

# ***Interactive comment on “Leaf phenology as one important driver of seasonal changes in isoprene emission in central Amazonia” by Eliane G. Alves et al.***

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Reply to Referee 1 The study by Alves et al. provides a context for phenological control over isoprene emissions in an Amazonian tropical forest. I think that the results are interesting, but only because this is a tropical forest. The potential for phenology and leaf age to control isoprene emission rates has been recognized in past studies going back 25 years. Studies by Fall, Monson, Harley, Litvak, Sharkey, Loreto and many others have clearly shown these relationships in temperate forest trees. The Alves et al. study is most interesting because it deals with a tropical forest, for which this type of insight is missing. The main critique I level against the study is that it is written to largely

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ignore this past body of work, and the broader context of phenological influences over isoprene emission, and instead makes it sound like this is a new relationship discovered since 2013. I recommend a major revision of the work that honestly takes into account the historical context of the phenology-emission relationship and its relevance to the observations made in the tropical forest. In this revision I recommend making it clear that the novel aspects of the current work are that it (1) is among the first to show the importance of the phenology-emission relationship in a tropical forest, and (2) that it allows for the MEGAN model to be modified to better predict emissions in tropical forests. Author's response: We now understand that the novelty of this manuscript was not clear in the text. Indeed, leaf phenology as one important driver for seasonal changes in isoprene emission is only new here with respect to a tropical rainforest. We do not want nor intend to ignore the well-established literature focusing on temperate forests. Therefore, the Introduction has been rewritten citing the relevant temperate forest literature and putting it within the context of this study. We appreciate all the comments made by the referee, and we think the manuscript has been improved after considering and accepting his/her comments and suggestions.

Referee's comment - Lines 66-68. The phrase "as BVOC emissions are regarded as highly significant for ecosystem productivity (Kesselmeier et al., 2002) with isoprene being the most emitted hydrocarbon, it thereby plays an important role in carbon balance", is worded strangely. What does "highly significant for ecosystem productivity" mean? Why is that part of the phrase supported with a reference, but the next part of the phrase, "it thereby plays an important role in carbon balance", is not supported by a reference? Does the Kesselmeier reference cover both parts of the phrase? If not, it seems that a second reference is needed for the second part of the phrase. I am especially interested in what is meant by "important role", as my understanding is that isoprene emission occurs as a small absolute flux compared to overall carbon fluxes (e.g., approximately 1000 times lower). Author's response – BVOC emissions are small when compared to net primary productivity and gross primary productivity, but the carbon emitted in form of BVOCs can be significant for net ecosystem produc-

tivity, and comparable to the magnitude of net biome productivity (Kesselmeier et al., 2002). Because isoprene is the most emitted BVOC, we suggest that its contribution to carbon balance is highly important when compared to other BVOCs. To make this clearer, these sentences have been rewritten in the manuscript. Author's changes in manuscript – Line 64. "Moreover, isoprene emissions could play an important role in the carbon balance, because it is the most emitted within BVOCs, which are regarded as highly significant for net ecosystem productivity, with their losses comparable to the magnitude of net biome productivity (Kesselmeier et al., 2002); and carbon dioxide is believed to be the fate of almost half of the carbon released in the form of BVOCs (Goldstein and Galbally, 2007).

Referee's comment - Lines 402-406. The phrase "and as isoprene emissions are strongly dependent on leaf age and mainly emitted by mature leaves (Alves et al., 2014), seasonal changes in the forest leaf-age fractions may also influence the seasonality of isoprene emissions, suggesting higher emissions in the presence of more mature leaves and during high ecosystem photosynthetic capacity efficiency." I found this to be a bit of an egregious claim by the authors. The implication is that the dependence of isoprene emissions on leaf age and phenology was only discovered by the authors in 2014 ignores a rich literature that has shown the effects of leaf age and phenology on isoprene emissions going back at least two decades. There are many past studies showing, in explicit terms, the effects of leaf age and phenology on isoprene emissions. The authors seem gracious in citing the rich literature connecting photosynthate to isoprene emissions, but then take sole credit for discovering the connection between phenology and isoprene emissions. This should be corrected so that the true scope of the problem and related past research is brought honestly into this paper. Author's response – This paragraph has been rewritten with more literature added. Author's changes in manuscript – Line 402. "...and as isoprene emissions are strongly dependent on leaf ontogenetic stage - due to the developmental patterns of isoprene synthase activity that gradually increases with leaf maturation and decreases with leaf senescence (Alves et al., 2014; Kuzma and Fall, 1993; Mayrhofer et al., 2005;

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Monson et al., 1994; Niinemets et al., 2004, 2010; Schnitzler et al., 1997) - seasonal changes in the forest leaf-age fractions may also influence the seasonality of isoprene emissions, suggesting higher emissions in the presence of more mature leaves and during high ecosystem photosynthetic capacity”.

