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Review

Effect of land-use change and management on biogenic volatile organic compound emissions – selecting climate-smart cultivars

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ABSTRACT

Land-use change (LUC) has fundamentally altered the form and function of the terrestrial biosphere. Increasing human population, the drive for higher living standards and the potential challenges of mitigating and adapting to global environmental change mean that further changes in LUC are unavoidable. LUC has direct consequences on climate not only via emissions of greenhouse gases and changing the surface energy balance but also by affecting the emission of biogenic volatile organic compounds (BVOCs). Isoprenoids, which dominate global BVOC emissions, are highly reactive and strongly modify atmospheric composition. The effects of LUC on BVOC emissions and related atmospheric chemistry have been largely ignored so far. However, compared with natural ecosystems, most tree species used in bioenergy plantations are strong BVOC emitters, whereas intensively cultivated crops typically emit less BVOCs. Here, we summarize the current knowledge on LUC-driven BVOC emissions and how these might affect atmospheric composition and climate. We further discuss land management and plant-breeding strategies, which could be taken to move towards climate-friendly BVOC emissions while simultaneously maintaining or improving key ecosystem functions such as crop yield under a changing environment.

Key-words: BVOCs; climate adaptation; climate mitigation; cultivar selection; genetic manipulation; isoprene; land management; monoterpenes; priming.

INTRODUCTION

Between 30 and 50% of the land surface today has been transformed as a result of human activities (Ellis *et al*. 2010). The need to sustain the world's human population with food, fibre, building material and energy was the main driver for converting natural vegetation into arable cropland and pastures (Ellis *et al*. 2010). This coincided with a global population increase from an estimated less than 30 million around 8000 before present (BP; Kaplan *et al*. 2011) to approximately 7 billion today. Most of this increase has happened over the last 400 years, preceded by a slower and (averaged over time) more linear increase starting from around 1000 BP (Kaplan *et al*. 2011). At the beginning of the 21st century, the rate of global net LUC is estimated to have totalled to 2×10^5 km^2 year^{-1} (Hurtt *et al*. 2011). However, the important driving factors of human-induced land cover changes go well beyond mere population dynamics, including technology (Kaplan *et al*. 2011), and changes in economics and social values. Present LUCs differ widely in character, from the conversion of tropical rainforest into pastures and oil palm plantations to the reforestation of abandoned croplands in North America and Eastern Europe. Despite possibilities of using marginal or abandoned land for crop production, or closing yield gaps in developing nations, it will likely be necessary to convert natural grasslands and forests to new agricultural land by 2050 (Hardacre *et al*. 2013). This need to provide food and fodder will be difficult to reconcile with the supply of other ecosystem services (Naidoo *et al*. 2008), for instance climate regulation via the inclusion of terrestrial ecosystems as part of international efforts to mitigate greenhouse gas (GHG) emissions (e.g. UN-REDD; United Nations 2009; Azar *et al*. 2010).

Other than via long-lived GHGs and altered surface radiation and energy balance, the atmospheric and climate effects of LUC and land-cover change have not yet shifted fully into the focus of the climate change community. However, with the increasing consideration of climate effects of atmospherically short-lived pollutants alongside air quality (AQ) concerns (Andreae 2007; Arneth *et al*. 2009; Shindell *et al*. 2012), this is beginning to change. Biogenic volatile organic compounds (BVOCs) are among the compounds receiving increasing attention in this context. Because of the large mass emitted globally from terrestrial vegetation, and in particular the high atmospheric reactivity of the volatile isoprenoids (i.e. isoprene and monoterpenes), it is well established that these compounds exert a strong control on the burdens of tropospheric ozone, methane and secondary aerosols (Atkinson & Arey 2003; Arneth *et al*. 2010). Longer-lived compounds such as methanol or acetone tend to be dispersed

