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**Mountain birch –
large source of
sesquiterpenes into
atmosphere**

S. Haapanala et al.

Mountain birch – potentially large source of sesquiterpenes into high latitude atmosphere

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Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Abstract

Emissions of volatile organic compounds (VOCs) from mountain birches were measured in Abisko, northern Sweden. Mountain birches make up majority of the tree biomass in Scandinavian high latitudes, area subject to significant climate warming.

5 The measurements were carried out in two growing seasons. The emissions of a branch from four individual trees were measured in June–August 2006 and one of them again in July 2007. The measurements were conducted using a dynamic flow through chamber covered with Teflon film. The studied mountain birches were found to emit substantial amounts of linalool, monoterpenes and sesquiterpenes. The monoterpene
10 emission was dominated by sabinene. The magnitude and composition of sesquiterpene emission changed dramatically between the years. For example, the average α -farnesene emission in 2006 was almost $2000 \text{ ng g}_{\text{dw}}^{-1} \text{ h}^{-1}$ while in 2007 the emission of α -farnesene was negligible. Also the emissions of other sesquiterpenes decreased in 2007 to a fraction of that in 2006. One possible explanation for the change in emis-
15 sions is the herbivory damage that occurred in the area in 2004. Herbivory is known to enhance the emissions of sesquiterpenes, especially those of α -farnesene, and the effect may last several years.

1 Introduction

20 Volatile organic compounds (VOCs) are a diverse group of hydrocarbons emitted to the atmosphere by both biogenic and anthropogenic sources (Guenther et al., 1995; Simpson et al., 1999; Piccot et al., 1992). Their double bonds give rise to high reactivities towards the hydroxyl radical (OH), ozone (O_3), and the nitrate radical (NO_3). Therefore the volatile organic compounds play an essential role in the regulation of the oxidizing capacity of the atmosphere. The VOCs also contribute to the formation and growth of
25 secondary organic aerosols (Kulmala et al., 2004; Tunved et al., 2006), and they may form long-lived oxidation products, with the potential of affecting atmospheric chemistry

BGD

6, 5409–5430, 2009

Mountain birch – large source of sesquiterpenes into atmosphere

S. Haapanala et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

in remote regions (Law and Stohl, 2007).

Biogenic VOC emissions in the tropical, temperate and boreal vegetation zones have been extensively studied while the high-latitude, e.g. subarctic, ecosystems have gained much less attention (Tiiva et al., 2008; Bäckstrand et al., 2008; Ekberg et al., 2009). However, the subarctic vegetation zone covers large areas on the globe and despite its relatively low biomass density it can have a significant impact on atmospheric VOC concentrations, at least on the local to regional scales. Largely as a result of the prevalence of short and cool summers, biogenic VOC (BVOC) emissions from the northern regions are likely to be relatively small compared to the global emissions. However, atmospheric reactions such as particle formation from biogenic pre-cursors and ozone destruction/formation occur on regional rather than global spatial scales (e.g. Tunved et al., 2006; Svenningsson et al., 2008).

Mountain birch (*Betula pubescens* ssp. *czerepanovii* (Orlova) Hämet-Ahti), a subspecies of downy birch, covers an area of almost 600 000 ha in the Scandinavian subarctic. The birch species in boreal and temperate regions have been found to emit substantial amounts of a wide range of C_5 to C_{15} VOCs (Isidorov et al., 1985; König et al., 1995; Hakola et al., 1998, 2001; Vuorinen et al., 2005). BVOCs emitted from the mountain birch in the subarctic may thus be of significant regional importance for the complex relationship between the ecosystem carbon flux, atmospheric chemistry and climate, but at the present there is only one emission study available (Steinbrecher et al., 1999).

The subarctic mountain birch forests are exposed to herbivory by caterpillars of the autumnal moth (*Epirrita autumnata*) and severe outbreaks often occur with intervals of about 9–10 years. In some cases, large forest areas have suffered from mortality of most of the trees (Trägårdh, 1939; Haukioja et al., 1988). Mechanical damage of leaf tissue is known to induce an immediately enhanced production and emission of volatiles (Juuti et al., 1990). However, it has also been suggested that an immunological memory effect of herbivore attacks, potentially affecting the composition of the emitted VOC mixture, may persist for several years after the actual defoliation event (Ruuholta

BGD

6, 5409–5430, 2009

Mountain birch – large source of sesquiterpenes into atmosphere

S. Haapanala et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

et al., 2007).

