Author Responses to Editor and Referee comments on "Emissions of BVOC from lodgepole pine in response to mountain pine beetle attack in high and low mortality forest stands" (BG-2012-209), 17 October 2012

Firstly, we thank the Editor and Referees for their thorough reviews and constructive suggestions. We have responded directly to each of the comments/suggestions made by the Editor and Referees by quoting the original comments and then responding to each of these in a bold typeset so as to make the text containing the author responses obvious.

Referee 1:

"The manuscript will need major revisions and concentrating on the main findings. Due to the complex samplings and the difficulties involved, the message of the study is not transparent and clearly argumented in the current ms. I get the impression that the authors were not able to decide what their main message was, and therefore decided to list all data without a proper analysis. Therefore the results section is in many places tedious to read, and in fact it occasionally is just listing the individual measurements, instead of summarizing the message in figures and tables. Further, the tables are far too detailed, and need to be condensed or changed to figures. The discussion should concentrate on the main findings and leave speculations out. In summary: the ms needs to be condensed, and concentrated around the main, significant results. "

Author response: We elected to present all of our results to the research community, largely because the initial responses to the manuscript from early internal reviews indicated that the relatively large amount of emissions data generated for lodgepole in this study could, in and of itself, justify publication. Although we are sorry that Referee #1 found the manuscript somewhat tortuous and complex, the main points and conclusions are, in the opinion of the authors, clearly and succinctly outlined in the abstract and conclusion sections of the manuscript; the rest of the story is available to interested readers if they want to mine the results section of the text. Additionally, we feel that extensive description and discussion of some of the results and related caveats were warranted in order to justify several of the conclusions reached in the manuscript. For instance, the conclusion that trees which survived historical MPB attack had higher late season SQT emission capacities than all other trees at the MRS site required a demonstration that it was not heat stress to enclosed branches during June-July sampling that caused differences in observed emissions in late-season samples, since it was coincidentally also the historical MPB survivors that were not subjected to enclosure overheating conditions during June-July sampling. Because of the potentially confounding variable of heat stress, a previously unsampled branch from one of the dedicated sample trees was sampled in September, along with the primary dedicated branch from the tree (which had been subjected to over-heating during mid-summer sampling) in order to demonstrate whether prior heat stress had an effect on emission capacity. In terms of addressing Referee #1's view that the tables are too detailed and should be condensed or presented as figures, the original submitted manuscript did in fact have most of the data presented graphically. The current tabular presentation of the compound ratio data

is in large part due to the helpful initial comments provided by the editor, who suggested that data presented in graphical format (such as pie charts) "only serve to make quantitative results qualitative," and we have come to agree with his position on this matter. In order to address Referee #1's comment that occasionally, the results section is merely listing the individual measurements, we have gone through the manuscript to confirm that in fact, we never present simple recapitulations of any emission rate data that can already be found in Table 3 (emissions results). We do, however, acknowledge that relatively more emphasis is placed on a detailed discussion of monoterpene ratio results for the two sites (Table 4), but since this was clearly one of the significant findings of this paper, we contend that this degree of emphasis is appropriate. Additionally, in our opinion, the qualitative discussion of compound ratios in the results section compensates for the visually-obvious qualitative conclusions that the reader could have made were the ratio data presented in a visual fashion. Finally, Referee #1 argues that the discussion section is too speculative, but this also is the result of an iteration of earlier reviews provided by other readers, who generally converged on the point of wanting to see more discussion about potential ramifications of the findings presented in our manuscript, especially in reference to the Amin et al. (2012) paper that is discussed in more detail in the author response to Referee #2, below (see comment #7). To maximize the objectivity of the paper (and in response to comments provided by Referees #2 and #4), we have now included a more quantitative description of beetle pressure at each site and have also expanded the discussion in terms of identifying and, when possible, excluding other potential causative factors that could have influenced observed discrepancies at each site including soil type, MPB pressure at the sites, etc. and hope that the inclusion of this information serves to justify as well as constrain some of the speculative aspects of the discussion section.

Specific comments:

How were the trees and the sampled branches selected? Was shoot growth quantified

between the samplings?

