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Interactive comment on "The emission factor of volatile isoprenoids: stress, acclimation, and developmental responses" *by* Ü. Niinemets et al.

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We thank the Anonymous referee and Alex Guenther for careful examination of the MS and for providing useful suggestions and critics of how to improve the MS. We have carefully examined all the comments and are hereby responding point-by-point to all these.

Reviewer one:

This reviewer mainly questions the timeliness of this review, especially regarding the excellent paper by Vickers et al (2009; Nature Chem Biol), and the recent special issue in TiPS to which 4 of the 6 co-authors of this MS have contributed. As for the TiPS special issue, this arouse as the result of BVOC science meeting on Induced

BVOC emissions held in Estonia in Jan. 2009. Thus, this special issue is mainly concerned with induced emissions, in particular, focusing on cellular mechanisms - gene expression, stress priming and proteome changes, although providing some suggestions of how to include such effects into models (e.g. Arneth and Niinemets opinion article about including insect outbreaks into models). However, given the TiPS special issue of which we have been very well aware, in this BGD MS we essentially do not address these effects at all and focus on modifications in constitutive emissions due to stress and seasonality and short-term and long-term environmental variations from perspective of including these into existing model algorithms. This has been a practical decisions given the special issue about induced emissions and also the circumstance that we are far from being able to start including induced emissions into mechanistic models.

Under stress section (2.1) on P1535, L11-12, we said "Here we focus on drought and heat stress effects on the constitutive isoprenoid emissions as these two factors have been studied in most systematic manner." Thus, we made it clear from the beginning that we intend to avoid any overlap. In fact, there is only half-page section 2.1.3. Other abiotic and biotic stresses and outlook, which considers induced emissions and which can be removed if it seems to be overlapping with some of the papers in TiPS special issue. Then the other sections are 2.2 ES in relation to long-term variations in environment; 2.3 ES in relation to short-term variations in environment; 2.4 Seasonal and age-dependent variations in ES; and finally 2.5 Philosophy of consideration of biological factors in models, all focusing on constitutive emissions from the modeling perspective. To our knowledge, these aspects have never been summarized this way together. In fact, none about the recent papers in the TiPS special issue discusses applicability of existing BVOC algorithms for quantitative ecosystem or global model applications.

Regarding the Vickers et al., their paper is devoted to understanding of how plant capacity to emit volatile isoprenoids protects plants from various abiotic stresses and the corresponding chloroplastic defense that involves the production of reactive oxygen species. Thus, their focus lies with the various anti-stress, especially antioxidant, properties of isoprenoids rather than in understanding emission controls for modeling purposes. As with the TiPS special issue, Vickers et al. center on the details of internal, cellular processes mainly targeting plant scientists. By contrast, we do not address the question of why plant emit isoprenoids, but rather target the BVOC modeling community.

The key task of our MS was to highlight what we perceive are crucial problems of modeling leaf and ultimately ecosystem and global BVOC emissions with current algorithms. We ask the question whether these algorithms really reflect current understanding of BVOC emission responses. We agree that this MS may have little to offer for a plant biologist, but we believe that the information summarized is of great value for those wishing to simulate BVOC emissions. It is clear that we must make this more clear in the Intro.

Specific issues

P1537,L2. Well, this is what 13C-labelling experiments demonstrate, i.e. activation of other carbon sources. We agree that we need to clarify the matters here.

P1538, L8. We are not aware of such a sudden drop and to our knowledge such effects have not been reported in the literature. In fact, very few transient temperature responses (e.g., maintaining a leaf under supraoptimal temperature for continued period of time) have been reported in the literature. The responses reported so far demonstrate a gradual decline. We admit that heat shock with temperatures wide above the physiological temperatures may result in rapid cessation of leaf life activity, but we do not believe that this will have significance for modeling BVOC emissions in the field.