The aim of the present study is to characterize the VOC emissions from a natural mountain birch forest. To obtain the emission parameters, usable in emission inventories and emission model development, the temperature and the photosynthetic photon flux density (PPFD) were carefully recorded during the measurements. In addition to the VOC emission measurements, ecosystem scale photosynthesis was measured simultaneously at the same site. From these data we also managed to study the link between delayed responses of herbivory damage and the atmospheric VOC emissions of plants.

2 Materials and methods

2.1 Measurement site

The measurements took place in Stordalen Nature Reserve, located near Abisko in northern Sweden (68°20' N, 19°03' E, 360 m a.s.l.). The long-term annual mean temperature at Abisko climate station (68°21' N, 18°49' E, 388 m a.s.l.) is -0.8°C with the warmest month being July (mean temperature 11.0°C) and the coldest January (mean temperature -11.9°C). The sheltered valley has a relatively dry microclimate with mean annual precipitation of 304 mm. The highest precipitation occurs in July (mean rainfall 54 mm) and the lowest in April (mean rainfall 12 mm) (Alexandersson et al., 1991). Snow accounts for about half of the precipitation.

The woody vegetation at the measurement site is dominated by mountain birch. The forest is limited by a mire in the north and continues in the other directions for hundreds of meters. There is a road with little traffic to the south of the measurement site. During the growing season of 2004 the area was affected by a massive outbreak of the autumnal moth. By the growing season of 2006, the trees were mostly recovered from the damage caused by the outbreak. Net CO₂ exchange was in the same order of

BGD

6, 5409–5430, 2009

Mountain birch – large source of sesquiterpenes into atmosphere

S. Haapanala et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

magnitude as in the growing seasons preceding the outbreak in 2004 (T. Johansson¹, personal communication, 2009).

In summer 2006 we conducted VOC emission measurements on four individual trees (numbered as 1–4) and, as a complementary measurement, one of them (number 4) was measured again in summer 2007. The measurements took place during 28 June–5 August 2006 and during 16–17 July 2007. During both of the campaigns the leaves of the studied trees were mature. Due to the fact that all the measurements were conducted in the middle of the growing season, the seasonal variation of the emission was not studied.

2.2 Sampling

For the VOC emission measurements a branch growing about 2 m above the ground level was placed in a transparent chamber made of Teflon film. The canopy is open and at that height, about half of total tree-height, the branch is sun-exposed. The enclosure installation took place at least one day before the measurements to avoid any effects of rough handling on the emission, has been shown to cause increased emissions (e.g. Juuti et al., 1990; König et al., 1995; Hakola et al., 2001). The enclosure was appropriately ventilated until just prior to sampling initiation. The volume of the cylindrical enclosure was about 15 l. Inflowing air was pumped to the enclosure at a rate of about 5 l min⁻¹. Ozone was removed from the inflow air using MnO₂ coated copper nets. Samples from both inflow and outflow air were collected by trapping C₅–C₁₅ hydrocarbons to cartridges filled with Tenax-TA and Carboxpack-B/Carboxgraph 1TD adsorbents. The samples were taken using a constant flow rate of about 0.1 to 0.2 l per minute and sampling times of 55 to 120 min resulting in 6 to 12 l sample volume. The adsorbent samples were analyzed using an automatic thermodesorption device (Perkin-Elmer ATD-400) connected to a gas chromatograph (HP-5890), with a mass-selective detector (HP-5972). The accuracy of the repeated adsorbent calibra-

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Mountain birch – large source of sesquiterpenes into atmosphere

S. Haapanala et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



tion sample analysis was estimated to be about 6% for each compound. This value was used as an accuracy estimate for the concentrations. Emission rates were determined based on differences in concentration between inlet and outlet air. For further description of the enclosure system and chemical analysis, see Hakola et al. (2006).

5 Despite the relatively high air flow through the enclosure, the temperature inside the enclosures increased during periods of strong solar radiation. The highest recorded temperature inside the enclosures was 31.4°C, with the corresponding ambient temperature being 18.0°C. During the measurements the temperature difference between the enclosure and the ambient air varied from 0 to 15°C, with the average increase being as high as 7.1°C. This should be taken into account when interpreting the regional
10 emission values.

3 Results and discussion

3.1 Measured emissions

15 Mountain birches were found to emit large amounts of mono- and sesquiterpenes. In addition, linalool emission was found to be substantial, about half of the monoterpene emission. Isoprene emission was negligible. Examples of the emissions of the different VOC groups are shown in Fig. 1 together with records of temperature, light intensity and net ecosystem CO₂ exchange from eddy covariance flux tower at the same site. From these results it is apparent that the emissions are strongly dependent on the
20 temperature inside the chamber.

