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Biogeosciences Discussions

Interactive comment on "Impact of heat stress on the emissions of monoterpenes, sesquiterpenes, phenolic BVOC and green leaf volatiles from several tree species" *by* E. Kleist et al.

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Interactive comment on "Impact of heat stress on the emissions of monoterpenes, sesquiterpenes, phenolic BVOC and green leaf volatiles from several tree species"

Kleist et al.

We thank both reviewers and in particular the interested reader Peter Harley for their comments. All remarks were considered.

Response to the remarks of Peter Harley (SC C3546):

We greatly appreciate Peter Harley's supportive comments. His remarks and suggestions were very helpful. The manuscript was changed according to his remarks and these changes indeed improved the manuscript:

Remark Peter Harley: "Heat stress" as used here is an ill-defined concept. I think most physiologists would agree that primary metabolism may be severely restricted, i.e., heat-stressed, well before significant effects on BVOC are apparent. "Heat stress" as used here represents some combination of high temperature and duration of exposure, but is really characterized by irreversible changes in BVOC and the induction of GLV, related to membrane damage. The emphasis on effects of 'heat-stress' as here defined tends to ignore the effects of increasing temperature on BVOC emissions prior to the onset of irreversible damage.

Our response: Indeed we defined heat stress as the appearance of effects that are irreversible on a time scale of hours to days. Reversible effects, i.e. well known temperature dependencies of BVOC emissions were not considered as stress effects. This "normal" and reversible behavior is often used to predict future trends but this procedure neglects that elevated temperatures may also cause deviations from exponential increases. Aim of our work is to show that the plants' responses to heat may differ from simple exponential increase of BVOC emissions with temperature. As obvious from Peter Harley's remark, this was not expressed as explicit as required. To make this point clearer we changed the respective paragraph in the introduction. This text now reads"

"The most obvious abiotic stressors to vegetation that are expected with on-going climate change are more intense and elongated heat waves and drought. Here we investigated impacts of heat stress on the emissions of BVOC. Projections of future BVOC emissions are often based on projected mean temperature increases. Considering only changes of BVOC emissions induced by changes of mean temperatures certainly projects higher BVOC emissions with on-going climate change. Mean temperature increase of few degrees will normally not lead to temperatures high enough to act as

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stress. But during heat waves temperatures might be much higher and may act as stress. Hence, procedures based on mean temperatures only neglect effects as described already by Guenther et al. (1993): If temperature reaches values disposing stress on plants, isoprene emissions drop. This might also be the case for other BVOC than isoprene. If so, it is furthermore possible that also emissions of monoterpenes, sesquiterpenes and phenolic BVOC drop in regions where future heat waves put stress on plants. We investigated the plants' responses at temperatures high enough to act as stress. As stress impacts we termed only those that were irreversible on a time scale of hours to days, meaning that BVOC emissions did not recover to the emission pattern and strength observed before heat application. Reversible impacts of enhanced temperatures were not considered as stress impacts in this study. By doing so we checked for possible deviations from projected increases of BVOC emissions with increasing mean temperatures."

We furthermore extended the last sentence of the abstract: "Otherwise the overall effect of heat stress will be a lower increase in BVOC emissions than predicted by algorithms that neglect stress impacts." Peter Harley is also correct assuming that primary metabolism may be severely restricted before impacts of heat on BVOC emissions may appear. But it may also be that primary metabolism recovers earlier than BVOC emissions (see also the new figure 7). The decoupling of plant responses in primary and secondary metabolism requires using BVOC emissions themself as the reference for our definition of stress.

Remark Peter Harley: The authors attempt to interpret their results in the context of future climate change and the expected increase in the frequency, magnitude and duration of high temperature events. To their credit, they acknowledge that their data is inadequate to predict specific consequences of increasing frequency of heat stress events, only generalizing that the impact on BVOC emissions will depend on the mix of de novo and pool emissions in a given region, which may lead to either an increase or decrease of total emissions. They fail to discuss the effect of generally increasing

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temperatures, below the hypothetical tipping point at which irreversible damage occurs, which, based on our current understanding, will clearly lead to large increases in BVOC emissions. Compared to these effects, the impact of these irreversible heat stress events is likely to be minor. Particularly since at least some of the stresses imposed in this study (e.g., 45 °C continuously for 48 h or 51 °C for 4 h) are unlikely to occur.