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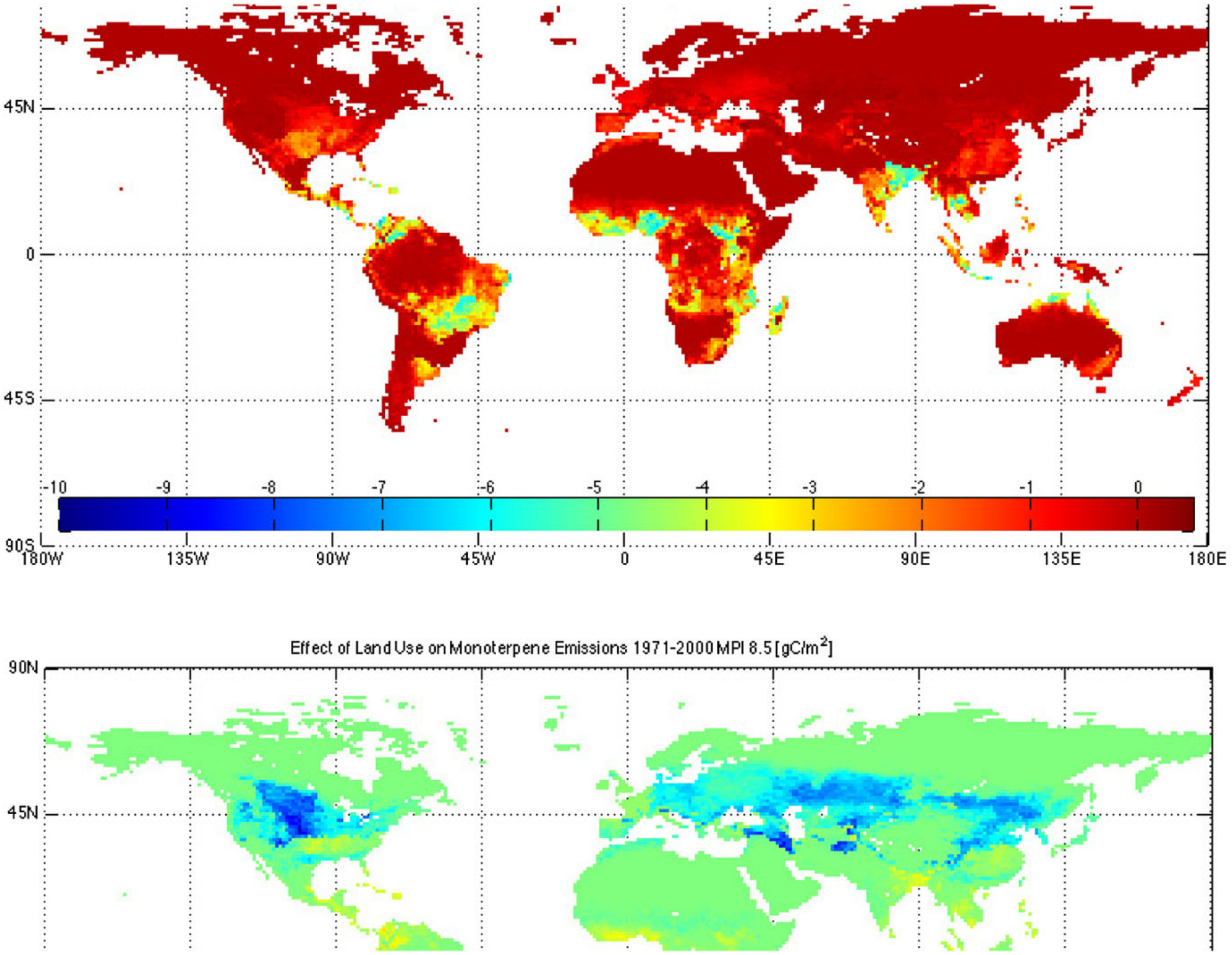
on a continental scale and throughout the troposphere before oxidation (Tie *et al*. 2003; Arnold *et al*. 2005), thereby diluting their impact.

Conversion of natural vegetation into cropland and pastures is expected to decrease isoprene and monoterpene emissions substantially, especially if this conversion is through deforestation (Fig. 1). Irrespective of the exact vegetation type, woody vegetation has much larger emission potential [defined as BVOC emissions under a set of standard environmental conditions (see, e.g. Niinemets *et al*. 2010a)] than herbaceous or crop vegetation (see, e.g. Kesselmeier *et al*. 2002). Reforestation, however, will have the opposite effect. Further, some species, such as oil palm and fast-growing tree species (poplar and willow), used in short-rotation coppice (SRC) have very high BVOC emissions, exceeding those of natural forests (Hewitt *et al*. 2009; Ashworth *et al*. 2012).

