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Tree Temperatures, Volatile Organic Emissions, and Primary Attraction of Bark Beetles

By

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S u m m a r y

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Bark beetles (*Scolytidae*) may be attracted by organic compounds emitted from tree barks and appear able to identify weakened trees, but the exact relationship between tree health and attraction is not known. This paper deals with possible connections between reduced sapflow, volatile emissions, and beetle colonisation of injured spruce trees. The hypothesis tested assumes that the cooling effect of sapflow on the phloem of healthy trees is sufficient to keep temperature-dependent emissions of terpenes below those of stressed trees with reduced transpiration.

Temperature profiles from the bark surface to the sapwood were measured on three trees over several weeks. One tree in a closed stand gave the natural temperature profile and the flow of xylem sap. The external temperature of a 1 m long stem zone of a second tree in the closed stand was kept constant by artificial heating to study the effects of sapflow on phloem temperature uncoupled from interaction with external heat fluctuations. In a third tree the effect of interrupting sapflow on temperature profiles and emissions of ethanol and monoterpenes was studied by transection of the sapwood.

Although sapflow had a significant cooling effect on the cambium temperature, it resulted in a maximum temperature difference of not more than 2.5 °C between a tree with high sapflow and one without transpiration, which does not appear sufficient for a substantial increase in emissions that might attract beetles to stressed trees.

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A strong correlation between bark temperature and emissions was corroborated and the daily maximum of emissions coincided with the maximum of sapwood temperature. Interruption of the sapflow gradually changed the emission spectrum, with pinene increasing relative to limonene, and ethanol detected in appreciable amounts only after several months. The emission spectrum was not identical with the terpene content of the bark. These findings raise the possibility that at least part of the emissions do not originate in the bark but in the sapwood. A survey of literature data on sapwood ethanol contents indicates a connection between sapflow, oxygen contents of xylem water and the emission of ethanol.

Introduction

Bark beetles are among the most serious pests in Central European forests and may significantly reduce returns. Mass infestations with bark beetles inflict severe damage to large forest tracts in a short time, but a prognosis of impending outbreaks, which would permit early countermeasures, proves difficult. Since conifers are the main host trees and spruce is the economically most important among them, research in Central Europe has concentrated on the interactions between spruce trees, bark beetles, and the environment. The predisposition of trees for attacks may be characterized by a number of parameters, among them resin content, phloem quality, nutrient supply, and concomitant stress events (SCHIMITSCHEK & WIENKE 1963, MATSON & al. 1987, WARING & PITMAN 1983).

Volatile organic compounds are main components of spruce resin and, being toxic for attacking beetles, constitute an important defense of trees. Nevertheless the insects utilize them as source materials for the synthesis of species-specific pheromones and are attracted by at least some volatiles, which they use to locate trees. The identification of trees suitable for breeding depends on the olfactory perception of volatile emissions (predominantly monoterpenes and ethanol) emitted by the tree (FÜHRER & al. 1991, BYERS & al. 2000). Felled trees are attractive and suitable for breeding beetles, a fact exploited to control them, but bark beetles also become attracted by emissions of standing and mechanically uninjured trees.

Monoterpene emission in conifers is a function of vapour pressure within plant tissues, which is controlled by air temperature and concentration within the tissues (LERDAU & al. 1997). The concentration in turn depends on many factors related to the health of the tree, possibly induced defense reactions and general metabolic activity. At least over short and possibly also over longer periods, the permeability of the bark will also affect the emissions (ROSNER & KARTUSCH 2003). The connection between the health status of the tree, the amount of emissions and their composition is as yet only insufficiently explored. However, in some cases the physiological weakness predisposing the tree for pest attacks and making it attractive to beetles was apparently related to a reduction or disruption of the water supply (KRAEMER 1953, SCHIMITSCHEK & WIENKE 1963, WARING & PITMAN 1983, CHRISTIANSEN & al. 1987). It is not yet clear whether there is a causal connection between reduced transpiration and pest attack or whether both have their origins in other stress phenomena. At any rate, a number of different stress situations (drought stress, pathogens, needle or root injuries) tend to reduce

the transpiration of plants, and at least some of these are also known to increase bark beetle attractiveness or infestation. In this context, we tested the following hypothesis relating the emission of volatiles to sapflow rates.