Our response: Same as above: we do not discuss the "normal" temperature dependence because it is quite well-known. We particularly investigated the deviations from "normal" temperature dependence. "Normal" temperature dependence is the base; we show effects on top of this "normal" temperature dependence. With respect to the temperatures chosen for the experiments we had to find compromises. This is described below.

Remark Peter Harley: The authors are, in my view, too quick to attribute heat stress induced declines in de novo emissions to enzyme denaturation. Although our understanding of the limitations to isoprene emissions at high temperatures remains controversial, there is good evidence that substrate levels can play a significant role. Although very little data is presented in this study related to net photosynthesis and stomatal conductance, it is quite likely that general physiology, electron transport in particular, is severely depressed during these stress events, and DMADP levels may well limit de novo BVOC synthesis.

Our response: This remark is correct. We added the possibility of substrate limitation where necessary to the text. Here the respective changes:

Former P. 9550 lines 2 ff (added text in red letters): Similar to isoprene, de novo MT emissions depend on the activity of the enzymes producing the respective BVOC as well as on substrate delivery. Such enzymes may denature at temperatures above 40 to 45 °C (Loreto and Schnitzler, 2010; Loreto et al., 2006) or substrate delivery may be reduced. Hence, the observed decreases of de novo MT emissions during heat stress

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can be explained by either of both mechanisms.

P. 9550 lines 22ff. whole sentence deleted.

P. 9951 lines 4 ff. Sentence was changed to (added text in red letters): Such threshold temperatures may depend on the heat sensitivity of the enzymes producing individual MT species, on reductions of substrate availability, on the individual plant as well as on the environmental conditions the plants experience.

P. 9551 lines 21 ff. The first half of the sentence deleted.

P. 9551 lines 24 – 9552 line 7. According to another remark of Peter Harley (see below) the total paragraph including our remark on enzyme denaturation was exchanged by the sentence: We furthermore did not find such pulses from plants not possessing resin ducts and we therefore conclude that the pulses in MT release from conifers were due to damage of resin ducts.

P. 9555 lines 5 ff. Sentence was left because this is a listing of possibilities already including lower substrate delivery.

P. 9556 line 15 ff. Sentence changed to: We believe that this behaviour was caused by a general decrease of the plants performance including e.g. denaturation of BVOC synthesizing enzymes or lowered substrate supply.

Remark Peter Harley: In general, the authors present convincing evidence that heat-stress, characterized by irreversible changes in BVOC emissions and the production of GLV, affects de novo emissions and emissions from storage pools in fundamentally different ways. This should be the thrust of the paper and certainly justifies publication. With that in mind, I think the paper could be shortened somewhat, eliminating speculation about the effects of future climate change on BVOC emissions. The data presented in this paper provides no way to address these questions except in a very general way. An assessment of future impacts will require a much more rigorous attempt to quantify the interacting effects of maximum temperatures, duration of exposure, water stress,

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etc.

Our response: We tried to stay as short as possible and also, as suggested by Peter Harley, a whole paragraph was deleted. However, the necessity to clarify that reversible effects were only neglected for our definition of stress but not for estimating future trends of BVOC emissions counteracted the reduction in text length. To eliminate text passages that might be misinterpreted as speculation about effects of future global change on BVOC emissions we changed the respective parts by exchanging "future climate change" by "heat stress". These changes should diminish the risk of misinterpreting our statements as speculations on global change.

Remark Peter Harley: The authors stress the possible importance of enzyme denaturation in explaining the observed declines in de novo emissions, but present no evidence for this assumption, which appears unwarranted to me. Any discussion of hypothetical causes should include the potential for substrate (DMADP) limitations. A more thorough discussion of the changes in primary metabolism (photosynthesis and transpiration) before and after the imposition of stress would be helpful in this regard.