Author response: To clarify the methods used to determine the infestation status and selection criteria for sampled trees, we have added the following text into Section 2 (Methods), Page 9129, line 16: "At both sites, the health and MPB-status of trees selected for sampling were determined visually and confirmed with the help of coauthors with expert site-specific knowledge of the local MPB dynamics and history. MPB infestation was determined by looking for visual indications of infestation, including bore-holes, boring dust on bark crevices or at the base of trees, missing patches of bark, red needles, and/or any other visually-apparent signs of infestation or distress. Mature trees with a minimum DBH of 15cm were selected for sampling." In answer to the question about whether shoot growth was quantified, we direct Referee #1 to the extensive discussion of this topic in the existing manuscript beginning on line 14 of p 9133 and ending on line 17 of p 9134.

Can you quantify the beetle-induced damage to sample trees somehow (e.g. x% of foliage turned red)?

Author response: For the "red beetle" (dead) trees sampled at CP, all of the foliage was red. There was no red foliage on the "beetle green" trees; descriptions of the foliage conditions of these sample trees are defined in Table 1 (column 1). To further clarify this, we changed the text on P. 9129, lines 8-16 to read "At CP, three classes of trees were sampled: healthy, uninfested trees (referred to hereafter as "Live Green" or "LG" trees), trees infested with the MPB but still containing predominantly live green foliage ("Beetle Green" or "BG" trees), and late-stage infested trees whose needles had all turned red but had not yet fallen ("Beetle Red" or "BR" trees). At MRS, where there were no "BR" lodgepole trees, we sampled BG trees (referred to as "old_beetle" or "OB" trees), apparently healthy uninfested trees before and after being baited with lures and subsequently attacked by MPB ("Before Baiting" or "BB", and "After Baiting" or "AB", respectively), and apparently healthy uninfested trees not baited with MPB lures (referred to as "control" or "CT" trees)". Additionally, average MPB bore-hole densities and tree mortality for the two sites are now presented in Table 1 and discussed in the discussion section.

The calculation of emission rates should be presented in the materials and methods (now in results).

Author response: We have moved this information to the methods Section 2.6 and have changed the name of this section to "Emission rate calculation and statistical methods".

Although this is one of the reasons why the number of samples is so small, it is not

necessary to describe the destroyed samples in such details (p 9137 lines 17-21).

Author response: We have shortened the description of why several of the CP samples had to be excluded from analysis.

Table 1 and 2: Currently there are too lengthy descriptions of sites (with even some

references!), these should be moved to the main body of the text.

Author Response: In the initial submission of this manuscript to BGD, the information now contained within Tables 1 and 2 was originally presented in the introduction (and took up quite a lot of additional space in the manuscript, especially since tables allow one to convey information using terse and condensed language), but after the first round of editor and referee reviews, Table 1 was expanded and Table 2 added, so it is difficult to reconcile the opinion of Referee #1 with the opinions of other reviewers who have encouraged the inclusion of this information in tabular format. To the knowledge of this author, there are many examples in the literature of references appearing in tables

(e.g. Guenther et al., Atmos. Chem Phys., 6, 3181-3210, 2006; Duhl et al., Biogeosciences, 5, 761-777, 2008) and this is not an inappropriate convention.

What does 'Stand-membership' (Table 2) mean?

Author response: We have changed the title of table 2 from "Stand-memberships and characteristics for trees sampled…" to "Stand characteristics for trees sampled…"

I suggest revision of the tables 1 & 2: TABLE 1: the most relevant characteristics of

the sites (infestation category, tree age, stand density, management, soil type, long-term T and precipitation etc.), and TABLE 2: conditions during measurements (date, T,

PAR), numbers of sampled trees, etc

Author response: If we were to move the enclosure temperature data from Table 3 (emission rates) into Table 2, we contend that our readers would have a much more difficult time making visual comparisons of the emission results between trees/sites since temperature is such a strong driver of emissions. We have, however, now included recorded PAR ranges observed during sampling as well as brief summaries of other meteorological variables including ambient temperature for the sample periods in Table 2 and have added additional site-specific climatic information as well as soil types present at each site to Table 1.

tables and figures should be self-explanatory with all abbreviations out-spelled in the

legend. Since there are quite many abbreviations used in the ms, it is very hard for the

readers to remember them by heart.