During daylight hours, the bark is warmed by the surrounding air and, in some cases, by direct radiation absorbed. The high sapwood water content dampens the daily temperature fluctuations in the bole, and the transpiration water passing through the sapwood, which enters the stem base at the temperature of the soil, will in addition remove heat and cool the cambium and the inner parts of the secondary phloem. This should reduce temperature-dependent emissions. In a stressed tree with diminished sapflow, on the other hand, temperatures and thus emissions will be higher than in healthy neighbouring trees, which could identify weakened trees to beetles and make them attractive.

Material and Methods

Measurements were made in a forest close to Kreisbach, Lower Austria (48°05'N, 15°39'E, 480 m a.s.l.) on or close to experimental plots 184 and 185a of the FWF Special Research Program 008 ("Forest Ecosystem Restoration"). The site is located on a northward slope with a stagnic cambisol and the stands were about 65 years old.

Natural tissue temperatures were measured at 10 m height and at the depths of 1 mm (bark), 5 mm (cambium), 25 and 40 mm (sapwood) in a spruce tree with a diameter at breast height (DBH) of 30 cm inside a spruce/beech forest. This tree was tree number 938 on plot 185a. In general, temperature profiles were measured in the tree crown because this is where bark beetles tend to invade and where higher irradiance should lead to higher phloem heating. Temperatures were measured with type-T thermocouples and a reference thermistor at intervals of 1 min and stored as 5 min averages with a Campbell CR10X datalogger (Campbell Scientific, Shepshed, UK). Sapflow was recorded with two tissue heat balance probes (EMS, Brno, Czech Republic, Čermák & al., 1973) installed on opposite sides of the stem at a height of about 2 m.

To measure the potential cooling effect of sapflow independent of external temperature variation, a stem zone of 1 m length at a height of 7 m was kept at a constant temperature of 34.1 °C (± 0.9 °C SD) by an adjustable heater in a second spruce tree with a DBH of 30 cm inside a pure spruce stand (tree number 112 on SRP plot 184). Tissue temperatures were measured as described above at depths of 1, 5, 15, 25 and 40 mm, and sapflow was measured with Granier-type heat dissipation sensors (GRANIER 1985). A third spruce tree standing on the northern edge of a small forest clearing was studied for the effect of sapflow on the emission of volatile organic compounds. The crown around the point of temperature measurement at a height of 16.4 m was slightly thinned out for permitting maximum irradiance of the stem and warming of the bark. Temperature profiles were measured as in the other trees at heights of 2 and 16.4 m and the parameters described below were measured over several weeks before and after the sapflow was interrupted by completely transecting the sapwood at a stem height of 0.65 m on August 17, 1998. Shortwave irradiance was measured on the sun-exposed side with a star pyranometer (Schenk, Vienna), and air temperature and humidity were measured on the shaded side and stored on a Tinytalk II datalogger (Gemini Dataloggers, Chichester, UK).

The emission of volatile compounds (mainly monoterpenes and ethanol) was measured with a device sucking a defined volume of air over a known area of bark for a standardized time and adsorbing volatiles on filters of activated charcoal (BAIER & BADER 1997, BAIER & al. 1999). Adsorbed compounds were eluted with n-hexan, analysed on a HP 6890 gas chromatographic system using a chiral column (CP-Chirasil Dex-CB) and quantified (BAIER & al. 1999, 2002). Identification of chromatographic peaks was made by comparing their mass spectra with reference mass spectra determined with a mass spectrometer system (HP G1800C GCD II and separating column HP5 and

for most of the compounds by comparing GC-retention times with those of pure reference compounds (BAIER & al. 2002). Emitted organic compounds were collected on three days (11 single measurements) prior to and on 11 days (22 measurements) after interrupting sapflow, with the last samples collected on May 27, 1999. Volatile organic compounds were also quantified from corresponding phloem samples using CLSA (LORBEER & al. 1984, BAIER & al. 1999, BAIER & al. 2002).