The average emission spectra of the most abundant compounds during the measurements in 2006 and 2007 are shown in Fig. 2. When considering single monoterpene species, the monoterpene emission was dominated by sabinene. Other abundant
25 monoterpenes were ocimene, trans-ocimene, terpinolene and α -pinene. The same compounds were identified by Hakola et al. (2001) from the emissions of downy birch in southern Finland. The total monoterpene emission averaged over all trees in 2006

Mountain birch – large source of sesquiterpenes into atmosphere

S. Haapanala et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



was $1100 \text{ ng g}_{\text{dw}}^{-1} \text{ h}^{-1}$ ($970 \text{ ng C g}_{\text{dw}}^{-1} \text{ h}^{-1}$), ranging from 0 to $14\,000 \text{ ng g}_{\text{dw}}^{-1} \text{ h}^{-1}$. In 2007 the average sum was almost equal, $1200 \text{ ng g}_{\text{dw}}^{-1} \text{ h}^{-1}$ ($1060 \text{ ng C g}_{\text{dw}}^{-1} \text{ h}^{-1}$), and varied between 0 and $4000 \text{ ng g}_{\text{dw}}^{-1} \text{ h}^{-1}$. In Fig. 3a we show the monoterpene emissions of birch 4 as a function of temperature. The results show that even though the average emission was almost the same, the emission patterns in different years were somewhat different. In 2006, clear increase above zero line can be distinguished during the warmest periods, whereas in 2007 some monoterpene release took place already at relatively cool temperatures around 15°C .

In 2006 sesquiterpenes were emitted in high amounts, the average sum emission being $2700 \text{ ng g}_{\text{dw}}^{-1} \text{ h}^{-1}$ ($2380 \text{ ng C g}_{\text{dw}}^{-1} \text{ h}^{-1}$). The sesquiterpene emission varied between 0 and $31\,000 \text{ ng g}_{\text{dw}}^{-1} \text{ h}^{-1}$. The dominant sesquiterpene compound was α -farnesene, followed by β -caryophyllene. In 2007 the sesquiterpene emission was reduced to a fraction of that in 2006. The average sum emission was only $16 \text{ ng g}_{\text{dw}}^{-1} \text{ h}^{-1}$ ($14 \text{ ng C g}_{\text{dw}}^{-1} \text{ h}^{-1}$), which is less than 1% of that in the previous year. The dominating compound was β -caryophyllene while α -farnesene was lacking completely. From Fig. 3b the differences between the magnitudes of the sesquiterpene emissions can clearly be seen.

The tree-to-tree variation of the emissions was high (see Table 1). Trees 1 and 4 had almost equal emissions of mono- and sesquiterpenes. Trees 2 and 3 had somewhat smaller monoterpene but significantly higher sesquiterpene emissions than the other trees. Mountain birch has several phenotypes, from small polycormic (multi-stemmed) shrubs to large monocormic (single-stemmed) trees (Vaarama and Valanne, 1973). Hybridization with dwarf birch (*Betula nana* L.) is common and it is one of the factors affecting the growth form. This variation may be one of the factors explaining the differences in the emissions between the trees. Also Hakola et al. (2001) point out the large variation in the emissions between the individual trees.

Mountain birch – large source of sesquiterpenes into atmosphere

S. Haapanala et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[⏪](#)[⏩](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

3.2 Temperature and light dependence of emission rates

To study the temperature and light dependence of VOC emission rates we performed nonlinear regression analysis using two widely applied emission algorithms. TEMP-algorithm (Guenther et al., 1993) is a simple exponential model of the form

$$E = E_0 \exp(\beta(T - T_0)), \quad (1)$$

where E is emission rate at temperature T , E_0 is emission potential at temperature T_0 , and β is an empirical coefficient describing the strength of the temperature dependence. It describes emissions from storage pools inside the plants and it is usually considered as the monoterpene emission algorithm. G97-algorithm (Guenther et al., 1993; Guenther, 1997) is both temperature and light dependent description of emission rate given by

$$E = E_0 C_T C_L, \quad (2)$$

where E is emission rate at temperature T and PPFD L , E_0 is emission potential at temperature T_0 and PPFD L_0 . Temperature dependence factor C_T is Arrhenius-type description of enzymatic activity having maximum above 35°C. C_L is light dependence factor following light dependence of photosynthesis, and saturating at 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. It is applied to isoprene and monoterpene emissions that are not stored but emitted rather directly from production (e.g. Rinne et al., 2002; Kuhn et al., 2004).