Author response: We have removed abbreviations from the figures but have kept abbreviations in the tables since these are consistent throughout the tables and all abbreviations for tree codes are defined in Table 1. We have also removed the stand codes from Table 2 in order to simplify that table and reduce the number of abbreviations/codes used.

most of the tables are very busy and should be condensed, or the results illustrated

in figures (and not all measured numbers need to be listed)

Author response: This issue has already been responded to in our response to Referee #1's main points, above.

table 7: give the degrees of freedom for the statistical tests

Author response: In deference to Referee #1's earlier contention that most of the tables are "very busy", we point out that this information can be inferred from the sample sizes given Table 6 (which appears just before Table 7).

figures 2-4 are poor quality and the legends are unclear

Author response: The authors will work with BG production office to ensure that figure quality is maximized. Additionally, the legends have been changed so that tree abbreviations are no longer used and are instead now identified by the full name of the sample class associated with each tree.

fig 3: which data was used for the regression lines? Did you combine the controls

and old beetle measurements?

Author response: As described in the manuscript within the text that explains and discusses Figure 3 (line 25, p. 9140-line 4, p. 9141), "Samples collected in early August (Figure 3) indicated a more or less linear relationship between emissions and temperature and less tree-to-tree variability in BERs (Table 7). The slope obtained when a linear regression was performed on all the data (0.07) had a much lower R^2 value (0.51) than when the baited trees were treated with a separate regression analysis. The baited trees exhibited lower MT emissions than both control and old-beetle trees at similar temperatures, and had a lower slope (0.07, R^2 = 0.80) than control and old beetle trees (0.11, R^2 = 0.84, Figure 3)." and we hope this explains that linear regressions and corresponding correlations were explored for (a) all three sample classes combined and then (b) after separating the baited trees into one class and combining the old-beetle and control trees into another class. We did notice a typographical error in the above excerpt (the 2nd appearance of "Figure 3" was originally erroneously referred to as "Table 3"), and this has been corrected in the revised text and should make it more clear that the regression procedures described are referring to Figure 3.

Referee 2:

My main concern with the article is the comparison of CP and MRS and subsequent interpretation of results. I assume that these sites are very different and have undergone very different beetle pressure. I am skeptical that the MRS trees have more heterogeneous emissions because of tree resistance to beetle pressure or blue stain fungus. Additional information in the discussion section would strengthen this aspect of the paper. As writing now, a few questions remain unanswered: Can the authors quantify that the sites had similar beetle pressure? For example, were number of pitch tubes counted on host trees? Were beetle flight traps used during attack? How confident are the authors in the baiting used at MRS matched actual beetle pressure at CP? These data may be available in the baiting paper referenced; however a more detailed description in this paper is needed.

Author Response: We have expanded the discussion to include measures of beetle pressure at each site and have included in Table 1 the average pitch tube counts for infested tree classes at CP and for the naturally infested as well as baited trees at MRS. We have also expanded the existing discussion of other factors that could contribute to some of the observed differences at the sites including MPB pressure at each site, soil characteristics, etc. We would like to emphasize that we are not implying that "MRS trees have more heterogeneous emissions because of tree resistance to beetle pressure or blue stain fungus", but rather that MRS trees have more heterogeneous emissions, period. This was observed among MRS trees prior to, and after baiting. We are implying that it could be this heterogeneity that makes MRS trees appear to be more MPB resistant, although we have refrained from making strong statements to this effect because of the low sample numbers. The trees baited at MRS had an average of ~52 attacks per square meter of bark surface. That's within the range of densities that occurred on unbaited trees attacked in the site as well, which had a mean attack density of ~97 pitch tubes per square meter of bark surface, therefore the trees selected for baiting were a bit lower on the defenses scale than the mean of lodgepoles but attack density is an imperfect measure of tree defenses. The attacked tree categories at CP (BG and BR) had average pitch tube counts of 60-87 pitch tubes per square meter, and although this metric alone is not a complete measure of beetle pressure, this range is obviously similar to what was observed at MRS. There are not beetle flight data available for CP, but for MRS several observations indicate that MPB pressure is relatively high there: MPB flight season in recent years at MRS has ranged from a low of 95 days (2009) to 115 days (2011) (Mitton and Ferrenberg, 2012) with first MPB attacks on trees beginning prior to July in all years 2008-2011. High levels of MPB activity (>10 individuals/day in single traps or on individual trees), measured by captures in flight traps and attacks on trees were observed consistently throughout July and August, 2009-2011 (Ferrenberg, unpublished data). Importantly, there were sufficient numbers of MPB still in flight in September of all years to successfully attack and kill trees en mass. This information suggests that beetle pressure has been relatively high at MRS, while the high mortality levels seen at CP suggest that beetle pressure has also been significant at that site.