Secondary phloem was sampled and fresh weight (F), saturated weight (S) and dry weight (D) were determined on a microbalance (ME22/BE22, Mettler, CH) and used for calculating the relative water content (R) from the equation

$$R (\%) = 100 (F - D) / (S - D)$$

The methods were described in detail by ROSNER & al. 2001.

Anatomy of secondary phloem and lenticels was investigated in microtome sections prepared after fixation in FAA (formalin, alcohol, glacial acetic acid 1:1:1, v:v:v), dehydration in an ascending alcohol series and imbedding in Technovit (Heraeus Kulzer GmbH, D). A rotary microtome (1165 Rotocut, Reichert Jung, D) was used for sections of 1 - 2 μm thickness. The sections were stained with Toluidine Blue (GERLACH 1984), dehydrated and embedded in Entellan. Sudan Black B (GERLACH 1984) served as an indicator of suberin. Resin flow was measured at breast height and at the crown base following the methods of MASON 1969.

Results

Although the surface of the stem could be kept at a rather constant temperature of about 34.1 °C by heating, the temperatures of the cambium, and even more so of the sapwood, showed large fluctuations with minima during daylight times, that is, the times of sapflow. While a cooling effect of sapflow was conspicuous under these semi-controlled conditions, the correlation between the magnitude of the cooling effect and the sap amount flowing was weak. There was a distinct cooling on the day with the highest sapflow (day 280), but also on days with very low sapflow due to high air humidity (days 279 and 281); on day 282 with moderate sapflow there was practically no temperature gradient (Fig. 1). A potential problem of the experimental design seems to be that the stem is artificially heated over a relatively short length only, and that some heat is lost in the upward and downward directions, which is difficult to account for. Besides, the reduced evaporative demand during cool periods forces less sap through the heated tissue, but this liquid draws the heat more rapidly because it enters at a lower temperature.

On the unheated tree the temperature profile was measured over a much longer period, which allows for a more thorough analysis. With the external temperature fluctuating, the potential cooling effect was evaluated as the temperature difference between the outermost measurement point in the bark (at 1 mm) and deeper layers. This temperature difference is clearly related to sapflow and highest in times of high flow (Fig. 2). In part, this is not an effect of sapflow per se but of the dampening of temperature fluctuations in deeper layers of tissue with high water content. To analyse the effect of sapflow and bark temperature on the cooling, a multiple linear regression was calculated, after checking for collinearity between

sapflow and bark temperature (QUINN & KEOUGH 2002, ANONYMOUS 2002). The Durbin-Watson statistic ($p = 0.335$) did not reject the assumption of no autocorrelation in the residuals, and the variance inflation factor ($VIF = 1.413$) also gave no indication of serious collinearity. The standardized regression coefficient is higher for sapflow (0.570) than for bark temperature (0.13), showing that sapflow has a stronger effect on the temperature difference than temperature near the surface.

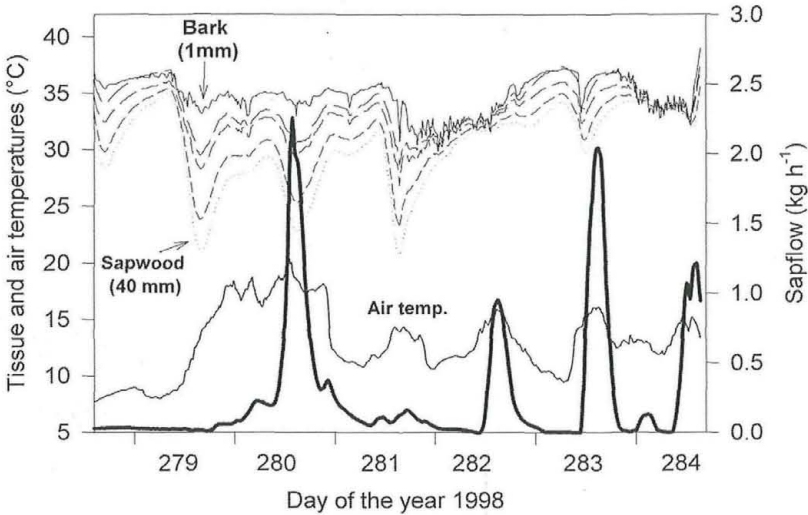


Fig. 1. Temperature profile at the depths of 1 mm (bark), 5 mm (cambium), 15, 25 and 40 mm (sapwood), and sapflow in a spruce stem heated from the outside to a constant temperature of 34.1 °C over a length of 1 m. The thin line between 6 and 20 °C is external air temperature, the bold line is sapflow.

