
◀ | ▶
Back | Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion

Abstract

Tree canopies are known to emit large amounts of VOCs (volatile organic compounds) such as monoterpenes to the surrounding air. The main source for these is considered to be the green biomass, i.e. foliage, but emissions from the woody compartments have not been quantified. A VOC emission anomaly has been observed during transition from winter to summer activity. We analyzed if non-foliar components could partially explain the anomaly. We measured the VOC emissions from Scots pine (*Pinus sylvestris* L.) stems and shoots during the dehardening phase of trees in field conditions in two consecutive springs. We observed a large, transient monoterpene burst from stems, while the shoot monoterpene emissions and transpiration remained low. The burst lasted about 12 h. Simultaneously, an unusual night-time sap flow and an anomalous diurnal pattern of tree diameter were detected. Hence, we suggest that the monoterpene burst was a consequence of the recovery of the stem from winter-time. This indicates that the dominant processes and environmental drivers triggering the monoterpene emissions are different between stems and foliage.

1 Introduction

The stems of mature coniferous trees contain significant quantities of oleoresin. 20–50 % of the conifer oleoresin consists of monoterpenes (Langenheim, 2003), and the monoterpene content of dry Scots pine (*Pinus sylvestris* L.) wood is about 0.5 % (Strömvall and Petersson, 2000). In addition to the volatile monoterpenes, oleoresin is composed of volatile sesquiterpenes and non-volatile diterpene acids. The composition and quantity of wood oleoresin depends on e.g. tree species, age, provenance, health status, and environmental conditions (Back and Ekman, 2000; Erbilgin and Colgan, 2012), and is likely linked to protection against stem-damaging herbivores (Lewinsohn et al., 1991; Philips and Croteau, 1999; Trapp and Croteau, 2001). Oleoresin flows out from a mechanically damaged site to protect the tree by sealing the wound. Once in

BGD
12, 7783–7814, 2015

contact with air, the volatile parts of oleoresin evaporate, and the residual compounds harden to make a solid protective seal over damaged tissues. Yet, a fraction of volatile part may react already on the oleoresin and form large polymers of low volatility.

It is well known that also the foliage of conifers contains several volatile isoprenoids (isoprene, monoterpenes, sesquiterpenes), as well as small oxygenated carbonyls, e.g. methanol, acetone and acetaldehyde, which are emitted at very variable rates (e.g. Isidorov et al., 1985; Christensen et al., 2000; Grabmer et al., 2004). Temperature is the main controlling factor for monoterpene emission, influencing their volatility in an exponential manner (Tingey et al., 1980), although recently light-dependent emissions from shoots have also been reported (Staudt and Bertin, 1998; Shao et al., 2001; Tarvainen et al., 2005; Ghirardo et al., 2010), indicating a close dependence with carbon assimilation. Emissions of monoterpenes from tree canopies have a typical seasonal pattern, normally peaking in summer (e.g. Hakola et al., 2006).

Surprisingly, despite abundant knowledge on emissions of volatile isoprenoids from foliage, very little is known about their emissions from woody plant tissue. From the viewpoint of the timber and paper industry, isoprenoid emissions from harvested and further-processed timber have been previously reported (Strömvall and Petersson, 1991, 1993; Granström, 2007), but living woody tree parts have gained only little attention. As the oleoresin storage pools in stems are large, emissions occur constitutively without any damage to the tree itself, but their seasonal patterns or driving factors have not been studied in detail.

Resin duct network and water transport system are both pressurized systems: resin is under positive pressure caused by cells surrounding the ducts and xylem water under negative pressure caused by the transpiration created tension linking the pressure to many physiological processes of a tree. Apart from transpiration the water status in stem is linked to repeated freezing and thawing cycles in winter. These can cause embolism in water conducting tracheids (Sperry, 1993) potentially hindering the stem water transport as transpiration commences at spring recovery of the canopy. Thus one requirement for trees living in cold environments is that the xylem conduits are refilled and the water transport capacity recovers in the spring (e.g. Améglio et al., 2002). The water pressure changes in xylem and phloem can be reflected to the radial changes of inner-bark and xylem (e.g. Mencuccini et al., 2013).

Interestingly, emissions from Scots pine branches can be very high in early spring, in many cases much higher than those later in the growing season (e.g. Tarvainen et al., 2005; Hakola et al., 2006). This implies that other factors, related to the tree physiological processes in spring may also influence emission rates, beyond the simple physical factors related to volatilization of VOCs.

To analyze the dynamics of stem monoterpene emissions and their possible relationship to the stem physiology in spring, we measured the emissions from a Scots pine stem during two springs in field conditions in a boreal pine forest. In addition, we measured sap flow, stem radial variation and leaf gas exchange (including emissions of monoterpenes) from the same tree. Our hypothesis was that the emissions from the stem are driven by several factors: one is related to incident changes in temperature and solar radiation and the second one represents the storage emission from different parts of the tree. The latter one is expected to be linked to tree water relations, and thus the onset of monoterpene emissions from the stem in spring is related to the recovery of tree water transport capacity. This can be characterized with dynamics in sap flow, transpiration and pressure changes in stem as reflected in its diameter variation.

2 Materials and methods

Measurements were done at the SMEAR II (Station for Measuring Forest Ecosystem–Atmosphere Relations, 61°51′ N, 24°17′ E) stand (Hari and Kulmala, 2005). The growing season there ranges, on average, from the end of April to mid-October (Table 1). Thermal spring, defined as a period when daily mean temperature stays between 0 and 10 °C, starts typically during the first half of April (Table 1). The start of the growing season takes place when snow has melted on open sites and mean daily air temperature rises above 5 °C. At our measurement site, this takes place around the turn from April to May. The temperature, snow depth and soil water content during the measurement periods in April–May 2012 and 2013 are shown in Fig. 1.

The measurement site is situated at the boreal vegetation zone in southern Finland. The stand is dominated by Scots pine with some Norway spruce (*Picea abies* (L.) Karst.), European aspen (*Populus tremula* L.), and birches (*Betula* spp.) as a mixture. The ground is covered with dwarf shrubs (*Vaccinium myrtillus* L., *Vaccinium vitis-idaea* L.) and mosses (*Pleurozium schreberi* (Brid.) Mitt., *Dicranum* spp.). Soil is haplic podzol formed from glacial till and its thickness on bedrock is quite low, on average only 0.5–0.7 m.

The tree-scale parameters were measured from a visibly healthy, representative Scots pine individual belonging to the dominating canopy layer. This tree was 18.6 m tall and had a diameter of 20 cm at breast height (in 2012), and has been measured for diameter change and sap flow since 2005. The lowest living branches grew at a height of 10 m.

The gas exchange of the stem was measured with a transparent enclosure (see below). The flux calculation of stem enclosure data was done according to Kolari et al. (2009). The top-canopy shoot gas exchange was measured at the height of about 17 m with a dynamic enclosure as presented by Aalto et al. (2014). The shoot gas exchange was calculated as in Kolari et al. (2012) with a transpiration correction as in Altimir et al. (2006). Until the end of April 2013 the H_2O and CO_2 exchange was measured with URAS 4 infrared light absorption gas analysers (Hartman and Braun, Frankfurt am Main, Germany), and from May 2013 onwards with a Li-840A analyser (Li-Cor, Lincoln, NE, USA). The replacement of the gas analysers did not cause any irregularity in the measurement data. Both the old and new analysers were calibrated with the same gas standards just before the replacement and after it, respectively. The stem CO_2 efflux was temperature-normalised to study linkages with other stem processes by fitting an exponential curve to measurements at above zero temperatures in April. The simple exponential model derived from the described plot was then used to estimate CO_2 efflux anomalies.