Sturgeon (1979) analyzed resin from dozens of ponderosa pine trees at each of 8 sampling sites in southern Oregon and northern California and found that in a significant portion (but less than 50%) of trees from populations with a history of pine beetle infestation, the resin contained high ratios of limonene, α- and β-pinene, with low levels of carene and noted that this particular chemotype was rare in populations with no history of beetle infestation. This suggests that, at least in ponderosa pine trees, there may be certain resin monoterpene chemotypes that are more common in populations with a history of beetle attack. If a similar pattern exists among lodgepole pine, and if this pattern were to extend to branch-level volatile monoterpene emissions, then understanding the MPB history at each site might explain some of the observed differences. The trees sampled at MRS are thought to be ~150 to 200 m above what was considered the elevational limit of MPB in 1973 (Amman, G.

Environmental Entomology), though outbreaks in nearby areas have been documented over most of the 20th century. MPB is also known to have been present at CP since the early 20th century. Since little is known about the short- and longer-term effects from MPB on branch-level VOC emissions, whether the resin phenomenon observed for ponderosa would carry over to lodgepole, or if these types of impacts would also be seen in foliar/branch-level emissions, we have elected not to include this information (i.e., on ponderosa resin chemistry) in the discussion section of our manuscript. The idea of relatively high heterogeneity observed at MRS in terms of monoterpene emission profiles is reinforced by the observations that (1) lodgepole pine resin monoterpene chemotypes are well-known to vary at least somewhat according to subspecies/variety (Zavarin et al., 1969; Lusebrink et al., 2011), and (2) the trees at MRS have higher heterozygosity than other stands of lodgepole sampled at other elevations (Ferrenberg, personal communication). Also, monoterpene diversity in terms of resin profiles appears to be much higher at MRS than other sites that report lodgepole chemistry (Ferrenberg, unpublished data); these observations suggest that the MRS trees might indeed be located in a unique pocket of diversity. We have now included a brief reference to these observations in the discussion section.

…On the other hand, can the differences in MT emission be due to site-to-site variability, or another mechanism? What is known about MT emission variability among Lodgepole pines in different soil types, precipitation, and temperature regimes? If this is an open question to be answered in a follow up study, I suggest the authors remove references to MPB resistance throughout the paper. I also suggest that the authors add other possible explanations for site-to-site variability.

Author response: We have added the following text describing the soil regimes at the two sites as well as the limited information available regarding effects of soil composition on BVOC emissions from pine: "The effects of soil type and nutrient availability on emissions from lodgepole are unknown, though Ormeño et al. (2007) observed higher emissions of α-pinene from a Mediterranean pine species (*P. halepensis*) growing in calcareous versus siliceous soils. At both the MRS and CP sites, soils are dominated by Typic Chryocrepts and Cryoboralfs (Table 1, Knight, 1991; Birkeland et al., 2003; Veblen and Donnegan, 2005), soils at the MRS study site are predominantly of a sandy-loam texture (with 10-15% clay content, Birkeland et al., 2003) with large cobbles and rocks present. The mineral soils at MRS are overlain by a fairly shallow organic layer (5-10 cm) which is also overlain by a forest litter layer that has high spatial variability depending largely on canopy conditions. Soils at the CP site are predominantly of a sandy-clay-loam texture and exhibit more vertical stratification than do the soils at the MRS site. Similar to the MRS site, CP soils under lodgepole pine stands have a significant litter layer covering a decayed organic layer of 5-10 cm thickness (Gochis, personal communication). The similarity of the soil types at the two sites makes it unlikely, in our opinion, that differences in observed emissions between the sites are driven by local geology."

We have also included some unpublished results from S. Ferrenberg along with information about differences in lodgepole resin monoterpene profiles observed among sub-species and varieties of lodgepole pine (from the literature), to add credence to the idea that the diverse monoterpene emission profiles at MRS might indeed be a function of higher diversity there (added to discussion

section): "Monoterpene resin profiles of lodgepole pines have been shown to be unique among most subspecies/varieties (Forest, 1980; Lusebrink, 2011), and analyses of monoterpene resin chemistry indicate that MRS specimens have higher heterozygosity as compared with a number of other stands sampled (Ferrenberg, unpublished data) although CP was not included in these resin samples. Nonetheless, these observations along with the site-specific comparisons of abiotic factors (above) suggest that the trees sampled at MRS may be more diverse than most other lodgepole populations." Finally, we have added average annual temperatures for each site to Table 1 addition to the precipitation summaries to show that climatologies between sites are not dramatically different.