A regression gives the relationship:

$$\Delta T \text{ (}^{\circ}\text{C)} = 0.0214 + SF * 23.50 + T_{\text{bark}} * 0.00583,$$

where ΔT is the cooling effect, SF sapflow per cm sapwood circumference ($\text{kg cm}^{-1} \text{h}^{-1}$) and T_{bark} the bark temperature ($^{\circ}\text{C}$). This means that a sapflow of 0.1 $\text{kg cm}^{-1} \text{h}^{-1}$, which is rather high for spruce, will result in a cooling of 2.35 °C only. Fig. 3 shows the relationship between cambium cooling, bark temperature and sapflow.

On very hot days in August 1998, cambium temperature reached up to 45 °C in the sun-exposed crown (concomitant with a bark temperature of 47 °C and a temperature of the surrounding air of 36 °C), and still up to 38 °C near the stem base. Because sapflow was completely interrupted, the potential cooling effect of

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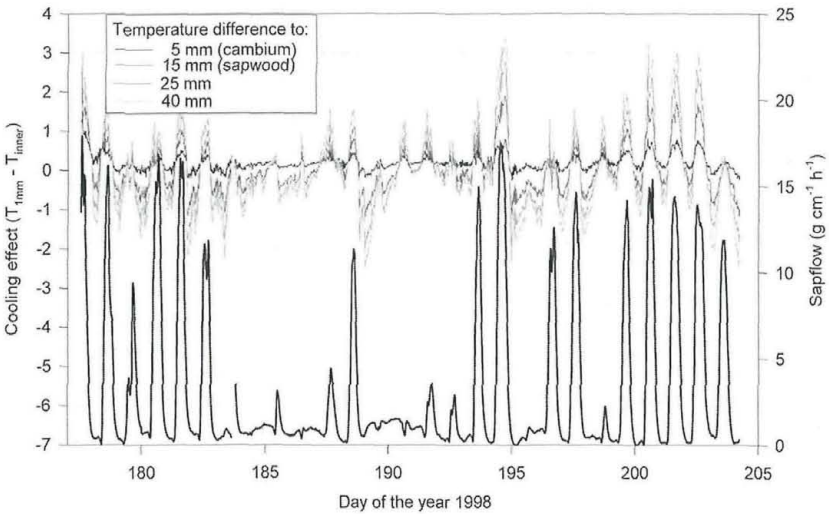


Fig. 2. Sapflow per cm sapwood circumference and temperature difference between outer bark (1 mm) and cambium and sapwood at different depths.

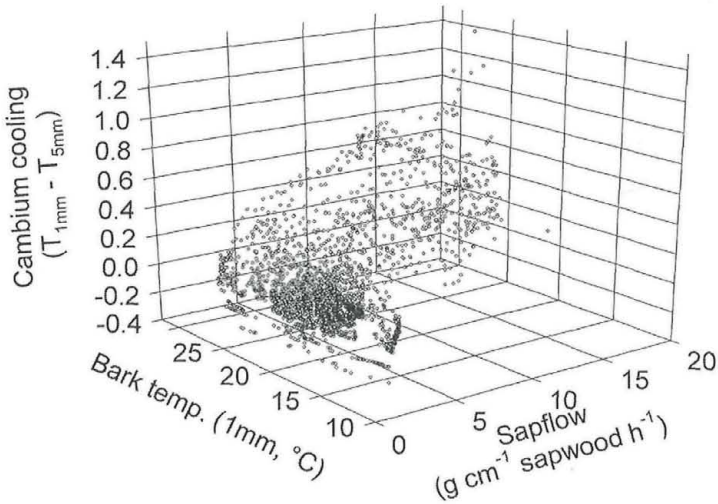


Fig. 3. The cooling effect in the cambium (ΔT : 1 mm - 5 mm) related to bark temperature in 1 mm depth and sapflow (per cm sapwood circumference).