The regression analysis was performed separately for each of the four studied birches and both years. The regression with the TEMP algorithm was performed both with a fixed and a variable strength of the temperature dependence. The selection of fixed β value is based on commonly used values for the emission rates. For monoterpenes, $\beta=0.09^\circ\text{C}^{-1}$ was used following the proposal of Guenther et al. (1993) and confirmed by several investigators thereafter for various plant species. For sesquiterpenes, a larger range of values has been reported. The average value from the studies listed by Duhal et al. (2008) is $\beta=0.18^\circ\text{C}^{-1}$, which was adapted to this study. A summary of the resulting regression parameters is given in Table 1. Figure 4 shows the

BGD

6, 5409–5430, 2009

Mountain birch – large source of sesquiterpenes into atmosphere

S. Haapanala et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



measured emission together with ones obtained from fittings of the two algorithms. In addition, the differences between the measured and predicted emissions are shown.

Both mono- and sesquiterpene emissions were slightly better explained by the solely temperature dependent algorithm (TEMP). In most cases, allowing the β coefficient to vary produces somewhat better regression statistics, especially for the monoterpenes. This method yield to the average correlation coefficients R^2 of 0.72 for monoterpenes and 0.65 for sesquiterpenes. Forcing the temperature coefficients to constants decreased the correlation coefficients R^2 to 0.48 and 0.63 for mono- and sesquiterpenes, respectively.

The temperature dependence coefficient β varied from 0.04°C^{-1} to 0.93°C^{-1} for the monoterpene emission and from 0.15°C^{-1} to 0.25°C^{-1} for the sesquiterpene emission. The average temperature coefficients for mono- and sesquiterpene emissions were 0.32°C^{-1} and 0.21°C^{-1} , respectively. Neglecting the non significant regression results with the P value >0.05 (marked n.s. in Table 1) the temperature coefficients become 0.39°C^{-1} and 0.23°C^{-1} for mono- and sesquiterpene emissions, respectively. For comparison, Hakola et al. (2001) reported β value of 0.11°C^{-1} for monoterpenes and $0.14\text{--}0.22^\circ\text{C}^{-1}$ for sesquiterpenes from their downy birch measurements. This temperature coefficient of sesquiterpene emission rate is in the same range with our results. The monoterpene emission rate, however, seems to be significantly more sensitive to temperature in mountain birch than in downy birch.

The temperature and light dependent algorithm (G97) was able to reproduce the measurement data reasonably well in most of the cases. This algorithm explicitly sets the emission to zero in total darkness. Similar behavior was also seen in the present data during nighttime for both mono- and sesquiterpenes (see Figs. 1 and 4). This is easy to understand since birches do not have resin ducts where terpenes could be stored in high amounts, and hence most of the emission must come almost directly from synthesis. This was also recently shown for silver birch (*Betula pendula* L.) by Ghirardo et al. (2009).

**Mountain birch –
large source of
sesquiterpenes into
atmosphere**S. Haapanala et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[⏪](#)[⏩](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

**Mountain birch –
large source of
sesquiterpenes into
atmosphere**S. Haapanala et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

In addition to the standard way of using these algorithms, we tried to reproduce the emissions using a linear combination of TEMP and G97 algorithms, following the approach used by e.g. Steinbrecher et al. (1999). This exercise was conducted only for the data from 2007 when the trees were supposed to function normally, without special resistance to herbivory. The hybrid algorithm slightly improved the fit, as expected. Holzke et al. (2006) used a hybrid algorithm, where they made use of the temperature dependence part of G97 algorithm as the pool emission, instead of the TEMP algorithm. In practice, the difference between these two approaches is small when applied in a narrow temperature range. However, the use of the TEMP algorithm allows setting the temperature dependence factor β to a value obtained from the current dataset.

3.3 Emission potentials

Emission potentials were calculated for each tree using both TEMP and G97 algorithms (see Table 1). The emission potentials were calculated at the temperatures of 20°C and 30°C. The emission potentials at 20°C are calculated to give the correct order of magnitude of the emission rates at the temperatures that really occur in the area. The values at 30°C are shown for easy comparison to other studies, and these values are discussed below. In all cases, tree-to-tree variations in the emission potentials were high.

Best fittings were obtained using the variable temperature coefficients in the TEMP algorithm. The resulting emission potentials for monoterpenes varied from 617 to 11 511 $\text{ng g}_{\text{dw}}^{-1} \text{h}^{-1}$, the average value being 5264 $\text{ng g}_{\text{dw}}^{-1} \text{h}^{-1}$. Emission potentials for sesquiterpenes varied between 255 and 15 801 $\text{ng g}_{\text{dw}}^{-1} \text{h}^{-1}$, the average value being 6526 $\text{ng g}_{\text{dw}}^{-1} \text{h}^{-1}$. The lowest sesquiterpene emission potential was obtained in 2007, when the sesquiterpene emission was clearly different from the emission in 2006.