Minor comments / questions:
1) The authors could provide more detail on quantitative measures of tree selecting at MRS for attacked trees. As written, readers are referred to a separate paper; however, a few additional sentences in this paper would be helpful in my opinion.

Author response: In order to clarify the methods used to determine the infestation status and selection criteria for sampled trees, we have added the following text into Section 2 (Methods), Page 9129, line 16: "At both sites, the health and MPB-status of trees selected for sampling were determined visually and confirmed with the help of coauthors with expert site-specific knowledge of the local MPB dynamics and history. MPB infestation was determined by looking for visual indications of infestation, including bore-holes, boring dust on bark crevices or at the base of trees, missing patches of bark, red needles, and/or any other visually-apparent signs of infestation or distress. Mature trees with a minimum DBH of 15cm were selected for sampling."

2) How does tree to tree communication alter results at CP? Because the beetle attack was more severe at CP, could tree to tree communication result in homogeneous emission? Perhaps this is too speculative, but what would the critical measurements be to determine this?

Author response: We don't know how tree-tree communication alters BVOC emissions in lodgepole, if at all. However, after inclusion of additional information regarding beetle pressure in the tables and text (as described above), we think it's reasonable to say that beetle pressure may not have been as different as one might expect between the sites if one were to deduce this from tree mortality rates alone…this conclusion is bolstered by the fact that MPB mortality among limber pines is much higher at MRS than for lodgepoles (Table 1). Also, since the trees at MRS were all growing within 40 m of each other (Table 2) while some of the CP trees were up to 475 m apart, we don't see why tree-to-tree communication should be a more compelling factor at CP as compared to MRS. After excluding the likelihood that abiotic factors such as soil types might also play a role in observed differences between the sites (in the new site-specific soils comparison added to the discussion section) and after including in the discussion section additional observations suggesting that MRS may indeed be somewhat more diverse than other sampled lodgepole stands (as mentioned above), we hope that Referee #2 will agree that a discussion of the potential role of tree-tree communication as an explanatory factor in observed differences would be highly speculative and not well supported.

3) What were the general meteorological conditions during each measurement period,
and would site differences prior or during measurements impact emissions? For ex-ample, was cloud cover similar at each site?

Author response: We have now included brief summaries of meteorological variables observed during sampling including ambient temperature, PAR ranges, and sky conditions in Table 2. Emissions of many of the compounds are highly dependent upon temperature; this is why we normalized emissions of mono- and sesquiterpenes to temperature. Cloud cover was similar for one of the two September sampling days at MRS compared to CP, and differed quite a lot on the other day. Much of this impact is reduced when emissions are normalized to temperature since one of the effects of cloud cover at high elevations in September is generally reduced air temperatures, although PAR would also be reduced under cloudy conditions. As PAR and meteorological conditions during sampling have now been included in Table 2, we see that PAR ranges were similar between the sites during September sampling. Ambient temperatures were lower at MRS than at CP during September sampling, however as mentioned already, these effects should be accounted for in the emission normalization process (for mono- and sesquiterpenes) and for compounds like MBO that were not normalized, readers can compare emission rates with observed temperatures in Table 3. Although the effects of past meteorological effects such as air temperature have been reported for isoprene (e.g. Guenther et al., ACP, 6, 3181-3210, 2006), these effects are much less well-constrained for other compounds and since our trees were not isoprene-emitters, we have not considered nor discussed this in the manuscript.

4) Why was PRISM data selected instead of on-site measurements?

Author response: PRISM provides a long-term context for general climate variability at the sites. The CP site does not have long-term records over the period detailed from 2001-2011. Niwot does and data from SNOTEL (for SNOwpack TELemetry) sites at Niwot are ingested by PRISM. Thus PRISM estimates over the Niwot site are very close to what was observed. PRISM estimates at the CP site are less accurate due to interpolation and regression errors. However, from a climatological perspective (i.e. inter-annual variability or seasonal rainfall variability) the PRISM product is reasonable at the CP site. Rather than mixing data sets we chose PRISM so as to have a consistent comparison product with respect to precipitation inputs.