sapflow should become evident in a comparison of the correlations between bark and cambium temperatures before and after transecting the sapwood. However, as far as an effect was perceptible at all, the cambium temperature at identical bark temperatures was even lower after transecting the sapwood (Fig. 4). With the highest air temperatures occurring in mid-August shortly before the transection of the sapwood, its temperature, which is far more inert than the temperatures of bark and cambium, was generally somewhat lower and could better buffer the peaks in the cambium caused by short episodes of insolation. A possible cooling effect of sap flow in this tree before sapwood transection might be inferred from the course of flow in the trees in the stand, which runs in parallel. Again, no clear cooling effect of sapflow on cambium temperatures becomes visible (data not shown).

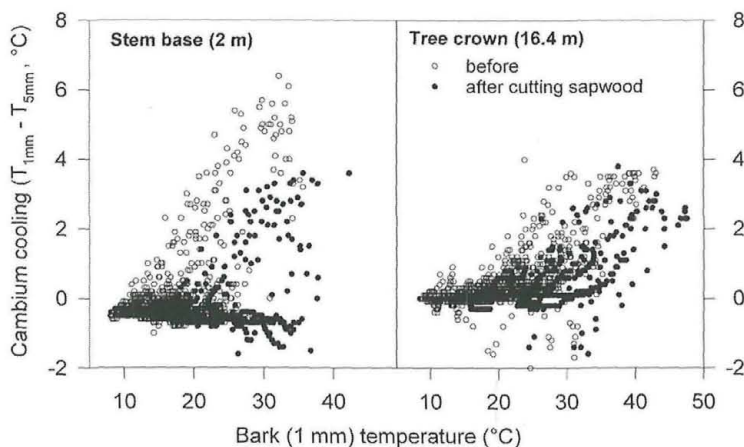


Fig. 4. ΔT bark surface (1 mm) - cambium (5 mm) at the stem base and in the crown of an insulated spruce tree before and after sapwood transection in relation to the bark surface temperature.

The total monoterpene content in the bark at the beginning of the emission measurements (1st sample, taken close to the measurement area for emissions on August 12, 1998) was only slightly lower than at the end of measurements after the sapflow had been interrupted, and the monoterpene pattern was also but little different (Table 1). The composition of the released monoterpenes did not at all reflect the internal monoterpene composition of the bark. Some of them, notably (-) and (+)-limonene, were relatively more emitted and others, such as (-)- α -pinene, (-)- β -pinene and (-)- β -phellandrene, less. Ethanol was not determined in the bark samples.

A significant change in the emitted substances occurred over the observation period. Among the main components, the relative fractions of (-)-limonene and

(+)-limonene declined significantly, while the fractions of (-)- α -pinene, (+)- α -pinene and (-)- β -pinene generally increased (Fig. 5). In most samples, ethanol could only be measured in very low concentrations. Only two samples taken on September 10, 1998 showed very high ethanol emissions of $> 3 \mu\text{g dm}^{-2} \text{h}^{-1}$, and on two days in the following spring, ethanol emissions of 1.78 and $0.51 \mu\text{g dm}^{-2} \text{h}^{-1}$ accounted for 73 and 32% of total emissions, respectively.