BVOC emissions can be controlled and/or manipulated by the selection of specific cultivars as well as by field management so that the next generations of crop and bioenergy cultivars could also be optimized during the breeding process for specific features of constitutive and inducible BVOC emissions. One aim could be to favour and/or create cultivars that impact less on atmospheric processes with low BVOC emission potential while at the same time selecting for BVOCs that could increase plant resistance against herbivores and pests, or the tolerance against abiotic stresses (Loreto & Schnitzler 2010; Mumm & Dicke 2010). Several novel biological and biotechnological tools are available to alter the BVOC emission potentials of cultivars/ecotypes, including genetic manipulation, priming by co-culturing or by using chemical elicitors. Cultivars with altered BVOC emission potentials might better tolerate, resist and overcome combined stressful conditions in the future.



Effect of Land Use on Monoterpene Emissions 1971-2000 MPI 8.5 [gC/m^2]

Figure 1. Present-day (average 1971–2000) isoprene (above) and monoterpene (below) emissions (g C a^{-1}) expressed as the difference of with without human land cover change. The shown examples are using the Dynamic Global Vegetation Model (DGVM) LPJ-GUESS, using land cover estimates as in Hurtt *et al*. (2011) and climate based on the General Circulation Model MPI-ESM (for more details, see Ahlström *et al*. 2012). Adapted from Hantson *et al*. (in prep.)

THE INTERPLAY BETWEEN LUC, CLIMATE CHANGE AND BVOC EMISSIONS FROM VEGETATION

The role of LUC in the climate system

Historical LUCs have contributed notably to climate warming (Le Quere *et al*. 2009; Kaplan *et al*. 2011) as carbon (C) emissions arising from past LUC activities to the atmosphere exceeded LUC-related land C sinks. Conversion of natural ecosystems into cropland and pastures, mostly through deforestation, has contributed an estimated release of more than 150 Pg C into the atmosphere, one-third of the approximate total anthropogenic C emissions since 1850 (Le Quere *et al*. 2009; Houghton *et al*. 2012). Large uncertainties are associated with these estimates due to the absence of observational constraints and methodological differences in the various model studies that seek to assess LUC effects (Houghton *et al*. 2012; T.A.M. Pugh *et al*. unpublished data). In addition, ca. 50% of the observed increase in atmospheric nitric oxide (N_2O) over the same time period has been attributed to agricultural fertilizer use (Zaehle *et al*. 2011), while anthropogenic methane (CH_4) emissions are dominated by agriculture, particularly from ruminants, rice paddies and manure management (Environmental Protection Agency 2012; Kirschke *et al*. 2013). CO_2, CH_4 and N_2O are potent GHGs and recent policy (Pittel & Rubbelke 2008; Jones *et al*. 2013; Mackey *et al*. 2013) has considered land management measures to mitigate global climate impacts as afforestation or avoided deforestation can either increase the terrestrial C sink strength or prevent additional C emissions to the atmosphere.

Climate change arising from changes in the sources and sinks of C- and N-containing GHGs continues to operate over centuries because these gases are long-lived in the atmosphere and also because changes in vegetation and soil C and N pools operate over decades to centuries. In addition, a LUC–climate response arises from changes in the land surface that alter biophysical processes controlling the surface energy balance. For instance, conversion of forest into crop vegetation decreases surface roughness and mixing of the near-surface air increases the fraction of radiation reflected back into the atmosphere and changes the partitioning of the net radiation received at the surface into evapotranspiration (latent heat flux) and sensible heat flux (Pitman *et al*. 2009; Arora & Montenegro 2011). Compared with the GHG climate impacts, the biophysical climate effects from LUC are thus stronger regionally, and realized over a period of a few months to several decades following a LUC event (Pitman *et al*. 2009; Arora & Montenegro 2011) as it is the initial changes in land cover that tend to have the strongest effects on the surface radiation and energy balances.