Our response: We added the possibility of substrate limitation (see above) and a new figure comparing net photosynthesis and de novo emission during and after heat application (new figure 7).

Detailed editorial suggestions: Page 9534 l. 3 need to define 'heat stress'; in this context, it is irreversible changes in BVOC emissions, associated with release of GLV; one might argue that 'heat stress' defined as deleterious effects on primary metabolism occur under far less stressful conditions

Our response: We changed the beginning of the abstract. To consider this remark we added the sentence: "Considering only irreversible changes of BVOC emissions as stress we found that.." to the abstract. In the new Figure 7 we show that impacts on BVOC emissions may be more deleterious than impacts on net photosynthesis indicating that our definition of stress indeed needs to use BVOC emissions itself as

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the reference (see above).

Page 9534 l. 7 ‘were’ instead of ‘being’ done

Page 9534 l. 10 suggest ‘release of monoterpenes from pools. . .’ done

Page 9534 l. 11 delete ‘of’ done

Page 9534 l. 20 It is important to distinguish between high temperatures (not defined as ‘heat stress’) and ‘heat stress’ itself. Thus, ‘heat waves’ will almost certainly increase BVOC emissions; only when conditions exceed some quite high threshold is there the potential for decreases or additional increases related to damage to resin canals.

Our response: To make this point clearer we added the paragraph to the introduction (see answer to Peter Harley’s remark no. 1). We furthermore extended the last sentence in the abstract to: “Otherwise the overall effect of heat stress will be a lower increase in BVOC emissions than predicted by algorithms that neglect stress impacts.“

Page 9536 l. 5 suggest ‘. . . in the study, although they may be expected to have a large impact on future BVOC emissions.’

Our response: See preceding remark. We added the paragraph clarifying that we did not neglect future increases of BVOC emissions due to increases of mean temperatures but neglected the reversible effects only for our definition of heat stress.

Page 9538 l. 25 ‘ . . . distance of the respective leaf from the chamber lamps. . .’ Done

Page 9540 l. 9 ‘Consistent with these observations, MT emissions . . .’ done

Page 9540 l. 15 I’m not sure I’d call 10-30 percent labeling ‘low’ Sentence was changed to: “Accordingly the degree of 13C labeling in the MT emitted from Scots pine was much lower than expected for pure de novo emissions.”

Page 9540 l. 19 Ghirardo misspelled Corrected, thanks for helping us avoiding a faux pas

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Page 9541 l. 4 ‘Consistent with the results of . . .’ done

Page 9541 l. 7 I believe this should be ‘A three-year-old beech seedling’ but I leave it to the copy editors. We leave this to the copy editors too

Page 9541 l. 15 When I look at Fig. 1, it appears to me that the data at 31oC, 40oC and 4oC (after heating) all fall on an exponential temperature curve with ïĄć =0.09 or so. I.e., no evidence of irreversible changes until returning to 31oC on day 8. One might suspect that the reduced rates at 31oC on day 8 are the result of the cooler temperatures on days 6 and 7 (as has been shown for isoprene emissions).

Our response: In principle correct. As shown for isoprene emissions cold temperatures may affect actual emissions. Thus cold temperatures might also impact monoterpene from beech irreversibly. Both, cold temperatures and heat might have the same impact. Nevertheless, our interpretation of the experiment shown here is different: In other experiments with beech we studied the temperature dependence of BVOC emissions and we found no effect of temperature history when measuring BVOC emissions at temperatures between 20 °C and 35°C. In case of the heat stress application shown here we always measured at temperatures above 20 °C (not 4°C). We therefore are convinced that the effect shown for beech was indeed caused by the heat application and not by cold temperatures.

Page 9542 l. 6 For the beech experiment, you report that net photosynthesis and transpiration were unaffected by the imposed stress. Was this also true in the case of oak?

Our response: In case of the oak net photosynthesis and transpiration were affected by the heat and a sentence was added with this respect: “Somewhat different to the observations on beech, rates of net photosynthesis and rates of transpiration were affected by the heat. Both quantities dropped by about 50 % (e.g. rate of net photosynthesis $\sim$3 / $\sim$1.5 μmol m-2 s-1 before / after the heat stress).”