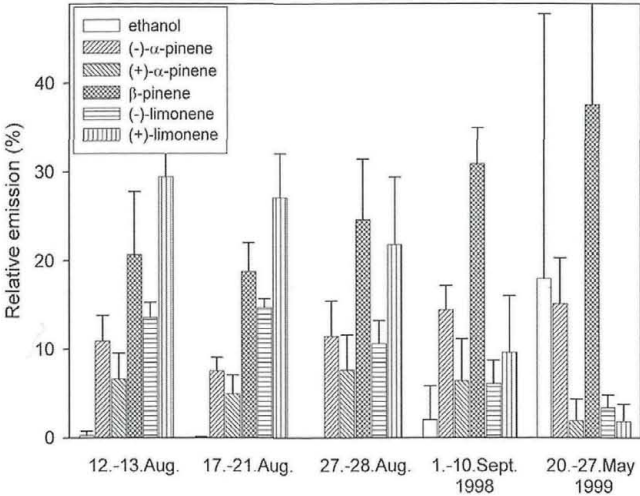


Fig. 5. Mean ($\pm$ SD) of relative fractions of the main components emitted before and after sapwood transection on August 17 1998 and during the following weeks with the last samples obtained in May of the following year. For absolute total emissions see Fig. 7.

The emission rates were highly variable (minimum: $1.31 \mu\text{g dm}^{-2} \text{h}^{-1}$; maximum: $48.65 \mu\text{g dm}^{-2} \text{h}^{-1}$), and, for the samples taken in 1998, were highly significantly ($r^2 = 0.50$, $p < 0.001$) correlated with temperature (Fig. 6). Emissions measured in spring 1999 never exceeded $3 \mu\text{g dm}^{-2} \text{h}^{-1}$ and were lower than for any samples in August and September 1998, even though the air temperatures ($20 - 25^\circ\text{C}$) were similar to those at many sampling dates of the previous year. Phloem water content did not change in the 23 days after interrupting sapflow and remained at $69\% (\pm 4\%)$ until September 10, but had declined to $46 - 56\%$ in May of the following year.

At the beginning of August, the development of the closing layers of the cork of the experimental spruce tree was still in progress. The final number of two to three cell rows had already been reached in most lenticels, the cell row last formed was however not yet completely differentiated and cells had not reached their final form, but suberin could already be detected as a cell wall layer. These suberized complementary cells had smaller intercellulars when compared to the more rounded fully differentiated cells.

Table 1. Absolute amounts and percentages of the total for volatile substances in the bark and relative emission rates. 1st sample: 12. 8. 1998, taken from the immediate vicinity of the emission site; 2nd sample: 18. 9. 1998, after the last measurement, taken from the emission site. The emissions are the mean of all emission measurements between August 12 and September 10 1998. - : not measured.

	sample 12.08.98.		sample 18.09.98		Emissions (%) mean ($\pm$ SD)
	$\mu\text{g/g FW}$	%	$\mu\text{g/g FW}$	%	
ethanol	-	-	-	-	0.73 (2.40)
α -thujene	0.98	0.10	0.98	0.10	0.43 (0.33)
(-)- β -myrcene	58.15	5.66	87.16	8.48	3.69 (0.72)
(-)- α -pinene	138.07	13.44	178.99	17.42	11.01 (3.89)
(+)- α -pinene	99.73	9.70	93.25	9.07	11.29 (6.12)
sabinene	3.79	0.37	4.91	0.48	0.32 (0.27)
tricyclene	2.29	0.22	2.59	0.25	0.63 (0.41)
(-)-camphene	2.28	0.22	2.11	0.21	0.17 (0.09)
(+)-camphene/(-)- α - phellandrene	1.54	0.15	1.81	0.18	0.17 (0.22)
α -terpinene	1.74	0.17	2.04	0.208	0.30 (0.29)
δ -3-carene	51.06	4.97	40.65	3.96	3.66 (1.58)
p-cymole	3.36	0.33	2.48	0.24	1.20 (0.31)
not identified	5.92	0.58	7.82	0.76	1.81 (1.47)
(-)- β -pinene	419.17	40.79	582.84	56.72	23.72 (7.27)
(-)-limonene	35.12	3.42	43.09	4.19	11.45 (4.09)
(+)-limonene	16.32	1.59	16.15	1.57	21.96 (10.18)
(-)- β -phellandrene	179.56	17.47	257.37	25.05	4.27 (0.65)
γ -terpinene	1.19	0.12	1.26	0.13	3.41 (1.72)
terpinolene	4.66	0.45	5.75	0.56	0.0 (-)
cineole	2.72	0.27	3.23	0.31	0.52 (0.33)
Total	1027.63		1334.47		

Resin flow at the crown base showed a strong reduction after sapwood transection. At breast height there was hardly any flow detectable immediately after the cutting of the conduits. In May of the following year, the flow had completely ceased at the base of the crown, too, and the tree could no longer resist the bark beetles by means of resin flow.