The role of BVOCs in the climate system

Like the biophysical LUC climate impacts, climate effects of BVOCs are regionally heterogeneous. Their climate importance is well acknowledged, operating via their effects on the burdens of CH_4, tropospheric O_3 and secondary organic aerosol (SOA) (Atkinson & Arey 2003; Arneth *et al*. 2010; Carslaw *et al*. 2013). However, the oxidation pathways of BVOCs are highly complex (e.g. Jenkin *et al*. 2003, 2012), and even for the most studied compounds such as isoprene, important aspects remain unclear (Di Carlo *et al*. 2004; Lelieveld *et al*. 2008; Crounse *et al*. 2011). In a number of field experiments in remote forests, detailed measurements of the hydroxyl radical (OH), the principal atmospheric oxidant, could not be reconciled with isoprene mixing ratios based upon state-of-the-art air chemistry (Lelieveld *et al*. 2008; Hofzumahaus *et al*. 2009; Pugh *et al*. 2010, 2011). Correct simulation of the impact of BVOCs on OH is crucial for determining the lifetime of CH_4 in the atmosphere, for which the influence of isoprene alone is of the order of 10% (Young *et al*. 2009). Recent work indicates strong evidence of hitherto unknown HO_x ($OH + HO_2$) regeneration under the low NO_x ($NO + NO_2$) mixing ratio typical of remote areas (Archibald *et al*. 2011; Taraborrelli *et al*. 2012), although the mechanism remains uncertain (e.g. Warwick *et al*. 2013). A strongly non-linear behaviour in relation to NO_x mixing ratios is typical of BVOC chemistry (Stevenson *et al*. 2006; Collins *et al*. 2010; Lamarque *et al*. 2010) and BVOCs can either increase or decrease tropospheric O_3 mixing ratios depending upon the local ratio of BVOCs to NO_x concentrations. Typically, increased BVOC emissions would suppress O_3 formation in remote locations where NO_x mixing ratio is low (known as NO_x-limited conditions) and increase it in polluted ones (known as VOC-limited) (Pyle *et al*. 2011). Besides their importance for gas-phase chemistry, isoprene (C5), monoterpenes (C10) and sesquiterpenes (C15) are crucial isoprenoid precursors for formation and/or growth of SOA (Bonn & Moortgat 2003; Claeys *et al*. 2004; Tunved *et al*. 2006; Laaksonen *et al*. 2008; Carslaw *et al*. 2010). Conversely, under some circumstances, isoprene emissions have been shown to suppress new particle formation from other isoprenoids (Kiendler-Scharr *et al*. 2009, 2012). As for O_3, the level of NO_x can be crucial for organic aerosol formation. Increasing NO_x tends to reduce biogenic SOA formation from isoprene and monoterpenes, while increasing it for some sesquiterpenes (Kroll *et al*. 2005, 2006; Ng *et al*. 2007; Wildt *et al*. 2014).

Improved understanding of BVOC emission patterns is crucial in the air chemistry–climate system. Firstly, for many of the short-lived climate pollutants (SLCPs), no observations of their pre-industrial baseline exist, calculations of the pre-industrial to present-day radiative forcing thus has to rely upon simulations of pre-industrial conditions, which introduces large uncertainties in the derived values (Mickley *et al*. 2001; Carslaw *et al*. 2013). Secondly, future changes in atmospheric BVOC loading have the potential to counteract some pollution and climate effects of anthropogenic emission control. For instance, a synthesis of field data identified potentially very strong regional climate cooling feedbacks from SOA formation by BVOCs (Paasonen *et al*. 2013), while other direct and indirect climate feedback can also be induced for isoprene–ozone interactions (Sitch *et al*. 2007; Arneth *et al*. 2010).

Future (and past) responses of isoprenoid BVOC emissions to climate and atmospheric CO_2 mixing ratio, in isolation and combined, are still under debate (Arneth *et al*. 2007a,b; Monson *et al*. 2007; Niinemets *et al*. 2010a). Briefly, warmer temperatures and higher light intensity stimulate leaf BVOC emissions – at least in short term directly by enhanced cellular production rates. Moreover, warmer environment can foster higher leaf area index and hence larger emitting leaf area. The response to enhanced CO_2 is more contentious for isoprene studies showing declining emissions at leaf scale in enhanced CO_2 environment (for a summary of studies, see Arneth *et al*. 2011). How these effects emerge on the canopy scale is less clear. Sun *et al*. (2013) combined observations under controlled-environment grown aspen with a simple growth model. While their study confirmed reduced leaf-level isoprene emissions for plants grown under above-ambient CO_2 mixing ratios, the simultaneously strongly enhanced canopy leaf dry mass, and leaf area index, counteracted the results obtained at single leaves. A number of older studies have pointed to similar interactions between measured leaf-based emissions and canopy structural changes (Centritto *et al*. 2004; Possell *et al*. 2005). These studies indicate that for projections of future isoprene and monoterpene emissions, plant growth dynamics are equally important as leaf-scale physiology, and that BVOC emission scenarios must be combined with dynamic global vegetation models (DGVMs) responding to environmental changes. Moreover, it remains to be shown whether simple CO_2 multipliers (Arneth *et al*. 2007b; Heald *et al*. 2009; Niinemets *et al*. 2010a), as currently used in BVOC emission modules, combined with DGVMs are sufficient, or whether a stronger process-based representation could be parameterized that internalizes BVOC emissions by linking them more strongly to photosynthesis (Morfopoulos *et al*. 2013). In addition, it is unclear how different variables (leaf physiology, canopy effects, climate change, LUC) simultaneously with atmospheric CO_2 mixing ratio affect BVOC emissions. Sharkey and Monson (2014) showed, for example, that the CO_2 effect on isoprene emission can be tempered by increasing temperature or heat waves.