The VOC emissions were measured online with a proton transfer reaction-quadrupole mass spectrometer (PTR-Q-MS, Ionicon, Innsbruck, Austria; Hansel et al., 1995) modified from the system described in Ruuskanen et al. (2005). The description and accuracy of the VOC measurement system has been reported in Kolari et al. (2012). Altogether, ten molecular masses (amu +1) were measured, but for this study we use data only on the m/z 137, which corresponds in Scots pine emissions mainly to monoterpenes. The other masses show so low signal-to-noise ratios and dependence on air humidity that their fluxes are insufficiently quantified. Calibrations of the PTR-Q-MS were carried out 2–3 times a month according to the method described in Taipale et al. (2008), including α-pinene as the representative monoterpene. The other gaps in the data originate from the momentary maintenance and malfunction of the measuring system. As the temperature variation in springtime is wide, the measured emissions were normalized to enable better comparison by applying the temperature normalization equation according to Guenther (1997) using an empirical beta-coefficient of $0.09\,^{\circ}\mathrm{C}^{-1}$ and a standard temperature of 30 °C. All the monoterpene emissions from the stem are expressed per m^2 of bark area and the emissions from the shoot per m^2 of all-sided needle area. The stem area was defined as a smooth cylinder surface ignoring the cracks of the bark.

The stem enclosure (Fig. 2) was designed specifically for this purpose with materials chemically inert to many VOCs to avoid detrimental signal losses. The enclosure covered $396\,\mathrm{cm}^2$ of the pine stem at the height of 12 m from the ground, which is close to the lowest living branches. The enclosure consists of a transparent and UV-permeable FEP foil (0.05 mm thick, Fluorplast, Maalahti, Finland) wrapped around the stem 2–3 times and tightened with binds on both ends. The vertical seal of the foil was made with FEP tape. Within the enclosure, a spiral of polyethylene-coated aluminium tube (Synflex, Eaton, USA) was wrapped around the stem to maintain an air space between the foil and the bark, and a FEP tape-covered aluminium brace for inlet and outlet connectors was placed between the spiral and the foil. Inside the enclosure, temperature was recorded with a copper-constantan thermocouple on the south-facing side of the stem. Rain water flow along the stem was blocked with a rain cover above the enclosure. Mounting of the enclosure was done well before the first measurements and without damaging the bark to avoid possible induced emissions. The bark at this height was rather smooth, so no levelling with a knife was needed. The measurements were done in steady state when the flow rate through the enclosure was about 1 L min^{-1}. The sampling time for emissions was 2 min 45 s, and samples were taken 24 times per day. To avoid accumulation of gases inside the enclosure, the enclosure was flushed between the samplings with above-canopy air at a rate of about 0.4 L min^{-1}.

Changes in stem radius were measured with two linear variable displacement transducers (point-dendrometers) (LVDT; model AX/5.0/S, Solartron Inc. West Sussex, UK), at a height of 15 m from the base of the sample tree. The point-dendrometers were installed to a rectangular stainless steel frame and were affixed onto the stem using two attachment plates. A detailed description of the dendrometers is provided by Sevanto et al. (2005). The head of the first dendrometer rested against a screw that was placed 10 mm through the bark surface, measuring xylem radial thickness (d_x). The head of the second dendrometer rested against the inner-bark, which was exposed by incising the outer-bark 3–4 mm deep with a scalpel. This dendrometer measured whole stem radial thickness (d_ws). As whole stem thickness also includes xylem thickness, the difference between these measurements is the inner-bark radial thickness (d_b). Inner-bark thickness, hence, includes the cambium and the phloem tissue towards the outside of the cambium. Dendrometer measurements (accuracy 1 µm) at 30 min intervals were used for the study and were offset to zero on 1 April of each year.

We used the radial measurements to calculate a dimensionless ratio, β, which is the ratio of the change in d_x to the change in d_b:

$$\beta = \frac{d_\mathrm{bMAX} - d_\mathrm{bMIN}}{d_\mathrm{xMAX} - d_\mathrm{xMIN}} \tag{1}$$

where d_bMAX and d_bMIN correspond to the maximum and minimum daily inner-bark diameter, respectively, and d_xMAX and d_xMIN corresponded to the maximum and minimum daily xylem diameter, respectively. This ratio is proportional to the ratio of the elasticity of the inner-bark tissues to xylem tissues. Note that an assumption is made here that the xylem and inner-bark tend towards water potential equilibrium with each other at the minimum and maximum diameters. As the elasticity of the xylem tissue is dependent mainly on the elastic properties of the dead xylem tracheids (Irvine and Grace, 1997; Perämäki et al., 2001) and the xylem and inner-bark (Sevanto et al., 2011) tend to approximately follow water potential equilibrium on a daily scale, the changes in β represent mainly the changes in the elasticity of the phloem.

Sap flow rate was measured with the Granier-type heat dissipation method at a height of about 13 m. Two probes, of 50 mm in length, were inserted in 2 mm wide brass cylinders into the sapwood approximately 10 cm apart. The upper probe (with 30 ohms resistance) was heated with constant power (approximately 0.2 W) and the sap flux density was calculated from the temperature difference between the two probes with a standard protocol (see e.g. Granier, 1987).

Air temperature was measured at 8 m height (Pt-100 sensor) and in soil A-horizon (5–10 cm depth with Philips thermistors). Precipitation was measured (Vector ARG-100 tipping bucket rain gauge and Vaisala FD12P Weather sensor) in an open site at 30 min intervals. Snow depth was measured once a week at seven locations below canopies at the study site and averaged for the forest stand.

3 Results

Weather patterns in both springs were rather normal (Table 1). Mean temperatures in April were somewhat below the long-time average, but May temperatures were slightly higher. The onset of the growing period was typical for the site. The maximum depth of snow was in both years higher than average, but snow was melting slightly earlier than normal.

The emission measurements show that very early in spring, already in early April, significant monoterpene emissions from pine stem and shoot could be detected

(Fig. 3). The emissions exhibited a clear diurnal cycle, with a maximum at midday and a minimum at midnight. Interestingly, a single, extremely high burst of monoterpene emission was observed from the stem on both years in April. At highest, the monoterpene burst was 13 ng $\mathrm{m^{-2}\,s^{-1}}$ in 2012 and 50 ng $\mathrm{m^{-2}\,s^{-1}}$ in 2013. The corresponding normalized (30 °C) emissions in the bursts were 77 and 500 ng $\mathrm{m^{-2}\,s^{-1}}$, respectively. In 2012, the peak occurred on 11 April, when the mean air temperature was 3.6 °C, and in 2013 on 19 April when the mean air temperature was 3.4 °C. The average, temperature normalized emission rate from the stem was 29 µg $\mathrm{m^{-2}\,day^{-1}}$ after the burst in April–May 2012. In 2013, the normalized emission rates were 79 µg $\mathrm{m^{-2}\,day^{-1}}$ before the burst in April and 47 µg $\mathrm{m^{-2}\,day^{-1}}$ after the burst in April–May, respectively. In 2013, the mean measured monoterpene emission from the stem in April before the burst was 0.7 ng $\mathrm{m^{-2}\,s^{-1}}$ (SD 0.6 ng $\mathrm{m^{-2}\,s^{-1}}$) and after the burst in April–May 1.3 ng $\mathrm{m^{-2}\,s^{-1}}$ (SD 1.5 ng $\mathrm{m^{-2}\,s^{-1}}$).

The high monoterpene emissions occurred after the freeze–thaw cycles, but their timing varied between years: in 2012, the highest values were measured in the afternoon, around 15:00 UTC+2, whereas in 2013 the highest values occurred in late evening, around 21:00 UTC+2. In 2012, the high emissions were recorded for 12 h, after which, emissions returned to their normal, low levels. In 2013, the emission measurements were unfortunately interrupted due to a communication error between the PTR-MS and the laptop controlling it during the peak emission. Before the break, the high emissions had continued for nine hours.