By mid-May of the following year, the bark beetles *Ips typographus* and *Pityogenes chalcographus* had started to attack the tree.

Discussion

The measurements broadly confirmed two requirements of the hypothesis tested, namely that emission rates are temperature-dependent (Fig. 6) and that, at least under certain conditions, sapflow can have a cooling effect on sapwood and cambium temperatures. However, given the small cooling effect that probably does not exceed 2.5 °C and the fact that emission rates in general are quite variable within one tree and certainly at least as much between trees, it appears now very implausible that the cooling through sapflow really will result in different emission

rates that would permit bark beetles to distinguish between healthy and weakened trees with reduced sapflow rates. It is also conspicuous that beetles did not attack until the end of September, when emission rates were high, but in spring, when emissions were lowest. Whatever the emission rates, bark beetles can only attack at a time when adult males and females are present and ready to mate. By that time the tree had severely dried, resin flow had ceased and provided no defense against beetles.

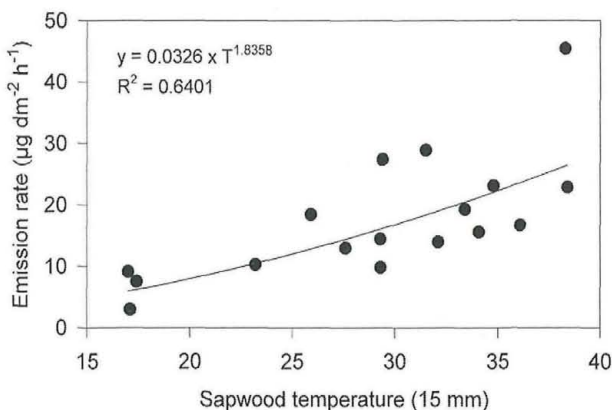


Fig. 6. Correlation between sapwood temperature at 15 mm depth and emission rates in August and September 1998. Emissions in spring 1999 were substantially lower (see Fig. 7).

If it is not the differences in absolute emission rates, the only cue that would enable beetles to locate weakened trees from a distance is the spectrum of volatile organic compounds emitted. Indeed, the terpene pattern emitted at the last measurements in September (Fig. 7) was similar to that of felled trap spruce trees attacked by *I. typographus* and *P. chalcographus*, although the absolute amounts were lower (BAIER & BADER 1997, BAIER & al. 1999). A bioassay with *Ips pini* showed that, while for most monoterpenes the number of beetles entering a phloem-based medium decreased with increased concentrations, pinene elicited increased beetle entry at moderate concentrations (WALLIN & RAFFA 2000); the proportion of just this compound increased in our experiment after interrupting sapflow.

As had been observed previously (SCHINDLER & KOTZIAS 1989, BAIER & BADER 1997), the spectrum of terpenes released differed from that of compounds stored in the bark. This may be a result of differences in volatility (if limonene is relatively more volatile than pinene and phellandrene), but also of the fact that an appreciable fraction of the volatiles emitted comes from the wood, where the pattern is probably different from the bark (PERSSON & al. 1993).