Interactions of LUC and BVOCs

Simulation experiments have demonstrated up to 40% reductions in global isoprene emission under future LUC (Heald *et al*. 2009; Ganzeveld *et al*. 2010; Squire *et al*. 2014), with much larger reductions regionally where the deforestation occurs (Lathière *et al*. 2006, 2010; Wu *et al*. 2012). One study projected a 7% reduction in global tropospheric O_3 from a 45% reduction in isoprene emissions (Squire *et al*. 2014), which would be consistent with an increase in CH_4 lifetime of several percentage (Young *et al*. 2009). However, the demonstrable effects of LUC on BVOC emissions do not necessarily lead to substantial global-scale changes in burdens of associated SLCPs, especially in model exercises that also account for the simultaneously occurring changes in climate and/or atmospheric CO_2 levels (Wiedinmyer *et al*. 2006; Wu *et al*. 2012; Hardacre *et al*. 2013; Tai *et al*. 2013). This arises because of the large spatial variability both in the influence of LUC on BVOC emissions and in the atmospheric chemistry. In a changing environment, the additional accounting of LUC-induced changes in BVOCs can result both in strong decreases and in increases of, for example, tropospheric O_3 or SOA, and resulting regional radiative forcing. In analogy to the biophysical climate effects of LUC, assessing radiative forcing impacts associated with BVOC-LUC interplay is misleading when solely a global total value is calculated, as warming or cooling forcing in different regions can cancel. Thus, regional-scale analyses are fundamental when analysing effects of altered BVOC emissions on pollution levels and climate change (Young *et al*. 2009; Wu *et al*. 2012; Hardacre *et al*. 2013; Tai *et al*. 2013).

Regional aspect of LUC–AQ–climate interactions

The strong and non-linear temperature and (in the case of isoprenoids) light dependence of many BVOC emissions means that the absolute influence exerted by a given form of LUC will be enhanced in warm regions with limited cloud cover. For instance, an isoprene emission rate increase of 1 mg (isoprene) $m^{-2}\ h^{-1}$ at 20 °C might become an emission of 4 mg $m^{-2}\ h^{-1}$ at 30 °C (e.g. Guenther *et al*. 2006). Likewise, because of the highly non-linear nature of the atmospheric chemistry, the effects of BVOCs depend strongly upon local atmospheric conditions, and thus, a given BVOC emission can generate a wildly different response in different regions. In addition to the local NO_x mixing ratio (see previous section), shortwave radiation flux density also strongly affects O_3 formation, with higher O_3 formation potential during summer or at lower latitudes. Here, a selection of real and hypothetical examples is used to illustrate the effects of some of the most common types of land conversion on BVOC emissions and atmospheric chemistry. The effects of these conversions on isoprene emissions, O_3 mixing ratios and SOA concentration are summarized in Fig. 2.

Forest-to-cropland conversion

Large-scale conversion of forested land to cropland has not only been a historical phenomenon (Kaplan *et al*. 2011; Klein Goldewijk *et al*. 2011) but it still continues today, especially in tropical areas (Houghton *et al*. 2012). Conventional agricultural crops, such as wheat (*Triticum* spp.), maize (*Zea mays*) and rice (*Oryza* spp.), which often replace the forested land, are regarded as being low-emitting species (Copeland *et al*. 2012, Table 1), as are sugarcane and soybean (Kesselmeier & Staudt 1999; Wiedinmyer *et al*. 2004; Winter & Rostás 2008; Moraes *et al*. 2009), the cultivation of which is expanding in the tropics due to the demand for biofuel and livestock feedstuff (Hardacre *et al*. 2013). In contrast, forests often contain strong isoprene- and monoterpene-emitting species, particularly in the tropics (Kuhn *et al*. 2004, 2007; Karl *et al*. 2007, 2009; Langford *et al*. 2010). Thus, a large-scale conversion of forest to crops leads to a strongly reduced emission of reactive BVOCs.