Referee’s comment - Lines 428-432. The phrase "This is consistent with previous studies that provide evidence that alternative non-photosynthetic pathways may contribute to isoprene synthesis under stress (Loreto and Delfine, 2000), which may then lead to a decoupling of isoprene emission from photosynthesis at high temperatures (Foster et al., 2014)." This seems to be a rather large and speculative jump in logic. There is no reason to suspect that the seasonal offset between GPP and isoprene emission rate is due to the use of stored carbon sources. In fact, the past literature (going back into the 1990s) shows that the leaf age effect is likely due to developmental (ontogenetic) patterns of isoprene synthase activity. Thus, the phenological constraint over isoprene emission (1) has the potential to override the correlation between photosynthesis rate and isoprene emission rate, and (2) this is due to an enzymatic limitation, not a limitation of carbohydrate availability. The authors seem to be unaware of this past literature as it is not mentioned in their paper. This should be corrected. Author’s response – We agree with this comment, and we decided to remove this whole paragraph. The relation between leaf age and isoprene synthase activity is mentioned in another part of the manuscript. We understand that this fits in better at lines 401-410. Author’s changes in manuscript – Line 401. Photosynthesis supplies the carbon to the methyl erythritol phosphate pathway to produce isoprene (Delwiche and Sharkey, 1993; Harley et al., 1999; Lichtenthaler et al., 1997; Loreto and Sharkey, 1993; Rohmer, 2008; Schwender et al., 1997), and isoprene emissions are strongly dependent on leaf ontogenetic stage - due to the developmental patterns of isoprene synthase activity that gradually increases with leaf maturation and decreases with leaf senescence (Alves et al., 2014; Kuzma and Fall, 1993; Mayrhofer et al., 2005; Monson et al., 1994; Niinemets et al., 2004, 2010; Schnitzler et al., 1997). Therefore, seasonal changes in the forest leaf-age fractions may also influence the seasonality of isoprene emissions, suggesting

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higher emissions in the presence of more mature leaves and during high ecosystem photosynthetic capacity efficiency.

Referee's comment - Lines 512-513. The phrase "However, less notable factors might also influence ecosystem isoprene emission." Once again, this phrase makes it seem like very few past studies have considered factors like phenology or leaf age as an important control over isoprene emissions. Actually, these factors have been recognized as just as important as temperature and light for over 25 years. The authors need to present their results in a way that embeds them honestly within the rich past tradition of isoprene emissions research. Author's response – This sentence meant to say that less notable factors might also influence ecosystem isoprene emission in tropical forests. Leaf phenology, with notable seasonal changes in the Amazonian rainforest, was just recently discovered (Huete et al., 2006; Lopes et al., 2016; Myneni et al., 2007; Saleska et al., 2016; Wagner et al., 2017), and there is still some debate about it (e.g. Morton et al., 2014; Samanta et al., 2010). The fact that for many years seasonal changes and leaf phenology were not thought to be important for tropical forests, given their evergreen condition state, led the scientific modeling community to assume that leaf phenology affects very little forest and atmosphere gas exchanges in tropical forests. However, after remote sensing studies showed seasonal biomass changes (Myneni et al., 2007) and seasonal changes in isoprene emissions (Barkley et al., 2009, 2013), models were improved in order to better represent seasonal biomass changes and leaf age in tropical forests. This is the case of MEGAN that uses variations in LAI to parameterize changes in leaf age, and then changes in the emission activity factor of isoprene emission (Guenther et al., 2012). However, because leaf phenology in tropical forests is not as notable as in temperate forests, some insights on how changes in leaf age over the year may affect seasonal isoprene emissions are still missing, and there is a lack of representation of this process in models. Here, we wanted to show that leaf phenology affects seasonal changes of isoprene emission and that is, in fact, new information for tropical forests. Author's changes in manuscript – Line 525. "However, less notable factors in tropical forests might also