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Page. 9542 l. 11 ‘constitutive de novo emissions were decreased. . .’ done

Page. 9543 l. 4 ‘In contrast’ instead of ‘contrary’ done

Page 9543 l. 9 resin ducts done

Page 9544 l. 7 Again, knowing whether photosynthesis and transpiration recovered from the (quite severe) 51oC heat stress would be useful. Was the plant even alive following several hours at 51oC?

Our response: In this case the plant did not recover to the level as observed before heat stress application within 6 days. Six days after the heat stress the rate of net photosynthesis was still only $\sim$ 15% of that before the heat stress and transpiration only $\sim$ 30 % of that before the heat stress. As the plant was removed from the chamber after that we have no information on the time it took until the plant recovered completely. With respect to severity of our stress applications see our detailed answer to this item below.

Page 9544 l. 19 delete ‘on’ done

Page 9545 l. 2 These emissions from apparently damaged resin canals must represent a large fraction of the total monoterpene pools within the needles. Can you estimate what fraction of the pools is lost as a result of the stress?

Our response: We can only crudely estimate that fraction to be less than 5 %. We removed needles from a pine, put them into the dark, cut them and measured the total amount of release of MT until this release was not measurable any more. Summing up the release and extrapolating this amount to the needle biomass of the living plant showed that the release from the living plant was by far lower than expectable when all pools were damaged and all stored monoterpenes would have been released. As this was a very crude estimation we do not include numbers with this respect to the manuscript.

Page 9545 l. 21 suggest ‘. . . confirming that they are de novo emissions.’ done

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Page 9545 l. 23 '... stored carbon, consistent with measured emissions in darkness.'

Our response: In case of MeSa there were nearly no emissions during darkness but the degree of labeling was low. Hence modulations of emissions with light and degree of labeling were not consistent in case of MeSa. We therefore left the sentence.

We interpret the emission of MeSa as a de novo emission as it may require just one light dependent step to cause a light dependent emission (possibly the methylation step) although the body of the molecule may be produced from a precursor with a considerable plant internal pool (during the respective experiment most probably phenylalanine).

Page 9546 l. 10 '. . . about 2-fold higher. . .' done

Page 9546 l. 12 Again, it would be nice to know whether or not net photosynthesis and transpiration recovered if that information is available.

Our response: This plant recovered within one day. We have added the new figure 7 to the manuscript showing the temperature pulse, the rate of net photosynthesis, and the response of a de novo emission – here MeSa emission - to this heat stress. During the heat MeSa emissions increased but net photosynthesis strongly decreased. Comparing the data from before and one day after the heat stress application shows no significant differences for net photosynthesis but a drop in MeSa emissions appearing another day later. This is an example where we found only minor impacts on primary metabolism but stronger impacts on BVOC emissions. On the one hand this example shows that our definition of stress impacts on BVOC emissions indeed requires using BVOC emissions itself as the reference. On the other hand this example shows that we did not "kill the plants" (remark referee#1).

p. 9547 l. 9 It's not surprising that no clear relationship between maximum applied temperature and stress impact emerges, since the duration of exposure also changed widely between treatments. Although we might expect greater stress from a 45oC exposure than a 40oC exposure, if the first is for one hour and the second for 6 hours,

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the effect might well be reversed. Also, the effect of elevated temperatures at night, something plants are unlikely to be exposed to in nature, confuses interpretation of the results. And p. 9547 l. 18 I think 51oC may be unrealistically high, although not inconceivable under water stress.