5) A table showing the level of mortality at each site / stand and its timing would be beneficial for comparing with other studies. As well as some description of beetle pressure.

Author response: These data have now been incorporated into the tables and text.

6) Information on drawbacks and potential errors associated with using enclosures may be helpful for some readers.

Author response: We have referred readers to [Ortega, J. and Helmig, D.: Approaches for quantifying reactive and low-volatility biogenic organic compound emissions by vegetation enclosure techniques – Part A, Chemosphere, 72, 343-364, 2008]. The following text has been added at the end of Section 2.4 (Sampling Methods): "Readers interested in more information about branch enclosure-based sampling are directed to Ortega and Helmig (2008)."

7) The authors briefly discuss the Amin et al., 2012 study published in Environmental Science and Technology in terms of SOA potential. Can the authors also discuss potential reasons why Amin et al., 2012 found a clear increase in MT from the trunk of beetle attack trees, and a similar increase was not found in the branches of this study? Does this result from additional resin production in the truck of trees during attack, and perhaps leaf emissions may not be as significant?

Author response: There are several reasons why the Amin et al. (2012) study might have missed a foliar signal in terms of MPB effects on emissions, which is why we did not include mention of that conclusion in our manuscript. We note that only 9 individuals were sampled in the Amin et al. (2012) study compared to 14 trees sampled in the present study. Furthermore, the nine trees sampled in the Amin study represented 6 sampling classes, with four of these sampling classes thus containing just one individual. In addition to the higher inherent uncertainty in the results from Amin et. al (2012) introduced by the smaller sample class sizes relative to our results, the authors were also unable to express their results as quantitative emission rates on a per unit biomass (or even per unit area) basis because they simply sampled air near healthy or infested trees, as opposed to employing a quantitative approach to sample collection in which the amount of biomass emitting the compounds of interest was isolated and quantified and therefore in Amin et al. the emissions from each individual were not isolated definitively (i.e., since only ambient air samples were collected). No light and temperature measurements were reported in Amin's study, despite the fact that these are the strongest drivers in emission variations within populations and emissions should therefore be normalized to temperature and/or light (for light-dependant compounds) whenever possible. In the Amin study, no statistical relationship was observed between canopy-level MT concentrations versus tree infestation status. The statistical analyses employed in Amin et al. relied on pooled measurements from a three-month period despite the observation that needle age and/or seasonality-related effects are known to dramatically alter emission capacities of many important compounds (e.g. MBO: Gray, Lerdau, and Goldstein, Ecology, 84(3), 765-776, 2003; Terpenes: Llusía and Peñuelas, Am. J. Bot., 87(1), 133-140, 2000). Therefore the approach used by Amin et al. might have missed infestation-related impacts on canopy-level emissions if the magnitude of the induced changes were below those arising naturally from seasonal changes in emission capacities.

Referee #2 poses an interesting question about whether leaf emissions are as significant as VOCs emitted from resin during MPB attack, based on Amin et al. (2012). In addition to the fact that the emissions data presented in Amin et al. (2012) were not expressed on a per-unit biomass basis nor as a function of light or temperature (and therefore could not be quantitatively compared with our data), emissions of MBO also were not considered in the Amin et al. (2012) study. MBO is emitted in great abundances from the pine forests of North America (e.g., Baker et al., JGR, 140(D21), 26107-26114, 1999) and since it is produced and emitted de novo, in comparable quantities as foliar monoterpene emissions, it would be an important compound to have data on to enable direct comparisons with Amin et al.'s results and to evaluate the source strength of foliar versus trunk-level emissions.

We can see why including some of the findings of Amin et al. in our manuscript could open a metaphorical 'can of worms', but we did not include references to Amin et al. in earlier versions of our manuscript and initial reviews suggested that some readers would like to have seen this study mentioned in our own work. Despite the various compelling reasons why Amin et al. might not have observed a relationship between MPB infestation and foliar emissions, we opted not to expound upon these in our own manuscript which is already long and, in our opinion, should not be a platform for dissecting a study whose findings cannot be compared with our own without substantial additional information.

Editorial comments:
1) page 9151, line 27: should this be "MPB resilience" not "MBP"?

Author response: We agree that this wording is better and have changed this in the current submission.