P1539, L13. This is what we are mainly targeting here, i.e. effects on constitutive emissions. However, we want to emphasize that the situation is not always that clear-cut. Many monoterpene synthase genes are present in plants, and biotic stress can

often result in elicitation of new synthases with similar emission profiles, e.g. Huber et al., 2005, Phytochemistry, 66: 1427-; Staudt and Lhoutellier, 2007, Tree Phys., 27: 1433-

P1540, L12. Yes, we agree and therefore did not address this that much here (plus this was partly considered in Peñuelas and Staudt in TiPS). We can include the statement about other nutrients and also that at any rate the effect of nutrients is indirect and likely mediated through overall changes in plant physiological activity.

P1540, L18. In fact, the data depicted are all from a long-term study, i.e. what is shown in this figure is the acclimation response. We must make this more clear.

P1541, L7. No, must be “below” (i.e. the experiment was conducted below the ambient CO2).

P1541, L11.We agree that the problem with many biological experiments is that the results are very difficult to invalidate. On the other hand, Sharkey and Loreto (1991) for one species and Li et al. (2009) for other species have also reported such an elevation of emissions under high CO2. Thus, although the majority of experiments do show one way response, there are outliers as also shown in Fig. 2. This is where we say “in contrast”. As for Tognetti et al. paper, their study was conducted with plants grown in the vicinity of CO2 springs and outside. In general, studies in CO2 springs can be hard to interpret because of lack of true replication. Many factors can vary for such a design, including differences in nutrient and light availabilities etc. So, it would be fair to point out in the revised MS that the study compared plants grown at different distances from a CO2 spring.

P1541, L14. Yes, we still cannot fully explain all the observations.

P1548. I think that this is what we intended to say, i.e. we need to directly include age and seasonality in ES. Seems that we need to clarify the MS quite a bit at this point and elaborate the message more clearly.

Reviewer two, Alex Guenther (AG):

It is somewhat unfortunate that this MS and the accompanying one (BGD-050) have followed temporally different paths. On the other hand, it is great that AG has been reviewing both of the MS.

Contrary to the first reviewer, AG believes that our review is timely. He challenges us to combine this paper together with a companion paper, that at that time was also under review in BGD. In fact, when we began writing the review(s) discussed at European Sciences VOCBAS conference in Montpellier, we did set out from one, single manuscript. But we quickly realized that the complexity of the issues we are dealing with made one manuscript by far too long, given that we wanted to do justice to the available information. We thus deliberately split the text into two separate independent pieces: one concentrating on the concept of the "emission factor", and its dynamic behavior regarding instantaneous changes in important environmental drivers (temperature, light, leaf-internal CO2 concentration) – and a second one (this manuscript) that discusses responses to the growth environment, including stress. These latter responses, many of which have only emerged relatively recently as chief determinants of seasonal variation in BVOC emissions, are much more difficult to quantify with the currently accepted modeling concepts. We argue that the often unknown sum of environmental influences prior to a leaf-measurement in the field (both in term of a stress, and in term of a more gradual variation in conditions) make determination of Es from these measurements difficult. On the other hand, as we also noted in response to Ref. 1, we are prepared to remove the redundant parts, e.g. the superficial consideration of induced emissions.

P1544, L10. Definition of the emission factor that includes growth conditions. This is an important point, and we clarified the text based on AG's comments as: "Nevertheless, within-canopy variation in ES has been occasionally included in emission models, varying ES with cumulative leaf area index from the canopy top to the bottom (Guenther et al., 1999). However, in models that attempt to account for effects of growth environment, within-canopy variation of Es is strongly reduced since variation is then

incorporated in long-term light response activity algorithms (Guenther et al., 2006).

AG criticizes us for viewing Es as a emission rate that is only adjusted by instantaneous light and temperature fluctuations (e.g. over the course of the day), and argues that Es should rather be also adjusted for these longer-term environmental modifications. His comments reflect very well some of the critical points that we would like to make with this review: the confusing and somewhat problematic use of the term emission factor for plant BVOC emissions over a wide range of space and timescales.