The stem monoterpene emission peaks in April were not coinciding with the highest emission periods from shoots (Fig. 3). The stem and shoot monoterpene emissions were momentarily at about the same level during the stem monoterpene burst in 2012, but in 2013, the stem monoterpene emissions clearly exceeded those from the shoots. Both the needles and the stem looked viable and no injuries or other abnormalities could be seen.

The observed inner-bark radial thickness (d_b) dynamics were very different before, during and after the observed emission burst. Thus, we separated them into three consecutive phases. The first phase began in early April, when large and reversible stem swelling and shrinkage was observed, which was associated with repeated freeze–thaw cycles (Figs. 4 and 5). These freeze–thaw cycles were observed over the first nine days of both Aprils, coinciding with daily minimum temperatures below −5 °C.

The second phase began once monoterpene emission started. Immediately after the stem monoterpene emission burst ceased, an acclimation response period lasting roughly one week was seen in d_b (Fig. 4a and b). Recovery of the d_b from the first period's freeze thaw cycles was detected, which occurred roughly three days after the burst in 2012 and almost immediately in 2013. On the 11–23 April 2012 and 19–25 April 2013, d_b and d_x were swelling and shrinking with no time lag, or even d_b swelling occurring before d_x. We considered the end of the second phase to take place once the d_x and d_b changes got more regular. Thus, the stem and its water transport got acclimated to external factors such as rising air temperature.

In the third phase, a regular swelling and shrinking of stem radius was observed: d_b followed d_x with a time lag of approximately 30–60 min. This kind of pattern is typical for the active growing period and is commonly observed in summertime at the study site. Moreover, irreversible d_b increment (i.e. radial growth) began shortly after the second phase.

Sap flow decreased and minimum occurred consistantly about 10 days after the peaks in monoterpene emissions, and then began to increase steadily to summertime levels following similar pattern in temperature (Fig. 6). Nighttime sap flow occurred concurrently with the stem monoterpene emission peaks (Fig. 5), which does not typically occur at any other time of the year at this site. In addition, shoot transpiration was very low during 2012 emission peak, although VPD was high, indicating closed stomata (data not shown).

β, reflecting the changes of inner-bark to xylem maximum daily amplitude showed large daily variations prior to the emission burst followed by a decline shortly after (Fig. 7). During the second phase, β exhibited noticeably smaller but abrupt changes lasting 2–3 days. After this response period, β reached a steady summer state.

The stem CO_2 efflux anomalies, i.e. the part of respiration value that is not explained by the regular response to temperature (Fig. 8), reveal that prior to the high monoterpene emission peak of both years, the stem CO_2 efflux anomaly increased relative to period before, or immediately after in 2012 (2013 measurements were missing at that period due to system problems). This suggests that in addition to regular maintenance respiration, CO_2 was released from some storage or there were some CO_2-producing processes occurring. This high CO_2 efflux during the monoterpene peak is not associated with growth since radial growth was observed with the point dendrometers approximately one month later.

4 Discussion

We showed that in a boreal forest, monoterpenes are emitted from Scots pine stems continuously at a low rate in spring, with a systematic daily pattern – maxima in the afternoon and minima during night-time. The stem monoterpene emissions differ from those measured from shoots in both magnitude and dynamics at the same time. The monoterpene emission from Scots pine shoots show clear seasonal pattern with several high transient emission periods in the beginning of the growing season (Aalto et al., 2014). The average level of the monoterpene emissions from the stem in springtime are in general lower than from the shoots (per area unit), which is likely due to lower oleoresin content and lower biological activity in stem than in shoot (Rockwood, 1973; Back and Ekman, 2000). The monoterpene emissions from the shoot were generally lower in 2013 than in 2012 (Fig. 3), but this is likely due to the aging of needles as the same shoot was enclosed in the measurement chamber in both years. Moreover, the dynamics of the monoterpene emissions from the stem and shoots seem to be driven by different factors.

In addition to the continuous low monoterpene emissions from the stem, we observed a rapid but large emission burst, lasting for several hours, after which the emissions decreased to the pre-burst levels, with a gradual emission increase towards summer concurrently with increasing ambient temperatures. The monoterpene emission burst coincided well with the recovery of stem radius from winter conditions. In both years studied, the burst occurred shortly after the last freezing period (Fig. 4). Around the time of the burst, stem radius fluctuations showed irregular behaviour in comparison to the regular pattern observed during summer condition, more noticeably in 2012. This behaviour included inner-bark fluctuations occurring before xylem fluctuations, both inner-bark and xylem changes occurring concomitantly and large daily fluctuations unlike summer-time behaviour. In both years, the inner-bark radius had a depression relative to xylem around the emission burst, but extremely so during 2012. This behaviour also coincided well with the changes in relative bark-xylem daily amplitude, β, where the largest changes were shortly before the burst (Fig. 7) and also more prominent in the year 2012 when the bark shrinking was more pronounced. Also the dynamics of sap flow behaved in similar manner relative to the burst event on both years (Fig. 6). This irregular behaviour in both relative timing, degree of swelling and relative amplitudes of xylem and inner-bark indicate other driving forces than during the regular diameter variation in summer when transpiration pull drives the pattern (Perämäki et al., 2001, 2005). The freeze/thaw cycles experienced during winter cause winter embolism: frozen gases (mostly air and CO_2) dissolve in xylem sap forming bubbles, which then expand during thawing and embolise the water conducting tracheids (Sperry, 1993; Pittermann and Sperry, 2006). In spring, xylem conduits are refilled with water by metabolic processes which are not yet fully understood, but most likely involve the interaction of living cells and radial interaction between xylem and phloem (Zwienieki and Holbrook, 2009; Nardini et al., 2011), resulting in the recovery of xylem transport capacity along with transpiration-driven tension propagation in stems. Cochard et al. (2001) demonstrated that an active mechanism for the recovery of shoot hydraulic conductivity via embolism refilling occurred early in the growing season, before cambial reactivation (i.e., before ring development).

Studies have shown that the inner-bark (i.e. phloem), plays a contributory role by providing the mechanism to drive radial water flow, ultimately aiding osmotic flow into embolised conduits (Salleo et al., 1996; Zwieniecki et al., 2000; Salleo et al., 2004). Also our results show that soon after the cessation of freeze–thaw events there occur changes, such as temporary shrinking of inner-bark relative to xylem and high inner-bark vs. xylem amplitude changes, which could suggest an active role of phloem in xylem recovery. Also the stem CO_2 flux anomalies might be related to this phloem activity. After this period, changes in stem radius achieved a general summer-time steady state, where changes in inner-bark follow xylem changes with a 30–45 min time lag (Sevanto et al., 2002). Also the sap flow rate starts to increase after this recovery period (Fig. 6), which indicates the initiation of tree growth.

The simultaneous dynamic changes in stem radius and deviation of xylem sap flow from normal conditions indicate that the changes in stem water relations are at least coinciding if not causing the emission bursts. Alternatively, the shrinking and swelling of phloem could indicate the growth of new phloem cells and the collapse of the old ones as phloem cells have been reported to start to form about 10 to 20 days before xylem cells in Scots pine (Antonova and Stasova, 2006). Furthermore, xylem microcore samples have indicated that xylem cells start forming at our measurement site after mid-May (Jyske et al., 2014). Thus, the potential reasons for these bursts are (1) volatilization from storages due to temperature increase, (2) changes in non-specific storage of monoterpenes; and (3) a rapid pressure-induced mobilization of volatiles from resin ducts in shrinking xylem tissue. We will discuss the three points in the following sections.