For comparison, Hakola et al. (2001) reported late summer monoterpene emission potentials of downy birch ranging from 170 to 5490 $\text{ng g}_{\text{dw}}^{-1} \text{h}^{-1}$. For sesquiterpenes, they measured emission potentials 310–6940 $\text{ng g}_{\text{dw}}^{-1} \text{h}^{-1}$. The emission potentials

of both mono- and sesquiterpenes obtained from our measurements are somewhat higher than those measured before for downy birch.

If we force the temperature dependence to a fixed value $\beta=0.09^{\circ}\text{C}^{-1}$, the resulting emission potentials are strongly decreased. For example birch 4, measured in 2007, had the monoterpene emission potential of $9965\text{ ng g}_{\text{dw}}^{-1}\text{ h}^{-1}$ when the temperature dependence coefficient was taken from the dataset. The emission potential was decreased to $4164\text{ ng g}_{\text{dw}}^{-1}\text{ h}^{-1}$ when the temperature dependence was forced to $\beta=0.09^{\circ}\text{C}^{-1}$.

The monoterpene emission potentials of G97 algorithm range from 490 to $10819\text{ ng g}_{\text{dw}}^{-1}\text{ h}^{-1}$, the average value being $3880\text{ ng g}_{\text{dw}}^{-1}\text{ h}^{-1}$. For sesquiterpene emission rate the emission potential vary between 98 and $14410\text{ ng g}_{\text{dw}}^{-1}\text{ h}^{-1}$, averaging at $5624\text{ ng g}_{\text{dw}}^{-1}\text{ h}^{-1}$. The lowest sesquiterpene emission potential comes from 2007 data, and it significantly differs from those of 2006 data, as with the TEMP algorithm.

3.4 Possible reason for high sesquiterpene emission

The change in the sesquiterpene emission between the years was dramatic. Climatic conditions did not heavily differ between the years. While sampling birch 4, the effective temperature sum ($+5^{\circ}\text{C}$ threshold) was between 150 and 320 d.d. (degree days) in 2006 and 270 d.d. in 2007. The effective temperature sum was calculated using the air temperature data from Stordalen mire, located a few hundred meters from the birch measurement site. A possible reason for the very high sesquiterpene emission might be herbivory damage that occurred in the area in 2004. Stress induced emissions can differ from normal emissions in both magnitude and composition. There is plenty of literature where a changed emission pattern, particularly increased emissions of the sesquiterpenes α -farnesene and β -caryophyllene, is linked to various stress factors of the plants (e.g. Paré and Tumlinson, 1999; Holopainen, 2004). Stress factors include for instance high temperature, drought and mechanical or biological damage. One of the most important stress factors is insect herbivore damage. Herbivore induced VOC

Mountain birch – large source of sesquiterpenes into atmosphere

S. Haapanala et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

emissions may help plants to defend themselves by repelling the insects, disturbing their growth and breeding, or by attracting the natural enemies of the insects. Staudt et al. (2007) studied the effects of gypsy moth (*Lymantria dispar* L.) feeding on VOC emission from holm oak (*Quercus ilex* L.). Feeding induced the emissions of new VOC compounds, consisting of sesquiterpenes, a homoterpene and a monoterpene alcohol. Also undamaged leaves of infested trees emitted new VOCs, but with a different composition and at lower rates.

In addition to the instant responses, plants have delayed responses. Immunological memory of mountain birch after the herbivory by autumnal moth is discussed by Ruuhola et al. (2007). They found out that delayed induced resistance lasted as long as five years. The trees exposed to herbivory five years earlier maintained decreased performance of moth larvae. In addition, some changes in the chemical composition of the leaves was observed. The quercetin to kaemferol ratio was increased whereas phenolic compounds were not significantly affected. The general features of plant memory were recently reviewed by Bruce et al. (2007). They define a plant memory, or stress imprint, as a genetic or biochemical modification of a plant that occurs after stress exposure. These changes in gene expression or plant metabolism cause the plant to respond in a different way to the future stress factors.

Our results suggest that also the changes in the VOC emissions may last several years. If a single insect outbreak affects the emissions for about three years and outbreaks occurs about once a decade, the mountain birch forest acts as high sesquiterpene emitter during about one third of the years. As sesquiterpenes are known to be important for formation and growth of secondary organic aerosols (e.g. Bonn and Moortgat, 2003) there may be link between occurrence of herbivores and aerosol particle formation events.