Our response: It was not our intention to find exact thresholds for temperatures above which they act as stress. These thresholds certainly depend on the duration of the heat application; in addition they might depend on the plant species, the history of the individual plant including the temperature history, the temperature gradient, and might depend on the water status of the plant. To determine such thresholds is really complicated and we therefore refrained from determining exact values. Instead we show the effects itself as this effect is not well known. To choose appropriate temperatures in measurements as described here certainly needs compromises for intensity and duration of the heat stress. Just two examples: Three short time exposures to beech showed only reversible effects (P. 9541 lines 2 to 7). Therefore the long lasting heat stress was applied although it seemed unrealistically harsh. The response of the plant was nevertheless comparably weak; however, the principle behavior was obvious. As second example: 51 °C for about 3 hours, the highest temperature we choose. This high temperature was applied during 13CO2 exposure. Such experiments are extremely expensive. We therefore made sure that the heat had the desired effect without taking too long time with 13CO2 exposure. Thus, the extreme temperature with the short duration was chosen. We agree with Peter Harley, that in combined heat and water stress situations the temperatures chosen here are conceivable. Furthermore we would like to point out, that comparing visible responses of plants treated here with those observed in the environment show that the plants in our experiment were less affected. During heat waves such as the summer 2003 in mid Europe many deciduous trees (we observed this in particular for Silver birch) lost most of their leaves. This behavior is well known and certainly due to the connected impacts of heat and drought. However, none of the plants used during our measurements showed visible stress symptoms of comparable severeness. We therefore conclude that the stress

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application (with heat alone) was less severe than the stress appearing periodically in the real environment. We are aware that both, heat and drought were responsible for the plants' responses in the environment. However to understand the impacts of both stresses requires to check the impacts separately in a first step and thereafter checking the combined effects. This was the reason to first determine impacts of heat for well watered plants although such situations will most probably be uncommon in the environment. More common will be combined effects. In combination both stresses will put much more stress on the plants than that we applied.

Page 9548 l. 3 '. . . release shortly after their biosynthesis. . .' done

Page 9549 l. 12 suggest '. . . during irreversible heat stress.' In fact, GLV emissions are basically the criteria by which you define 'heat stress'.

Our response: According to a remark of referee #1 the whole sentence was changed to: "GLV emissions are related to the degree of membrane damage (Fall et al., 1999; Beauchamp et al., 2005; Behnke et al., 2009). Assuming that heat stress does not repair damaged membranes consequently leads to the hypothesis that heat stress cannot cause decreasing GLV emissions. We therefore propose that future heat waves will either increase GLV emissions or leave them unaffected."

Page 9549 l. 24 suggest '. . . de novo MT emissions can drop. . .' done

Page 9549 l. 25 The authors acknowledge that reductions in isoprene emission above the temperature optimum result from 'an overall reduction of biosynthetic activity' which includes both reductions in available substrate (i.e., DMADP) and isoprene synthase activity (whether by regulation or denaturation). In the next paragraph however, they seem to suggest that reductions in de novo MT emissions result from denaturation alone. I don't think this is supported by any evidence.

Our response: We added the possibility of reduced substrate availability, see above.

Page. 9550 l. 8 Were net photosynthesis and electron transport reversible or was gen-

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eral metabolic activity irreversibly affected by the heat stress and presumed membrane disruption?

Our response: The plants' responses with respect to changes of net photosynthesis show a high variability. For example, in case of one experiment (no. 4 in table 3 discussion paper p. 9543 lines 20 ff.) the impact on net photosynthesis was irreversible on a time scale of few weeks. In another experiment (no. 6 in table 3 and new figure 7) irreversible impacts on net photosynthesis were only observable on the same day i.e. the plant recovered during the night following the heat application. Due to the high variability of the observed effects no quantitative answer can be given from our results, however, qualitatively the responses were always the same.

Page 9551 l. 19 resin ducts done

Page 9551 l. 21 I don't understand this sentence. Any 13C labeled emissions of MT prior to stress were presumably de novo emissions, and would be eliminated by the heat stress (either by denaturation or in my view more likely by substrate limitations). The labeling experiment tells us nothing about emissions from pools.

Our response: We believe that labeling experiments can tell us about pool emissions. Labeling was observed before the stress but not thereafter implying that de novo emissions decrease to low amounts. Therefore increases of emissions in parallel to ceasing labeling indicate that the increase is due to release from damaged pools. This was explained in the paragraph following this sentence (see next remark)

Page 9551 l. 24 This entire paragraph seems difficult to understand and unnecessary. The conclusion (p. 9552, line 7) seems straightforward and obvious. As shown in Fig. 3, the labeled emissions fall to near zero after the imposition of stress, while the total emissions, presumably from unlabeled pools, increase to extraordinary levels, in parallel with increased GLV emissions.