4.1 Effect of temperature

Monoterpene volatilization is a temperature-driven process (Guenther et al., 1993; Guenther, 1997; Lerdau et al., 1997; Tarvainen et al., 2005) and thus the seasonality of monoterpene emissions from vegetation is often linked to changes in ambient temperatures. Temperature-dependent emissions are especially important in species with large storage pools, such as conifers (e.g. Lewinsohn et al., 1991; Lerdau et al., 1997). The accumulation of monoterpenes in stem storage pools over winter and their release due to higher temperatures in spring could possibly lead to high emission rates. However, the temperatures at the day of the burst were not by any means higher than in spring on average: in 2012 the maximum temperature was 10 °C and in 2013 8 °C. In 2012 it was the warmest day until that date, but in 2013 there was somewhat warmer day three days before. We could not identify any extraordinary weather conditions which could have caused such high emission peak. No anomalous temperatures for the season were detected, neither any other unusual environmental factors. The emission burst had on both years almost similar timing compared to the growing season: the growing season started on 12 April 2012 and 16 April 2013. The burst took place on 11 April in 2012 and 19 April in 2013. Also the daily mean temperatures of the peak emissions days were almost identical in both years.

The bark surface temperature follows ambient air temperature with a short time lag, but may occasionally rise well above ambient temperature due to direct irradiation on the bark surface. However, inside and especially below the canopy this happens only occasionally and only on one side of the stem at a time. Furthermore, deeper inside the stem the response to changes in ambient temperatures is very slow. Measurements on a 60 cm thick Monterey pine have shown that diurnal temperature range inside the stem is only about one third of the range in ambient air (Neher, 1993). Thus, the oleoresin-rich heartwood (Strömvall and Petersson, 2000) stays in more stable conditions than the sapwood with lower oleoresin content. On the other hand, sapwood includes the living cells of the xylem and thus its temperature changes might be more significant for monoterpene emissions, especially in the case of de novo emissions. Our stem enclosure was situated inside the living canopy, so there apparently was only living sapwood and no heartwood enclosed.

Niinemets and Reichstein (2003a, b) concluded that the physico-chemical and structural factors explain well the shoot emission bursts of water-soluble VOCs such as methanol (with rather low Henry's law constant, H) when stomata open in the morning. On the other hand, fast temporal kinetics and liquid/gas phase transfer is reasonably irrelevant for compounds such as monoterpenes with rather large Henry's law constants, which generally have gas and liquid phase pools in a steady state. Thus, direct temperature effect is not capable to explain the bursts.

4.2 Changes in non-specific storage of monoterpenes due to changes in membrane permeability during spring

Monoterpenes are lipophilic and a dynamic, non-specific storage pool exists in cellular membranes (Niinemets and Reichstein, 2002, 2003; Ormeño et al., 2011). This pool may either influence or be affected by membrane permeability changes. At high concentrations monoterpenes may alter the properties of membrane proteins (Wink, 2003) and thus also affect the permeability and other bioactive features of the membrane. It has been suggested that monoterpenes affect membrane permeability and may cause leakage of intracellular materials of pathogenic microbes, which could explain their antimicrobial activity (Trombetta et al., 2005; Cristani et al., 2007).

Parallel to xylem refilling described above, the dehardening process of symplasm during spring involves many biochemical changes affecting membrane transport properties, e.g. the decrease in phospholipid content and biophysical changes of the membranes, changing membrane permeability (Pukacki and Kaminska-Rozek, 2013; Martz et al., 2006), which likely also influences the water relations between symplasm and apoplasm in stem, and hence, also xylem refilling. It is likely that changes in membrane properties (e.g. elasticity and permeability) were seen, in our case, as changes in stem radius measured with point dendrometers. It is possible that the properties of the cell membranes in xylem and phloem tissues changed due to dehardening, leading to a release of membrane-accumulated monoterpenes. The change in permeability is also reflected to the water status of the living cells of the stem, which may have caused the changes in sap flow rate as well. On the other hand, if the irregular inner-bark dynamics were associated with the collapse of previous years phloem associated with new phloem growth, then the monoterpene burst may originate from storages in there.

4.3 A rapid mobilization of volatiles from resin ducts

Resin ducts are located both horizontally and vertically in the stem, and thus they are in contact with both heartwood and sapwood. Based on our measurements, it is impossible to conclude from which stem tissues (e.g. tracheid cells, resin ducts, bark etc.) the observed monoterpenes originate. The spring-induced rapid change in water transport and related pressure changes in stem could potentially be leading to a pressure change in the xylem resin ducts and a consequent release of oleoresin. Such an effect could be corresponding to a damage-induced, transient release of monoterpenes from herbivory or mechanical wounding. However, after a steady diurnal water transport rate is obtained (in some hours after the recovery of the xylem), the resin ducts are no longer experiencing strong pressure effects and emissions go down to “normal” diurnal pattern.

One more possibility could be that monoterpene emissions originate from the gases inside embolised tracheids. A large proportion of tracheids is embolised after the winter as gas bubbles get trapped inside the frozen xylem sap during freezing and expand to embolise the tracheids during thawing (e.g. Pittermann and Sperry, 2003). Supposedly the air inside the embolised tracheids has a high concentration of monoterpenes as the turnover rate of the gases is low and there is ample time for the monoterpenes to diffuse from the neighbouring resin ducts and plasma membranes. Once the conduits refill with water in the spring, the gases, including monoterpenes, within the embolised tracheids diffuse out from the stem (Yang and Tyree, 1992; Vesala et al., 2003). It is unclear how large are the changes in stem gas content during the spring at our site, and if monoterpene concentrations can get high enough to sustain a burst for several hours. However, substantial changes in the volume of gas inside the stem are very likely as the volumetric water content of the stem is known to vary a lot during winter months (Sparks et al., 2001) and can increase by up to tens of percent’s during the springtime (Wullschleger et al., 1996).

Title Page
Abstract Introduction
Conclusions References
Tables Figures
◂ ▸
Back Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion

Yet, an explanation could be that once embolised tracheid cells fill up with water in spring, the filling causes extra pressure on resin ducts and this causes damages on the ducts and the subsequent oleoresin flow is seen as elevated monoterpene emissions. In this case the damages would be so remarkable that they release volatiles, but so small that they are not visible on the bark surface.

5 Conclusions

The irregular diurnal pattern of stem radial change compared to summer conditions, as well as night-time sap flow, accompanied by low shoot transpiration rates during the monoterpene burst was observed in two consecutive years. We also detected a difference in the ratio of the daily amplitude of phloem to xylem radial thickness and/or osmotically driven swelling before and after the burst. These dynamic changes indicate a phase change in stem water transport capacity that precedes the physiologically active summer state of the tree. The measurements show that there was a water transport acclimation period of a few days after the monoterpene burst occurred. After this period, the water transport capacity reached a steady summer state and daily patterns of stem radial change and sap flow rate stabilized. This suggests that there is a significant mechanism involved in the described physiological process. The spring-time as well as other phenological responses of woody plant parts to environmental drivers have been discussed recently by Delpierre et al. (2015).

This study is the first to show that monoterpene emissions from Scots pine stems are linked to changes in stem water relations during the spring recovery, indicated by sudden changes in stem radius and disruption of the normal diurnal cycle of xylem sap flow during the highest emission burst. The stem emissions are in general much lower than those from green plant parts, but our study indicates that the mechanisms related to stem emissions are less related to changes in environmental conditions than to the physiology of the tree, especially during the winter dehardening phase. The results open interesting new insights on the measurements of monoterpene emissions: although emission measurements on shoots using branch enclosures abound, we know practically very little of the detailed emission patterns and their driving factors of the woody parts of the shoots, which may be very different than in leaves or needles. The emission dynamics in leaves may follow the traditional temperature (pools) and light (synthesis) responses, but in woody compartments the large oleoresin reservoirs are less directly affected by these incident factors, and more likely reflecting a longer term adjustment of the tree physiology. Furthermore, the future directions on the topic should address the studies on cellular-level processes in tree stems.