**Mountain birch –
large source of
sesquiterpenes into
atmosphere**S. Haapanala et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

4 Conclusions

We measured the branch scale emissions of various VOC compounds from mountain birch, a dominant tree species of the European subarctic ecosystems. The mountain birch leaves were found to emit a large quantity of VOCs, with rates higher than those from downy birch. The data of Tarvainen et al. (2005) suggests that also a Scots pine forest in the north may emit more sesquiterpenes than similar trees in the mid-latitudes. This may be, at least partly, explicable by the short but intensive growing season in the north.

Herbivory damage is supposed to significantly affect the sesquiterpene emission. Ideally, this variability between the years should be taken into account in the emission inventories. Even small changes in the emissions of sesquiterpenes may influence the local atmospheric chemistry strongly due to the fact that sesquiterpenes are chemically very reactive. These interactions raise also questions for future climate change impacts in insect outbreaks and herbivory, and their interactions with atmospheric processes, but today the available data is far too limited to comment on whether such changes will be substantial. In our case, our dataset is limited to just two growing seasons. While it indicates possible substantial effects in response to insect attacks, much more further research is needed for more accurate predictions.

From the present data it is obvious that both monoterpene and sesquiterpene emission of mountain birch approaches zero in the darkness. This suggests that majority of the emission originates directly from synthesis rather than from pools. The exact behavior is difficult to characterize from field data, as temperature and PPFD are strongly correlated.

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BGD

6, 5409–5430, 2009

Mountain birch – large source of sesquiterpenes into atmosphere

S. Haapanala et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

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BGD

6, 5409–5430, 2009

Mountain birch – large source of sesquiterpenes into atmosphere

S. Haapanala et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

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Mountain birch – large source of sesquiterpenes into atmosphere

S. Haapanala et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

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BGD

6, 5409–5430, 2009

**Mountain birch –
large source of
sesquiterpenes into
atmosphere**

S. Haapanala et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

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BGD

6, 5409–5430, 2009

**Mountain birch –
large source of
sesquiterpenes into
atmosphere**

S. Haapanala et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Mountain birch – large source of sesquiterpenes into atmosphere

S. Haapanala et al.

Table 1. The results of the nonlinear regression analysis of the monoterpene and sesquiterpene emission rates using both the temperature dependent TEMP algorithm (Guenther et al., 1993) and the temperature and light dependent G97 algorithm (Guenther et al., 1993; Guenther 1997). E_0 ($\text{ng g}_{\text{dw}}^{-1} \text{h}^{-1}$) are the emission potentials at temperatures of 20°C and 30°C and incident PPF of $1000 \mu\text{mol}_{\text{photons}} \text{m}^{-2} \text{s}^{-1}$ in the G97 algorithm. β ($^{\circ}\text{C}^{-1}$) is the coefficient describing the strength of the temperature dependence in the TEMP algorithm. R^2 is the regression statistic and the P values for fitted β are indicated using asterisks. The values in the parentheses are the standard errors. N indicates the number of samples in each subset.

Measurements	TEMP, $\beta_{\text{MT}}=0.09^{\circ}\text{C}^{-1}$, $\beta_{\text{SQT}}=0.18^{\circ}\text{C}^{-1}$				TEMP, variable β			G97		
	$E_{0,20^{\circ}\text{C}}$	$E_{0,30^{\circ}\text{C}}$	R^2	β	$E_{0,20^{\circ}\text{C}}$	$E_{0,30^{\circ}\text{C}}$	R^2	$E_{0,20^{\circ}\text{C}}$	$E_{0,30^{\circ}\text{C}}$	R^2
Birch 1, (N=21) 28.6.–21.7.2006										
Monoterpenes	289 (98)	710 (240)	0.46	0.270 (0.042)***	191 (47)	2846 (698)	0.77	291 (35)	1033 (125)	0.62
Sesquiterpenes	389 (60)	2352 (364)	0.71	0.207 (0.035)***	374 (90)	2818 (679)	0.72	428 (49)	1520 (174)	0.63
Birch 2, (N=7) 1.7.–4.8.2006										
Monoterpenes	188 (100)	461 (246)	0.53	0.928 (0.229)**	1 (0)	1379 (322)	0.92	137 (26)	490 (92)	0.62
Sesquiterpenes	1721 (972)	10412 (5882)	0.45	0.185 (0.189) n.s.	1649 (673)	10488 (4281)	0.45	2535 (694)	9046 (2478)	0.43
Birch 3, (N=6) 2.7.–29.7.2006										
Monoterpenes	281 (215)	692 (529)	0.03	0.042 (0.065) n.s.	405 (108)	617 (164)	0.12	195 (38)	698 (137)	0.00
Sesquiterpenes	2721 (3010)	16462 (18761)	0.18	0.150 (0.222) n.s.	3526 (2147)	15801 (9622)	0.18	4037 (1781)	14410 (6358)	0.19
Birch 4, (N=6) 3.7.–5.8.2006										
Monoterpenes	4093 (789)	10066 (1940)	0.73	0.193 (0.040)**	1671 (151)	11511 (1043)	0.94	3028 (334)	10819 (1193)	0.89
Sesquiterpenes	544 (58)	3292 (349)	0.95	0.242 (0.027)***	291 (14)	3268 (162)	0.98	853 (112)	3044 (401)	0.84
Birch 4, (N=16) 16.7.–17.7.2007										
Monoterpenes	1693 (333)	4164 (818)	0.66	0.182 (0.026)***	1615 (353)	9965 (2180)	0.86	1790 (124)	6362 (440)	0.86
Sesquiterpenes	25 (11)	151 (16)	0.87	0.248 (0.032)***	21 (5)	255 (60)	0.91	28 (2)	98 (7)	0.87