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influence ecosystem isoprene emission. Here, we suggest that leaf phenology, especially when accounting for the effect of leaf demography (canopy leaf age composition) and leaf ontogeny (age-dependent, isoprene emission capacity), has an important effect on seasonal changes of the ecosystem isoprene emissions, which could play an even more important role in regulating ecosystem isoprene fluxes than light and temperature at seasonal timescales in tropical forests. To the best of the author's knowledge, these results are among the first to show the importance of leaf phenology on seasonal isoprene emissions in a tropical forest". References Alves, E. G., Harley, P., Gonçalves, J. F. C., Moura, C. E. S. and Jardine, K.: Effects of light and temperature on isoprene emission at different leaf developmental stages of *eschweilera coriacea* in central amazon, *Acta Amaz.*, 44(1), 9–18, doi:10.1590/S0044-59672014000100002, 2014.

Barkley, M. P., Palmer, P. I., De Smedt, I., Karl, T., Guenther, A. and Van Roozendaal, M.: Regulated large-scale annual shutdown of Amazonian isoprene emissions?, *Geophys. Res. Lett.*, 36(4), L04803, doi:10.1029/2008GL036843, 2009.

Barkley, M. P., Smedt, I. De, Van Roozendaal, M., Kurosu, T. P., Chance, K., Arneth, A., Hagberg, D., Guenther, A., Paulot, F., Marais, E. and Mao, J.: Top-down isoprene emissions over tropical South America inferred from SCIAMACHY and OMI formaldehyde columns, *J. Geophys. Res. Atmos.*, 118(12), 6849–6868, doi:10.1002/jgrd.50552, 2013.

Delwiche, C. F. and Sharkey, T. D.: Rapid appearance of  $^{13}\text{C}$  in biogenic isoprene when  $^{13}\text{CO}_2$  is fed to intact leaves, *Plant. Cell Environ.*, 16(5), 587–591, doi:10.1111/j.1365-3040.1993.tb00907.x, 1993.

Goldstein, A. H. and Galbally, I. E.: Known and Unexplored Organic Constituents in the Earth's Atmosphere, *Environ. Sci. Technol.*, 41(5), 1514–1521, doi:10.1021/es072476p, 2007.

Guenther, A. B., Jiang, X., Heald, C. L., Sakulyanontvittaya, T., Duhl, T., Emmons, L. K.

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and Wang, X.: The Model of Emissions of Gases and Aerosols from Nature version 2.1 (MEGAN2.1): an extended and updated framework for modeling biogenic emissions, *Geosci. Model Dev.*, 5(2), 1503–1560, doi:10.5194/gmdd-5-1503-2012, 2012.

Harley, P., Monson, R. and Lerdau, M.: Ecological and evolutionary aspects of isoprene emission from plants, *Oecologia*, 118, 109–123, 1999.

Huete, A. R., Didan, K., Shimabukuro, Y. E., Ratana, P., Saleska, S. R., Hutyra, L. R., Yang, W., Nemani, R. R. and Myneni, R.: Amazon rainforests green-up with sunlight in dry season, *Geophys. Res. Lett.*, 33, 2–5, doi:10.1029/2005GL025583, 2006.

Kesselmeier, J., Ciccioli, P., Kuhn, U., Stefani, P., Biesenthal, T., Rottenberger, S., Wolf, A., Vitullo, M., Valentini, R., Nobre, A., Kabat, P. and Andreae, M. O.: Volatile organic compound emissions in relation to plant carbon fixation and the terrestrial carbon budget, *Global Biogeochem. Cycles*, 16(4), 73-1-73–9, doi:10.1029/2001GB001813, 2002.

Kuzma, J. and Fall, R.: Leaf Isoprene Emission Rate Is Dependent on Leaf Development and the Level of Isoprene Synthase., *Plant Physiol.*, 101(2), 435–440, 1993.  
Lichtenthaler, H. K., Rohmer, M. and Schwender, J.: Two independent biochemical pathways for isopentenyl diphosphate and isoprenoid biosynthesis in higher plants, *Physiol. Plant.*, 101(3), 643–652, 1997.

Lopes, A. P., Nelson, B. W., Wu, J., Graça, P. M. L. de A., Tavares, J. V., Prohaska, N., Martins, G. A. and Saleska, S. R.: Leaf flush drives dry season green-up of the Central Amazon, *Remote Sens. Environ.*, 182, 90–98, doi:10.1016/j.rse.2016.05.009, 2016.

Loreto, F. and Sharkey, T. D.: On the relationship between isoprene emission and photosynthetic metabolites under different environmental conditions, *Planta*, 189(3), 420–424, doi:10.1007/BF00194440, 1993.