Acknowledgements. This work was supported by the Finnish Center of Excellence “Physics, Chemistry, Biology and Meteorology of Atmospheric Composition and Climate Change” (projects 1118615 and 272041), Nordic Center of Excellence CRAICC and Helsinki University Centre for Environment HENVI. We highly acknowledge the assistance given during the measurements by the staff of the SMEAR II station.

References

Aalto, J., Kolari, P., Hari, P., Kerminen, V.-M., Schiestl-Aalto, P., Aaltonen, H., Levula, J., Siivola, E., Kulmala, M., and Bäck, J.: New foliage growth is a significant, unaccounted source for volatiles in boreal evergreen forests, Biogeosciences, 11, 1331–1344, doi:10.5194/bg-11-1331-2014, 2014.

Altimir, N., Kolari, P., Tuovinen, J.-P., Vesala, T., Bäck, J., Suni, T., Kulmala, M., and Hari, P.: Foliage surface ozone deposition: a role for surface moisture?, Biogeosciences, 3, 209–228, doi:10.5194/bg-3-209-2006, 2006.

Améglio, T., Bodet, C., Lacointe, A., and Cochard, H.: Winter embolism, mechanisms of xylem hydraulic conductivity recovery and springtime growth patterns in walnut and peach trees, Tree Physiol., 22, 1211–1220, 2002.

Antonova, G. F. and Stasova, V. V.: Seasonal development of phloem in Scots pine stems, Ontogenez, 37, 368–383, 2006.

Back, E. L. and Ekman, R.: The variability of wood resin, in: Pitch Control, Wood Resin and Deresination, edited by: Back, E. L. and Allen, L. H., TAPPI Press, Atlanta, xii–xiv, 2000.

Christensen, C. S., Hummelshøj, P., Jensen, N. O., Larsen, B., Lohse, C., Pilegaard, K., and Skov, H.: Determination of terpene flux from orange species and Norway spruce by relaxed eddy accumulation, Atmos. Environ., 34, 3057–3067, 2000.

Cochard, H., Lemoine, D., Améglio, T., and Granier, A.: Mechanisms of xylem recovery from winter embolism in *Fagus sylvatica*, Tree Physiol., 21, 27–33, 2001.

Cristani, M., D'Arrigo, M., Mandalari, G., Castelli, F., Sarpietro, M. G., Micieli, D., Venuti, V., Bisignano, G., Saija, A., and Trombetta, D.: Interaction of four monoterpenes contained in essential oils with model membranes: implications for their antibacterial activity, J. Agr. Food Chem., 55, 6300–6308, 2007.

Delpierre, N., Vitasse, Y., Chuine, I., Guillemot, J., Bazot, S., Rutishauser, T., and Rathgeber, C. B. K.: Temperate and boreal forest tree phenology: from organ-scale processes to terrestrial ecosystem models, Ann. For. Sci., doi:10.1007/s13595-015-0477-6, 2015.

Erbilgin, N. and Colgan, L. J.: Differential effects of plant ontogeny and damage type on phloem and foliage monoterpenes in jack pine (*Pinus banksiana*), Tree Physiol., 32, 946–957, 2012.

Ghirardo, A., Koch, K., Taipale, R., Zimmer, I., Schnitzler, J.-P., and Rinne, J.: Determination of de novo and pool emissions of terpenes from four common boreal/alpine trees by $^{13}CO_2$ labelling and PTR-MS analysis, Plant Cell Environ., 33, 781–792, 2010.

Grabmer, W., Graus, M., Wisthaler, A., Rappenglück, B., Steinbrecher, R., and Hansel, A.: Disjunct eddy covariance measurements of monoterpene fluxes from a Norway spruce forest using PTR-MS, Int. J. Mass Spectrom., 239, 111–115, 2004.

Granier, A.: Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements, Tree Physiol., 3, 309–320, 1987.

Granström, K. M.: Wood processing as a source of terpene emissions compared to natural sources, WIT Trans. Ecol. Envir., 101, 263–272, 2007.

Guenther, A.: Seasonal and spatial variations in natural volatile organic compound emissions, Ecol. Appl., 7, 34–45, 1997.

Guenther, A., Zimmerman, P., Harley, P., Monson, R., and Fall, R.: Isoprene and monoterpene emission rate variability: model evaluations and sensitivity analyses, J. Geophys. Res., 98, 12609–12617, 1993.

Hansel, A., Jordan, A., Holzinger, R., Prazeller, P., Vogel, W., and Lindinger, W.: Proton transfer reaction mass spectrometry: on-line trace gas analysis at ppb level, Int. J. Mass Spectrom., 149, 609–619, 1995.

Hari, P. and Kulmala, M.: Station for Measuring Ecosystem–Atmosphere Relations (SMEAR II), Boreal Environ. Res., 10, 315–322, 2005.

Irvine, J. and Grace, J.: Continuous measurements of water tensions in the xylem of trees based on the elastic properties of wood, Planta, 202, 455–461, 1997.

Isidorov, V. A., Zenkevich, I. G., and Ioffe, B. V.: Volatile organic compounds in the atmosphere of forests, Atmos. Environ., 19, 1–8, 1985.

Jyske, T., Mäkinen, H., Kalliokoski, T., and Nöjd, P.: Intra-annual tracheid production of Norway spruce and Scots pine across a latitudinal gradient in Finland, Agr. Forest Meteorol., 194, 241–254, 2014.

Kolari, P., Kulmala, L., Pumpanen, J., Launiainen, S., Ilvesniemi, H., Hari, P., and Nikinmaa, E.: CO_2 exchange and component CO_2 fluxes of a boreal Scots pine forest, Boreal Environ. Res., 14, 761–783, 2009.

Kolari, P., Bäck, J., Taipale, R., Ruuskanen, T. M., Kajos, M. K., Rinne, J., Kulmala, M., and Hari, P.: Evaluation of accuracy in measurements of VOC emissions with dynamic chamber system, Atmos. Environ., 62, 344–351, 2012.

Langenheim, J. H.: Plant Resins: Chemistry, Evolution, Ecology, and Ethnobotany, Timber Press, Portland, Cambridge, 586 pp., 2003.

Lerdau, M., Litvak, M., Palmer, P., and Monson, R.: Controls over monoterpene emissions from boreal forest conifers, Tree Physiol., 17, 563–569, 1997.

Lewinsohn, E., Gijzen, M., and Croteau, R.: Defence mechanisms of conifers, Plant Physiol., 96, 44–49, 1991.

Martz, F., Sutinen, M.-L., Kiviniemi, S., and Palta, J. P.: Changes in freezing tolerance, plasma membrane H^+-ATPase activity and fatty acid composition in *Pinus resinosa* needles during cold acclimation and de-acclimation, Tree Physiol., 26, 783–790, 2006.

Mencuccini, M., Hölttä, T., Sevanto, S., and Nikinmaa, E.: Concurrent measurements of change in the bark and xylem diameters of trees reveal a phloem-generated turgor signal, New Phytol., 198, 1143–1154, 2013.

Nardini, A., Lo Gullo, M. A., and Salleo, S.: Refilling embolized xylem conduits: is it a matter of phloem unloading?, Plant Sci., 180, 604–611, 2011.

Neher, H. V.: Effects of pressures inside Monterey pine trees, Trees, 8, 9–17, 1993.

Niinemets, Ü. and Reichstein, M.: A model analysis of the effects of nonspecific monoterpenoid storage in leaf tissues on emission kinetics and composition in Mediterranean sclerophyllous *Quercus* species, Global Biogeochem. Cy., 16, 1–26, 2002.