Our response: Peter Harley is correct, the conclusion is indeed straightforward. How-

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ever we had to find a compromise for this remark and his second last remark. We deleted the sentence referred to in the second last remark and the paragraph referred to in the last remark and added the text: “We furthermore did not find such pulses from plants not possessing resin ducts and we therefore conclude that the pulses in MT release from conifers were due to damage of resin ducts.”

Page 9552 l. 11 this comparison ignores the time of exposure; Tingey presumably exposed needles to 46 °C for just long enough to make an emission measurement, whereas in this study, needles were kept at high temperatures for hours to days.

Our response: Correct. We deleted the sentence: Such differences may be explained by different heat stress tolerance of different species . . . and deleted the word “But” at the beginning of the following sentence.

Page l. 29 resin ducts done

Page 9554 l. 1 widespread done

Page 9554 l. 5 ‘to aphid infestation’ done

Page 9554 l. 17 delete ‘respective’ done

Page 9555 l. 1 ‘. . . emissions to heat stress. . .’ done

Page 9555 l. 4 ‘decreases of constitutive de novo MT emissions;’ done

Page 9556 l. 15 Again, I think the emphasis on enzyme denaturation is too strong. While denaturation is certainly possible (at 51°C in particular) denaturation at 31°C or 35°C seems unlikely. I think a greater emphasis should be placed on potential substrate limitations, which should be related to declines (and recovery) of primary metabolic activity, in particular electron transport capacity.

We followed this suggestion, see above.

Page 9557 l. 1 delete ‘from’ done

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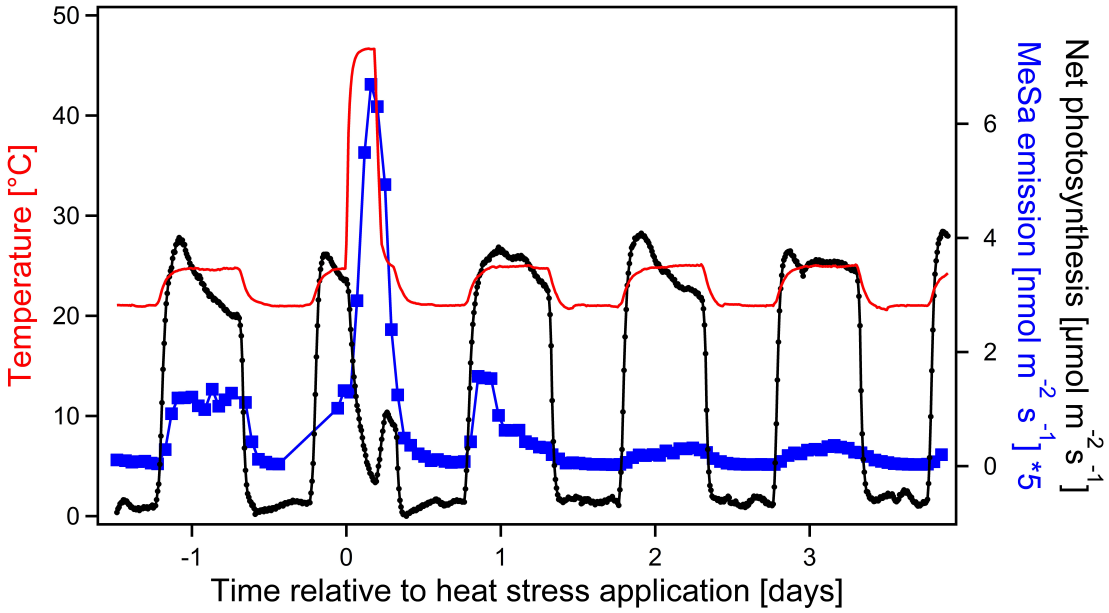

Fig. 1. Fig. 7: Temporal shape of temperatures applied to Scots pine in experiment No. 6 (red line, left hand scale), net photosynthesis (black circles, right hand scale), and MeSa emissions (blue squares, ri

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