*** $P < 0.001$ ** $P < 0.01$ * $P < 0.05$

n.s. not significant.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Mountain birch –
large source of
sesquiterpenes into
atmosphere

S. Haapanala et al.

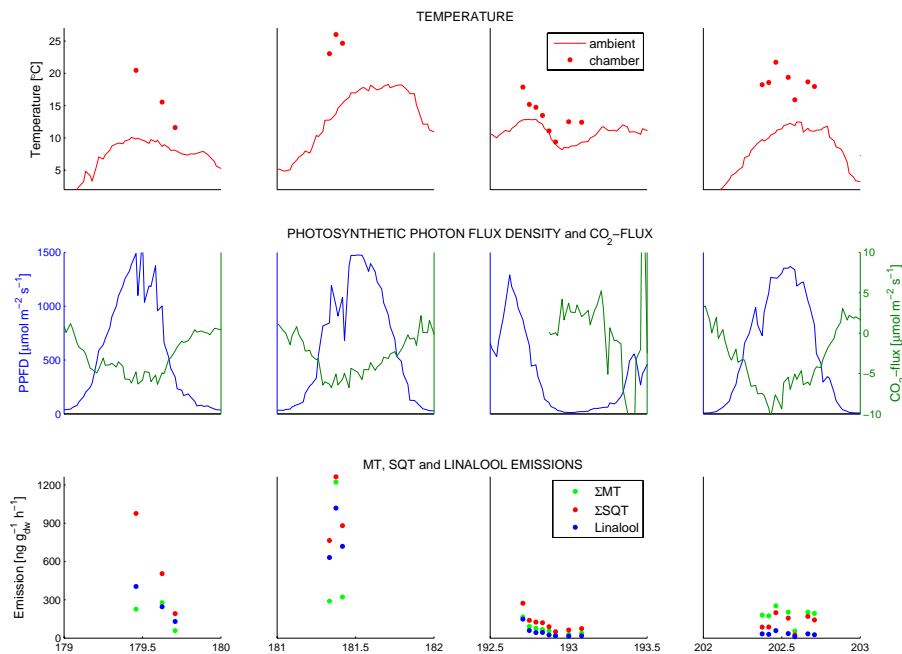


Fig. 1. A timeseries of the meteorological variables together with the ecosystem scale CO₂ flux and the emissions of different VOC groups from birch number 1. The properties plotted with dots are measured inside the chamber. The values on x-axis are day-of-year in 2006.