Niinemets, Ü. and Reichstein, M.: Controls on the emission of plant volatiles through stomata: differential sensitivity of emission rates to stomatal closure explained, J. Geophys. Res., 108, 4208, doi:10.1029/2002JD002620, 2003a.

Niinemets, Ü. and Reichstein, M.: Controls on the emission of plant volatiles through stomata: a sensitivity analysis, J. Geophys. Res., 108, 4211, doi:10.1029/2002JD002626, 2003b.

Ormeño, E., Goldstein, A., and Niinemets, Ü.: Extracting and trapping biogenic volatile organic compounds stored in plant species, TRAC-Trend. Anal. Chem., 30, 978–989, 2011.

Perämäki, M., Vesala, T., and Nikinmaa, E.: Analysing the applicability of the heat balance method for estimating sap flow in boreal forest conditions, Boreal Environ. Res., 6, 29–43, 2001.

Perämäki, M., Vesala, T., and Nikinmaa, E.: Modeling the dynamics of pressure propagation and diameter variation in tree sapwood, Tree Physiol., 25, 1091–1099, 2005.

Phillips, M. A. and Croteau, R. B.: Resin-based defences in conifers, Trends Plant Sci., 4, 184–190, 1999.

Pirinen, P., Simola, H., Aalto, J., Kaukoranta, J.-P., Karlsson, P., and Ruuhela, R.: Tilastoja Suomen ilmastosta 1981–2010, Finnish Meteorological Inst. Rep. 2012/1, Finnish Meteorological Institute in Helsinki, Finland, 1–96, 2012.

Pittermann, J. and Sperry, J.: Tracheid diameter is the key trait determining the extent of freezing-induced embolism in conifers, Tree Physiol., 23, 907–914, 2003.

Pittermann, J. and Sperry, J. S.: Analysis of freeze–thaw embolism in conifers. The interaction between cavitation pressure and tracheid size, Plant Physiol., 140, 374–382, 2006.

Pukacki, P. M. and Kaminska-Rozek, E.: Differential effects of spring reacclimation and deacclimation on cell membranes of Norway spruce seedlings, Acta Soc. Bot. Pol., 82, 77–84, 2013.

Rockwood, D. L.: Variation in the monoterpene composition of two oleoresin systems of loblolly pine, Forest Sci., 19, 147–153, 1973.

Ruuskanen, T. M., Kolari, P., Bäck, J., Kulmala, M., Rinne, J., Hakola, H., Taipale, R., Raivonen, M., Altimir, N., and Hari, P.: On-line field measurements of monoterpene emissions from Scots pine by proton transfer reaction – mass spectrometry, Boreal Environ. Res., 10, 553–567, 2005.

Salleo, S., Lo Gullo, M. A., DePaoli, D., and Zippo, M.: Xylem recovery from cavitation-induced embolism in young plants of Laurus nobilis: a possible mechanism, New Phytol., 132, 47–56, 1996.

Salleo, S., Lo Gullo, M. A., Trifilo, P., and Nardini, A.: New evidence for a role of vessel-associated cells and phloem in the rapid xylem refilling of cavitated stems of *Laurus nobilis* L., Plant Cell Environ., 27, 1065–1076, 2004.

Sevanto, S., Vesala, T., Perämäki, M., and Nikinmaa, E.: Time lags for xylem and stem diameter variations in a Scots pine tree, Plant Cell Environ., 25, 1071–1077, 2002.

Sevanto, S., Hölttä, T., Markkanen, T., Perämäki, M., Nikinmaa, E., and Vesala, T.: Relationships between diurnal xylem diameter variation and environmental factors in Scots pine, Boreal Environ. Res., 10, 447–458, 2005.

Sevanto, S., Hölttä, T., and Holbrook, N. M.: Effects of the hydraulic coupling between xylem and phloem on diurnal phloem diameter variation, Plant Cell Environ., 34, 690–703, 2011.

Shao, M., Czapiewski, K. V., Heiden, A. C., Kobel, K., Komenda, M., Koppmann, R., and Wildt, J.: Volatile organic compound emissions from Scots pine: mechanisms and description by algorithms, J. Geophys. Res., 106, 20483–20491, 2001.

Sparks, J. P., Campbell, G. S., and Black, R. A.: Water content, hydraulic conductivity, and ice formation in winter stems of Pinus contorta: a TDR case study, Oecologia, 127, 468–475, 2001.

Sperry, J. S.: Winter xylem embolism and spring recovery in *Betula cordifolia*, *Fagus grandifolia*, *Abies balsamea* and *Picea rubens*, in: Water Transport in Plants under Climatic Stress, edited by: Borghetti, M., Grace, J., and Raschi, A., Cambridge University Press, Cambridge, UK, 86–98, 1993.

Staudt, M. and Bertin, N.: Light and temperature dependence of the emission of cyclic and acyclic monoterpenes from holm oak (*Quercus ilex* L.) leaves, Plant Cell Environ., 21, 385–395, 1998.

Strömvall, A.-M. and Petersson, G.: Conifer monoterpenes emitted to air by logging operations, Scand. J. For. Res., 6, 253–258, 1991.

Strömvall, A.-M. and Petersson, G.: Monoterpenes emitted to air from industrial barking of Scandinavian conifers, Environ. Pollut., 79, 215–218, 1993.

Strömvall, A.-M. and Petersson, G.: Volatile terpenes emitted to air, in: Pitch Control, Wood Resin and Deresination, edited by: Back, E. L. and Allen, L. H., TAPPI Press, Atlanta, 77–99, 2000.

Tarvainen, V., Hakola, H., Hellén, H., Bäck, J., Hari, P., and Kulmala, M.: Temperature and light dependence of the VOC emissions of Scots pine, Atmos. Chem. Phys., 5, 989–998, doi:10.5194/acp-5-989-2005, 2005.

The Finnish Meteorological Institute: Open Data, available at: en.ilmatieteenlaitos.fi/open-data (last access: 19 February 2014), 2014a.

The Finnish Meteorological Institute: Climate in Finland, available at: http://en.ilmatieteenlaitos.fi/climate (last access: 12 February 2014), 2014b.

Trapp, S. and Croteau, R.: Defensive resin biosynthesis in conifers, Annu. Rev. Plant Physiol. Plant. Mol. Biol., 52, 689–724, 2001.

Trombetta, D., Castelli, F., Sarpietro, M. G., Venuti, V., Cristani, M., Daniele, C., Saija, A., Mazzanti, G., and Bisignano, G.: Mechanisms of antibacterial action of three monoterpenes, Antimicrob. Agents Ch., 49, 2474–2478, 2005.

Vesala, T., Hölttä, T., Perämäki, M., and Nikinmaa, E.: Refilling of a hydraulically isolated embolized xylem vessel: model calculations, Ann. Bot., 91, 419–428, 2003.

Wink, M.: Evolution of secondary metabolites from an ecological and molecular phylogenetic perspective, Phytochemistry, 64, 3–19, 2003.

Wullschleger, S. D., Hanson, P. J., and Todd, D. E.: Measuring stem water content in four deciduous hardwoods with a time-domain reflectometer, Tree Physiol., 16, 809–815, 1996.

Yang, S. and Tyree, M. T.: A theoretical model of hydraulic conductivity recovery from embolism with comparison to experimental data on *Acer saccharum*, Plant Cell Environ., 15, 633–643, 1992.

Zwieniecki, M. A. and Holbrook, N. M.: Confronting Maxwell's demon: biophysics of xylem embolism repair, Trends Plant Sci., 14, 530–534, 2009.