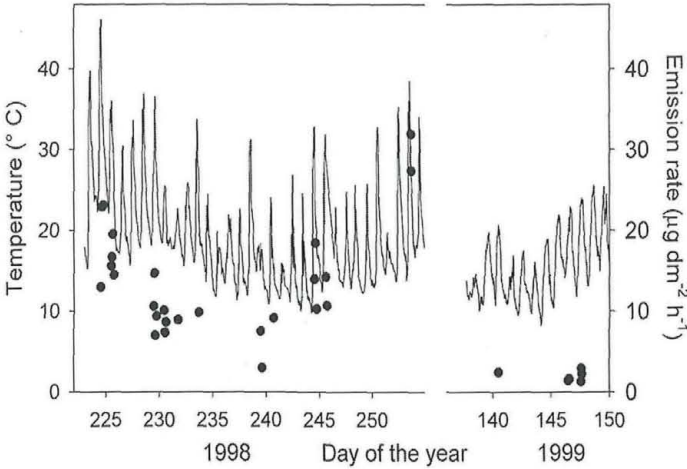


Fig. 7. Air temperature measured at the crown base of an exposed tree in 1998 and within the canopy of a closed spruce forest in spring 1999, and emission rates from the exposed canopy between August 12, 1998, and May 27, 1999. Note that within the closed canopy the short-term extremes of the exposed stem were not reached. Sapwood was transected on August 17, 1998 (day 229).

The low emission rates in spring can result from reduced production of monoterpenes in a dying tree and from a reduced permeability of the bark due to low water content and reduced turgescence of the lenticels (ROSNER & FÜHRER 2002). On the other hand, the highest ethanol emissions were measured at this time, which can be attributed to a reduced gas exchange via lenticels and consequently a lower oxygen supply of bark and sapwood tissues. When terpenes are combined with ethanol, the attraction is reinforced synergistically (BORDEN 1985), a behavior common to many bark beetles (MOECK 1970, PHILLIPS & al. 1988, SCHROEDER & LINDELÖW 1989). The production of ethanol is not related to the metabolic pathway of monoterpenes and generally results from fermentation under hypoxic or anoxic conditions. Some metabolic activity consuming oxygen is likely to continue for an extended period in the living cells of the sapwood and bark. Sapflow has been shown to be a major pathway of oxygen to the sapwood (GANSERT 2003, DEL HIERRO & al. 2002, EKLUND 2000), and cutting the sapwood may result in oxygen being consumed faster than it can be resupplied by diffusion via the bark, and consequently in the production and emission of ethanol when temperatures rise in spring. In living trees, oxygen concentrations under most conditions are high enough to ensure aerobic respiration (SPICER & HOLBROOK 2005), but at least in one case declined to < 1% during summer in spruce trees subjected to drought stress (EKLUND 2000), which was interpreted as a consequence of lower oxygen supply via reduced sapflow. In an experiment with cut logs, ethanol content was

higher in rain-wetted logs, where the diffusion of oxygen was reduced by the high bark water content, than in dry logs, and wetted logs were consequently preferred by bark beetles (KELSEY & JOSEPH 1999). Similarly, water stress resulted in higher ethanol contents and more attacks than in control or defoliated branches of Douglas fir (KELSEY & JOSEPH 2001).

Oxygen deficiency and the resulting ethanol production may also be the cause in the attractiveness for bark beetles of trees suffering from other types of stress. Spores of blue-stain fungi are carried by bark beetles and usually enter a tree together with their vector (WHITNEY & FARRIS 1970, CHRISTIANSEN & HORNTVEDT 1983). These fungi cause blue-stain of the sapwood of conifers by colonisation of the ray parenchyma cells and aid their insect vectors by weakening the tree's defense system. Although most species are only weakly pathogenic and will not kill a tree without a simultaneous infestation with bark beetles, a few species have been shown to be able to overcome the defense systems of host trees if inoculated at sufficiently high dosages by growing into the sapwood and disrupting the water-conducting system. The spruce bark beetle *Ips typographus* is associated with several species of blue-stain fungi and one of these, *Ceratocystis polonica*, is a virulent pathogen able to kill spruce trees (KIRISITS & OFFENTHALER 2002). The disruption of sapflow may lead to reduced oxygen supply to the living parenchyma cells inside the cambium and thus to ethanol production, which, together with pheromones, will attract more beetles to the weakened tree. In contrast, the fungus *Phaeocryptopus gaeumannii*, causing Swiss needle cast, results in reduced ethanol concentrations and less numerous beetle landings, although the tree is weakened, has low oleoresin pressure and beetles that did attack were more successful (KELSEY & MANTER 2004). The relationship between tree stress, oxygen content, ethanol production and bark beetle attraction remains to be investigated, it is however unlikely that any one mechanism or combination of volatile substances can completely explain the sometimes enigmatic relationship between bark beetles and their hosts.

Acknowledgements

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