Referee 4:

Some minor questions:

1. The authors mention that lower, reachable branches were sampled from the trees, which may suggest generally shaded conditions of sampling. However, the presence of MBO points at de novo synthesis of BVOCs. What were the PAR values for the sampled branches, and would this variation explain the scattered appearence of some compounds (other than MBOs), or suggesting that part of the emission is synthetized besides it being released from storage pools?

Author response: Yes, definitely the presence of MBO indicates de novo production and release. However, all of the trees sampled at the MRS site were located in an open canopy and each branch received full sun (PAR > 1000) for several hours each day between mid-day and late afternoon at least once during the sampling campaign. We did attempt to explain some of the observed variability in MBO (including the extreme emission bursts) by examining PAR values incident on the enclosure during sampling. However, PAR values did not explain the observed emissions behavior. In order to

reduce the likelihood that readers will erroneously think that only partial sun or shade-adapted branches were sampled (since the measurements were all conducted in more or less open canopies), we have removed the sentence "Many of the trees growing at CP offered little or no access even to their lowest branches, making the selection of trees for sampling challenging." (P. 9130, lines 1-3). Although by now most folks agree that some monoterpenes are light-dependent, it is extremely difficult to constrain these relationships in the field where PAR can be almost constantly changing. We did not find good correlation between total monoterpenes and PAR, but since the correlations for temperature were generally good, we did not attempt to determine which, if any, individual monoterpenes that were emitted might have been light dependent.

2. pg 9129/ 2. Methods and Table 1: How were BG and OB trees distinguished from healthy LG and CT trees? What visual signs used? Were the trees infested at the time of sampling? (BG, OB, BR or neighbouring trees)

Author response: In order to clarify the methods used to determine the infestation status of sampled trees, we have added the following text into Section 2 (Methods), Page 9129, line 16: "At both sites, the health and MPB-status of trees selected for sampling were determined visually and confirmed with the help of local ecologists with expert site-specific knowledge of the local MPB dynamics and history. MPB infestation was determined by looking for visual indications of infestation, including bore-holes, boring dust on bark crevices or at the base of trees, missing patches of bark, and/or any other visually-apparent signs of infestation or distress. Mature trees with a minimum DBH of 15cm were selected for sampling." As described (and slightly modified from the previous wording) on P. 9129, lines 8-16 to read "At CP, three classes of trees were sampled: healthy, uninfested trees (referred to hereafter as "Live Green" or "LG" trees), trees infested with the MPB but still containing predominantly live green foliage ("Beetle Green" or "BG" trees), and late-stage infested trees whose needles had all turned red but had not yet fallen ("Beetle Red" or "BR" trees). At MRS, where there were no "BR" lodgepole trees, we sampled BG trees (referred to as "old_beetle" or "OB" trees), apparently healthy uninfested trees before and after being baited with lures and subsequently attacked by MPB ("Before Baiting" or "BB", and "After Baiting" or "AB", respectively), and apparently healthy uninfested trees not baited with MPB lures (referred to as "control" or "CT" trees)". We did not survey surrounding trees at MRS for their infestation statuses during each visit to MRS (just the first visit), but we can say that it was quite difficult to find a specimen that had been infested there while at CP it was difficult to find un-infested trees.

3. pg 9130/ line 22: Was there any effect of the baiting on tree emissions before the MPB attack? If this information can not be concluded from the current dataset, could the authors give a view on this based on previous observations maybe?

Response: One could imagine the potential for both indirect and direct effects on tree emissions caused by the pheromone-containing lures used to ensure MPB attack on the baited trees. In terms of indirect effects, if lures were more successful than natural cues at attracting MPB to trees, then any