Zwieniecki, M. A., Hutyra, L., Thompson, M. V., and Holbrook, N. M.: Dynamic changes in petiole specific conductivity in red maple (*Acer rubrum* L.), tulip tree (*Liriodenron tulipifera* L.) and northern fox grape (*Vitis labrusca* L.), Plant Cell Environ., 23, 407–414, 2000.

Table 1. Environmental variables at the study site during statistical period 1981–2010 and in studied years 2012 and 2013.

	1981–2010[1]	2012[2]	2013[3]
Annual mean air temperature, °C	3.5	3.3	4.9
Minimum air temperature, °C	−38.1 (Jan 1987)	−31.7 (4 Feb)	−29.5 (18 Jan)
Maximum air temperature, °C	33.1 (Jul 2010)	27.5 (29 Jul)	29.6 (26 Jun)
Annual precipitation, mm	711	907	615
Annual maximum snow depth, cm	43	76	68
Duration of snow cover, days	227	157	179
First snow[3]	15 Oct	28 Nov	26 Oct
Snow melt	15–30 May	4 May	24 Apr
Thermal spring start	5 Apr	10 Apr	12 Apr
Start of the growing season	27 Apr–2 May	25 Apr	27 Apr
Annual cumulative temperature sum, degreedays	1200–1300	1161	1388
April mean temperature, °C	2.3	1.5	1.7
April minimum temperature, °C	−19.7	−16.5	−14.5
April maximum temperature, °C	23.4	13.9	11.9
April precipitation, mm	37	60	42
May mean temperature, °C	8.9	9.4	12.2
May minimum temperature, °C	−7.1	−2.9	−2.7
May maximum temperature, °C	28.2	23.8	24.9
May precipitation, mm	45	56	16

[1] Statistical data for years 1981–2010 is collected from Pirinen et al. (2012) and from Finnish Meteorological Institute (FMI) webpages (2014a, b).

[2] Data from FMI open access data (2014a).

[3] Date in the previous year.

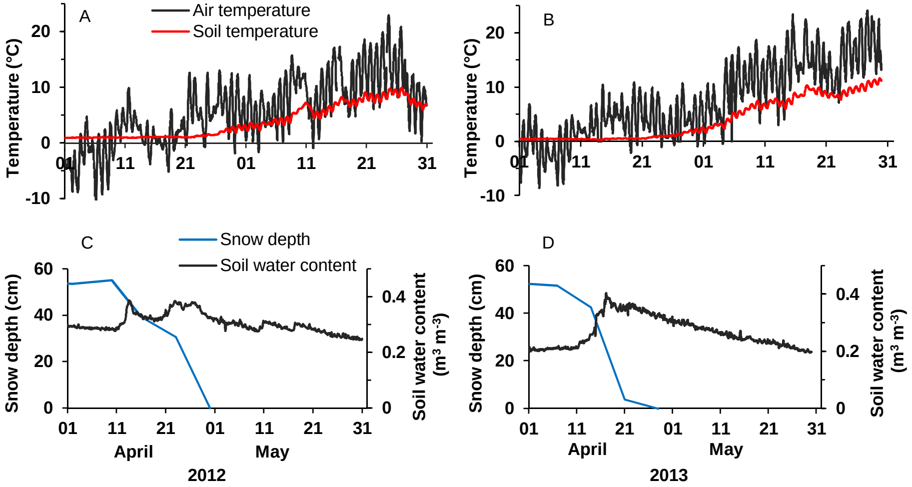

Figure 1. (a, b) Temperature at 8.4 m in air and in soil A horizon (°C). **(c, d)** Weekly snow depth (cm) and volumetric soil water content in A horizon ($m^3\,m^{-3}$). Left-hand panels are for April–May 2012 and right-hand panels for April–May 2013.

Figure 2. The stem enclosure around a Scots pine stem at a height of 12 m (left) and a linear variable displacement transducer to measure stem radius changes (right).

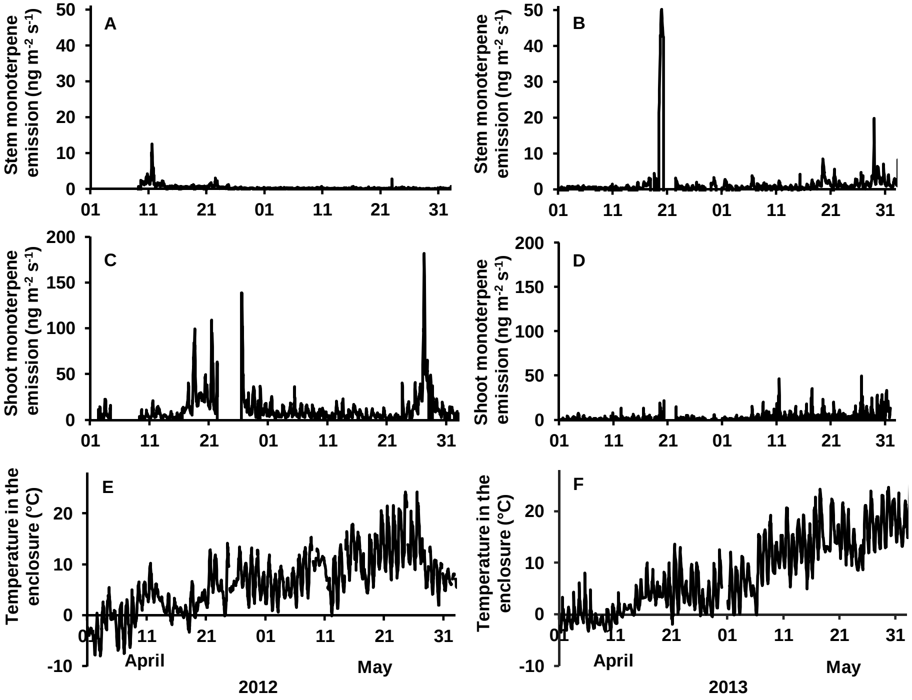

Figure 3. (a, b) Measured monoterpene emission (m/z 137, $\mathrm{ng\,m^{-2}}$ bark area $\mathrm{s^{-1}}$) from the pine stem (same location on the stem in both years). **(c, d)** Measured monoterpene emission (m/z 137, $\mathrm{ng\,m^{-2}}$ total needle area $\mathrm{s^{-1}}$) from a pine shoot (same shoot in both years). **(e, f)** Temperature (°C) in the stem enclosure. Left-hand panels for April–May 2012, right-hand panels for April–May 2013.

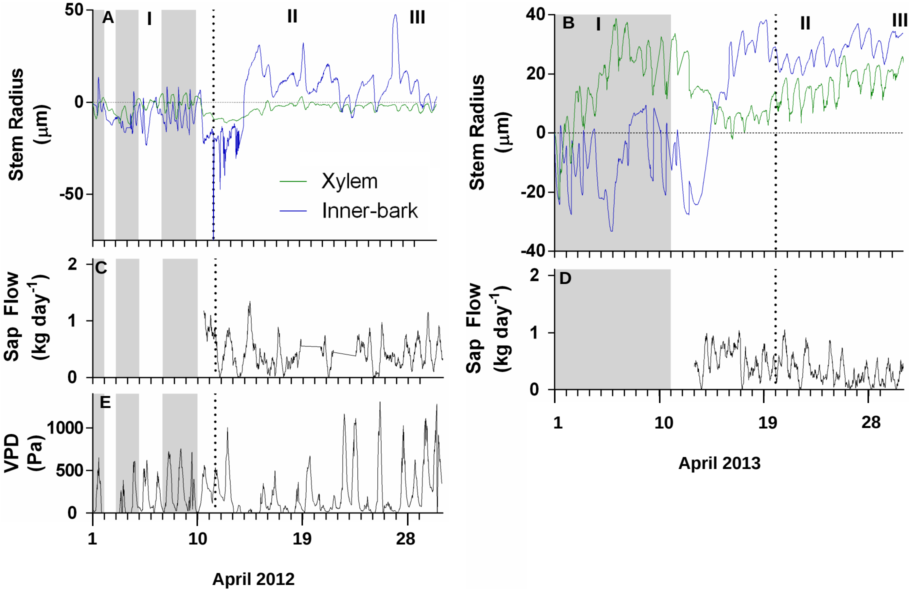

Figure 4. (a, b) Pine stem xylem and inner-bark radius changes (µm). **(c, d)** Stem sap flow (kg day^{-1}). **(e)** Vapor pressure deficit (VPD, Pa). Left-hand panels for April 2012 and right-hand panels for 2013. The grey shading refers to the periods when the stem was frozen. The timing of the monoterpene burst is marked with dotted lines. A closer look on the burst period is provided in the Fig. 5. The Roman numerals refer to the three phases of inner-bark radial changes discussed in the text.