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

Mountain birch –
large source of
sesquiterpenes into
atmosphere

S. Haapanala et al.

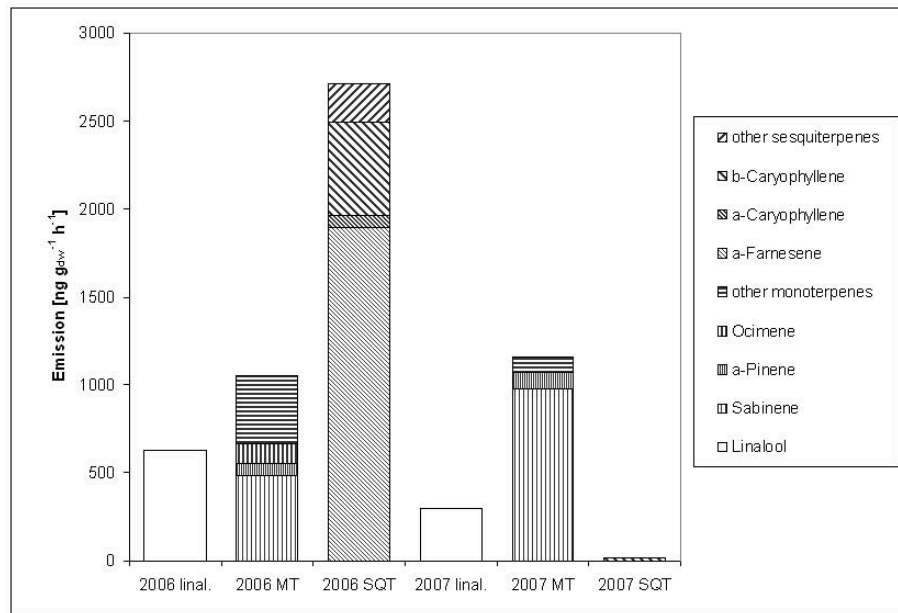


Fig. 2. The average emissions of different VOC groups in 2006 and 2007.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

**Mountain birch –
large source of
sesquiterpenes into
atmosphere**

S. Haapanala et al.

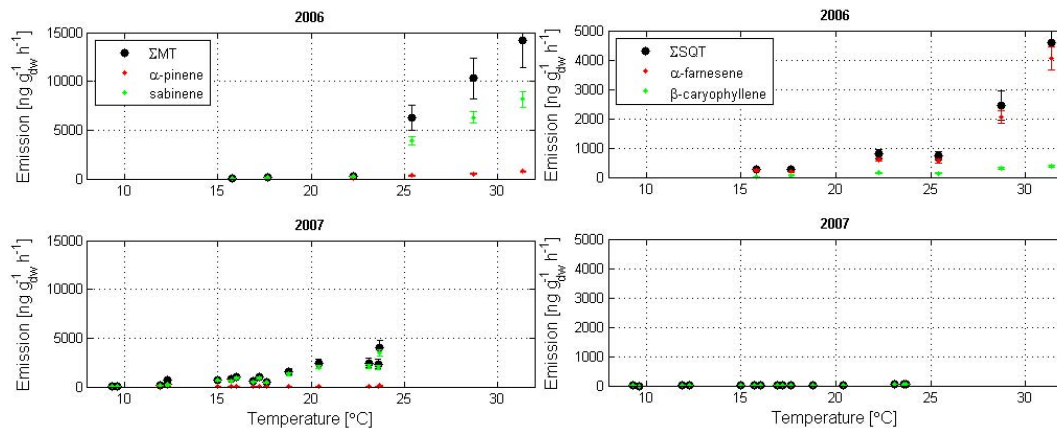


Fig. 3. (a) Monoterpene and **(b)** sesquiterpene emissions from the mountain birch number 4 in 2006 and 2007.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[⏪](#)[⏩](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

Mountain birch –
large source of
sesquiterpenes into
atmosphere

S. Haapanala et al.

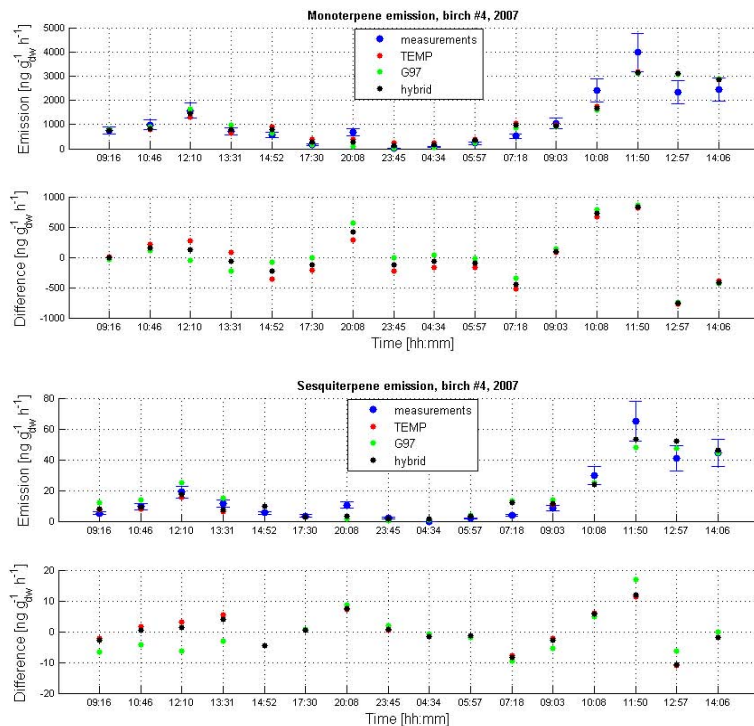


Fig. 4. The measured and predicted emissions of (a) monoterpenes and (b) sesquiterpenes from the mountain birch number 4 on 16–17 July 2007. The lower panels show differences between the measured and predicted emissions.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