emissions related to infestation could potentially be altered more than what might naturally occur if lures had not been used. The trees we baited had an average of 51.8 attacks per square meter of bark surface. That's within the range of densities that occurred on unbaited trees attacked in the site as well (pitch tube counts now appear in Table 1). In fact, un-baited lodgepole pines had a mean attack density of 97.2 (SEM = 15.0) pitch tubes per square meter of bark surface, therefore the trees we baited were a bit lower on the defenses scale than the mean of lodgepoles (but attack density is an imperfect measure of tree defenses). This suggests that reported MPB infestation effects on emissions should be on the conservative side and thus indirect effects on emissions from the lures is not expected to be a cause for concern. The possible direct effects of baiting on tree emissions (i.e., some sort of chemical communication between trees based on the specific monoterpenes contained in the lures, which include oxidized alpha pinene and myrcene) has never, to our knowledge, been established or observed. Although plant-plant chemical signaling has been observed in some species (e.g., *Baldwin et al.*, (2006) *Science*, 311 (5762), 812-815, DOI: 10.1126/science.1118446; *Dicke et al. (2003), Trends Plant Sci. 8, 403*), we've not seen reports supporting any assertion that the lures alter tree emissions. Unfortunately, we did not sample the trees post-baiting but pre-MPB attack, however, by the time the baited trees were sampled, they were being actively attacked, and given the intrusive process of MPB boring, it seems reasonable to assume that this influenced observed emissions more than the presence of a lure packet on an individual tree. Since none of the trees sampled at MRS were growing more than 40 meters apart from each other, we suspect that if the lures were influencing emissions, they could have affected all of the sampled trees, which would not explain the discrepancies in emissions observed among the baited and un-baited trees at MRS.

4. pg 9146/ 1st paragraph: How did AB1 (long time heat stressed branch) change its emission during the stress period (August)? Was the emission observed in September (AB1) similar to that in August before overheating?

Author Response: This branch was heat-stressed starting near the beginning of the first sample collected during the August sampling visit, and the enclosure remained at high temperatures throughout the sampling period until the enclosure was removed (~4.5 hrs), therefore we were unable to evaluate the short-term effects of heat stress on this individual. We have changed the text in Section 3.2.8 to "A second branch from baited tree #1 ("AB1b") was sampled during the September sampling period to evaluate potential long-term effects on emissions following a period of extreme heat stress, as the primary branch sampled from this tree was exposed to the longest period (~4.5 hours; the entire duration of the sampling period for this branch) of heat stress during August sampling. " so that readers will understand why the short-term effects of the heat stress were not examined on this branch.

The August MT BER and SQT BER (i.e. temperature-adjusted emission capacities) from AB1; (0.40, σ= 0.14 and 0.260, σ= 0.183 μgC g_{dw}^{-1} hr^{-1}, respectively) were within the same range as the BERs for the other AB tree (for MT) as well as both of the controls (for SQT) during this sampling period, as is evident from Table 3. September samples collected from this branch (also in Table 3) indicate that this branch was again in the range of SQT BERs (0.019, σ= 0.023) observed among the other AB tree

and both controls, while MT BER from this branch was within the same range as all trees except the OB trees, and, to a lesser extent, the secondary branch sampled from AB1 ("AB1b"). Since all of this information can be deduced from Table 3, we have not changed anything else in response to this comment.

5. Table 3: Due to the complexity of the current study, a remark of the experienced accidental influences of branches (heat stress, possible fungal infestation) could be marked besides the trees in Table 3. It would make the reader easier to have an overview why specific trees show unexpectedly high/low emissions.

Author Response: We agree and have modified Table 3 accordingly.

6. Table 5: Be more consistent with compounds names; assumed that "a-bergamotene“ means "cis“ isomer, as "a-trans-bergamotene“ is listed afterwards. Better to use the "E/Z“ isomer labeling instead of cis/trans; eg. c-beta-farnesene is Z-beta-farnesene. C3716

Author Response: We thank Referee #4 for pointing this out and have followed the convention "E/Z" for all instances of isomer labeling throughout the manuscript and in the tables, where applicable.

7. pg 9137/ line 6: Specify what linear regression was applied for.

Author Response: As stated in lines 5-6 (p. 9137) of the results section, "For all compounds, we report ranges of observed [emission rates] ERs and, if appropriate, results from linear regressions." Since some fraction of our potential readers may seek to use our reported emission rates and the observed relationships between emissions and temperature quantitatively, we wanted to present as much data as possible without making the already lengthy manuscript longer. As described in line 5-6 (p. 9137) of the results section, the expected exponential relationships between ERs and temperature were not always observed. In some cases however, linear correlations were high enough that slopes of the regressions could be given along with observed average ERs, which can be used by those parties interested in sensitivity analyses or other applications requiring quantitative means with which to describe relationships between emissions and the empirically-determined environmental drivers of variations in emissions (such as temperature). We have not included a lengthy explanation in the manuscript regarding our choice to report the results of these exploratory analyses, but we do feel that we have already alluded to why these might be useful enough in the paper without adding more text.

8. pg 9140/ line 5: Table 3 instead of Table 2

Author Response: Thanks for bringing this typo to our attention; it has been changed.