BGD
12, 7783–7814, 2015

Title Page
Abstract | Introduction
Conclusions | References
Tables | Figures
I◀ | ▶I
◀ | ▶
Back | Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion

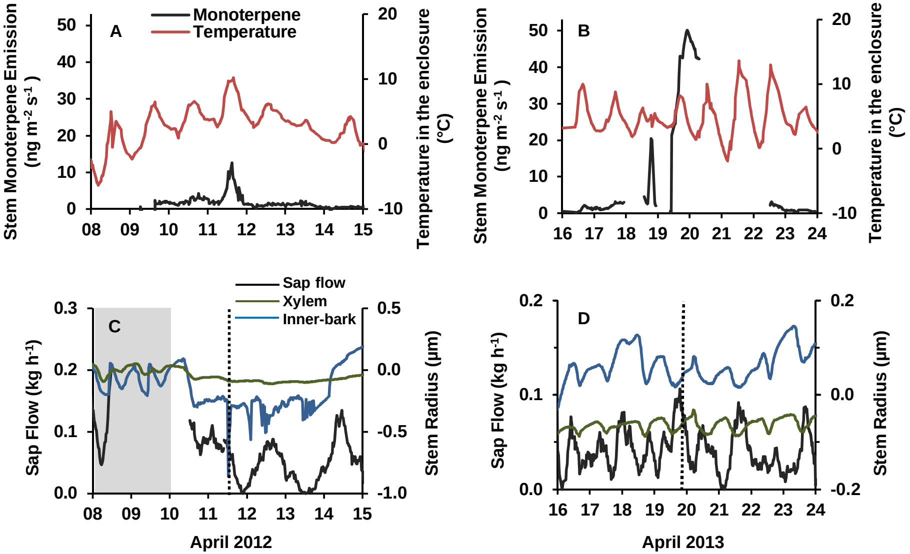

Figure 5. (a, b) Monoterpene emission from the stem (m/z 137, ng m^{-2} bark area s^{-1}) and the air temperature (°C) inside the enclosure. **(c, d)** Stem sap flow (kg h^{-1}) and inner-bark and xylem radius (µm). Left-hand panels for April 2012 and right-hand panels for April 2013. The grey shading refers to the periods when the stem was frozen. The timing of the monoterpene burst is marked with dotted lines in the lower panels.

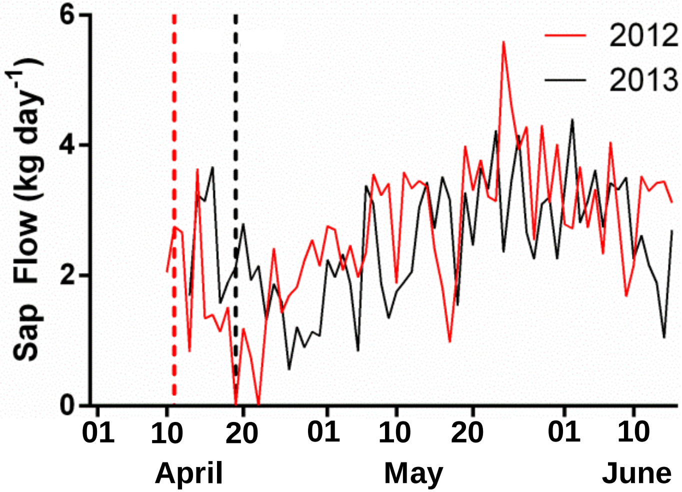

Figure 6. The daily sum of pine stem sap flow in 2012 (red) and 2013 (black). The timings of the monoterpene bursts are marked with dashed lines. The days when the stem was frozen are removed from the figure.

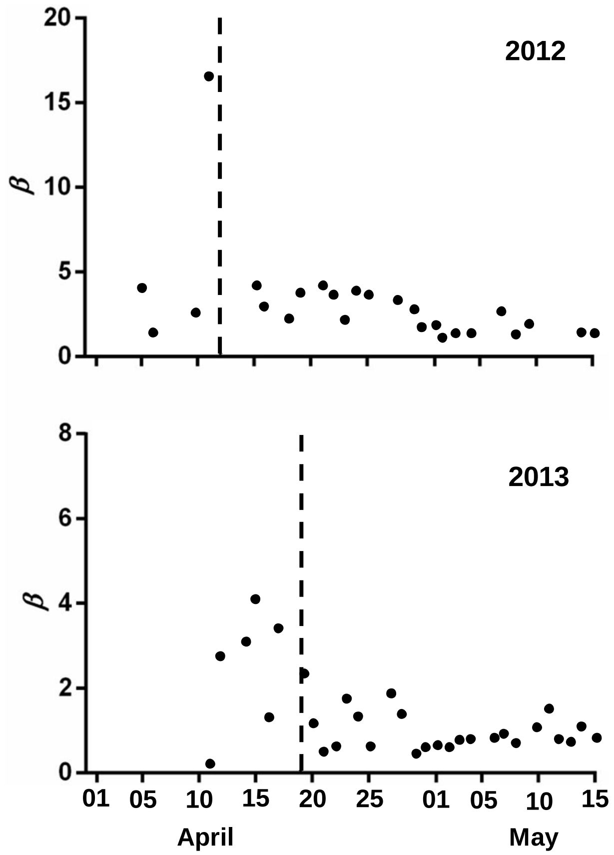

Figure 7. β as a function of time in 2012 and 2013. Figure shows that β (see Eq. 1), i.e. the daily amplitude of the phloem vs. xylem radial change, had its maximum value briefly before and during the monoterpene emission burst (dashed line). Days with occurrences of rain and frozen stem were removed.

Title Page
Abstract
Introduction
Conclusions
References
Tables
Figures
◂
▸
Back
Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion

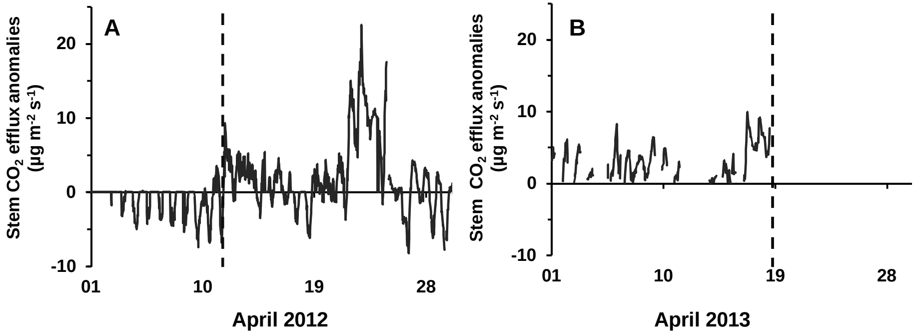

Figure 8. Temperature-corrected stem CO$_2$ efflux anomalies for April 2012 **(a)** and 2013 **(b)**.