Mayrhofer, S., Teuber, M., Zimmer, I., Louis, S., Fischbach, R. J. and Schnitzler, J.-P.: Diurnal and seasonal variation of isoprene biosynthesis-related genes in grey poplar

[Printer-friendly version](#)[Discussion paper](#)

leaves., *Plant Physiol.*, 139(1), 474–484, doi:10.1104/pp.105.066373, 2005.

Monson, R. K., Harley, P. C., Litvak, M. E., Wildermuth, M., Guenther, A. B., Zimmerman, P. R. and Fall, R.: Environmental and developmental controls over the seasonal pattern of isoprene emission from aspen leaves, *Oecologia*, 99(3–4), 260–270, doi:10.1007/BF00627738, 1994.

Morton, D. C., Nagol, J., Carabajal, C. C., Rosette, J., Palace, M., Cook, B. D., Vermote, E. F., Harding, D. J. and North, P. R. J.: Amazon forests maintain consistent canopy structure and greenness during the dry season, *Nature*, 506(7487), 221–4, doi:10.1038/nature13006, 2014.

Myneni, R. B., Yang, W., Nemani, R. R., Huete, A. R., Dickinson, R. E., Knyazikhin, Y., Didan, K., Fu, R., Negrón Juárez, R. I., Saatchi, S. S., Hashimoto, H., Ichii, K., Shabanov, N. V, Tan, B., Ratana, P., Privette, J. L., Morisette, J. T., Vermote, E. F., Roy, D. P., Wolfe, R. E., Friedl, M. A., Running, S. W., Votava, P., El-Saleous, N., Devadiga, S., Su, Y. and Salomonson, V. V: Large seasonal swings in leaf area of Amazon rainforests, *Proc. Natl. Acad. Sci. U. S. A.*, 104(12), 4820–4823, doi:10.1073/pnas.0611338104, 2007.

Niinemets, U., Arneth, A., Kuhn, U., Monson, R. K., Penuelas, J. and Staudt, M.: The emission factor of volatile isoprenoids: stress, acclimation, and developmental responses, *Biogeosciences*, 7(7), 2203–2223, doi:10.5194/bg-7-2203-2010, 2010.

Niinemets, U., Loreto, F. and Reichstein, M.: Physiological and physicochemical controls on foliar volatile organic compound emissions., *Trends Plant Sci.*, 9(4), 180–6, doi:10.1016/j.tplants.2004.02.006, 2004.

Rohmer, M.: From molecular fossils of bacterial hopanoids to the formation of isoprene units: Discovery and elucidation of the methylerythritol phosphate pathway, *Lipids*, 43(12), 1095–1107, doi:10.1007/s11745-008-3261-7, 2008. Saleska, S. R., Wu, J., Guan, K., Araujo, A. C., Huete, A., Nobre, A. D. and Restrepo-Coupe, N.: Dry-season

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greening of Amazon forests, *Nature*, 531(7594), doi:10.1038/nature16457, 2016.

Samanta, A., Ganguly, S., Hashimoto, H., Devadiga, S., Vermote, E., Knyazikhin, Y., Nemani, R. R. and Myneni, R. B.: Amazon forests did not green-up during the 2005 drought, *Geophys. Res. Lett.*, 37(5), 1–5, doi:10.1029/2009GL042154, 2010.

Schnitzler, J.-P., Lehning, A. and Steinbrecher, R.: Seasonal Pattern of Isoprene Synthase Activity in *Quercus robur* Leaves and its Significance or Modeling Isoprene Emission Rates, *Bot. Acta*, 110, 240–243, 1997.

Schwender, J., Zeidler, J., Gröner, R., Müller, C., Focke, M., Braun, S., Lichtenthaler, F. W. and Lichtenthaler, H. K.: Incorporation of 1-deoxy-D-xylulose into isoprene and phytol by higher plants and algae, *FEBS Lett.*, 414(1), 129–134, doi:10.1016/S0014-5793(97)01002-8, 1997.

Wagner, F. H., Hérault, B., Rossi, V., Hilker, T., Maeda, E. E., Sanchez, A., Lyapustin, A. I., Galvão, L. S., Wang, Y. and Aragão, L. E. O. C.: Climate drivers of the Amazon forest greening, *PLoS One*, 12(7), 1–15, doi:10.1371/journal.pone.0180932, 2017.

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