In principle, the BVOC emission community faces the dilemma that –at least for large scale models- a truly mechanistic approach (e.g., like for photosynthesis modeling) is not available. All existing concepts start with a plant's (or plant functional unit's) capacity to emit under predefined standard conditions, which is then modified up- and downwards based on a number of multiplicative, empirical functions.

Originally, the chief approach to BVOC emission modeling (Guenter et al. 1991, 1993) could be described by

(1) E = Es X f(short-term) = Es X f(Tinst) X f(Qinst) =, with E being the emission rate, Tinst and Qinst being instantaneous (e.g., diurnal) variation in light and temperature, "f" denoting an appropriate empirical algorithm.

But more recently, with increasing field experiments, it became apparent that the simple concept of a "constant" Es is not applicable; Es is not constant throughout the year but varies in response to environmental conditions across a number of time scales (days to weeks). The question of how to deal best with this emerging knowledge is a matter of debate and underlies the current state of confusion as regards to Es.

In a simple mathematical view, the current Es concepts may be viewed as

(2) E = Es' X f(short-term) X f(medium- to long-term)

versus

(3) Es" = f(past average climate, leaf age, seasonality) and E = Es" X f(short-term)

There is a distinct difference between these two concepts. According to (2) (Es') is standardized not only for immediate fluctuations in environment, but also for longer-term variations, including environmental and leaf-age-dependent drivers. Thus, one species-specific or canopy-specific value is scaled to different conditions using generalized instantaneous-to-medium-to-long-term environmental algorithms. According to (3), which is commonly used for simulation of carbon gain in regional and world-scale models, Es (Es") is only standardized for short term environmental controls (i.e. is defined as the emission capacity), and thus, is varying with medium-to-long-term environmental drivers. From modeling perspective both (2) and (3) can be parameterized to predict the emission rates with similar degree of predicted variance. However, there is a clear distinction from experimental perspective and from the perspective of parameterization the models. (2) provides an impression that only one spot measurement is all that is needed. In reality, what is needed is a generalized value that is standardized for variations in all the instantaneous to longer-term factors. In the case of (3), any value measured under standardized instantaneous environmental controls at some point during the season is Es, but these values are inherently variable and accordingly, repeated sampling is needed to parametrize the functions describing these long-term controls. We advocate for the use of (3) as this way we can more efficiently link BVOC modeling to models of carbon gain, but we do not say that (2) is somehow inferior. In fact, many scaling exercises conducted have not considered any of the longer-term environmental controls, and including such controls either by (2) or (3) is clearly superior to not including those. In this respect, MEGAN has probably the most advanced approach so far and is doing great job in including the medium- to longer-term controls. However, we believe that it is highly important to be aware of these contrasting approaches and also that ES values defined by (2) and (3) are not the same. Cleary, we need to clarify things more at this point in the MS.

P1539,L16-19. Characterization of stresses. This is an important point. Standard

physiological measurements such as photosynthesis and stomatal conductance attached with emission measurements can be already very useful. Better having green leaf volatile or MeSa emissions (e.g., Karl et al 2008 paper on MeSa fluxes in Biogeosciences). We intend to include this point.

P1548, L21. AG is correct in that the canopy emission factor can be assessed if conditions like leaf age, past weather history or stress status are known. However, this can be done only by a combination of measurements and modeling. What we mean on P1550, L1, is that it is essentially impossible to directly measure canopy scale emission factors, since it is impossible to encounter standard conditions (e.g., as defined in MEGAN) at one field location, let alone at a number of sites. As said above, we do not see a problem that ES is defined according to (2), but then also one must be aware that getting a representative ES value requires much more measurements and modeling than just one spot measurement. This needs more emphasis in the BVOC community. One cannot take the existing parameterizations for certain location "as is" and immediately transfer to another setting.

P1551, L12. We agree here with AG that our common intention is to reduce the variability. The MS needs to be reworded at this point.

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