Using a future land-use scenario (IPCC A1B), Wu *et al*. (2012) simulated a decrease in surface isoprene mixing ratio

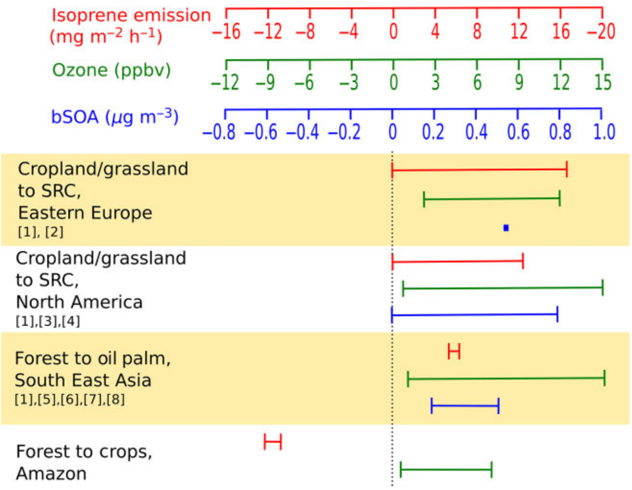


Figure 2. Range of changes in basal emission rate of isoprene, mean ozone mixing ratios and mean biogenic secondary organic aerosol (bSOA) concentration for four different land-use change scenarios, as reported by published studies. Ozone and aerosol changes are presented at the highest spatial and temporal resolution reported by the study (ca. 10–100 km, and either 8 h, daily or monthly). Underlying studies are indicated by numbers: [1] Ashworth *et al.* (2012), [2] Ashworth *et al.* (2013), [3] Porter *et al.* (2012), [4] Chen *et al.* (2009), [5] Hewitt *et al.* (2009), [6] Hewitt *et al.* (2010), [7] Pyle *et al.* (2011), [8] Warwick *et al.* (2013), [9] Hardacre *et al.* (2013), [10] Wu *et al.* (2012), [11] Squire *et al.* (2014), [12] Guenther *et al.* (2006).

over the Amazon region resulting from forest-to-cropland conversions. Due to the low NO$_x$ mixing ratios over much of this region, they calculated increases in the June–August mean O$_3$ mixing ratio of up to 7 ppbv in 2100, as compared to that in 2000. Squire *et al.* (2014) reported similar results based upon the same scenario, but using a different suite of models. On a more immediate timescale, Hardacre *et al.* (2013) used a land-use model to project a range of plausible cropland scenarios for tropical South America for 2030, and reported a strong reduction in isoprene emissions, leading to a 0.4–1 ppbv increase in tropospheric O$_3$.

Substantial variations in the size of modelled O$_3$ mixing ratio changes result from (1) differences in LUC scenario; (2) model grid size (Ito *et al.* 2009; Pugh *et al.* 2013); and (3) chosen emission factors for plant species (Niinemets *et al.* 2010a,b), but (4) also the treatment of organic nitrates, which are formed during BVOC oxidation. NO$_x$ loss due to organic nitrate formation can substantially reduce O$_3$ formation in low NO$_x$ regions, but the details remain poorly understood (Ito *et al.* 2009; Wu *et al.* 2012). A decrease in nitrate formation following forest-to-cropland conversion, and associated lower isoprenoid BVOC emissions, may be counteracted to some extent by a decrease in uptake of NO$_x$ in the lower crop canopies (e.g. Ganzeveld *et al.* 2010) or increased emissions of oxidized nitrogen due to fertilizer use.

Considering present-day O$_3$ mixing ratios in the remote Amazon of ca. 20 ppbv (e.g. Lelieveld *et al.* 2008), an addi-

Table 1. Biogenic volatile organic compound emission potentials of different crop and forestry species

	Species		Isoprene		Monoterpenes (or estragole when noted)	
	Latin	Common	Leaf scale (µg g DW^{-1} h^{-1})	Canopy (µg m^{-2} h^{-1})	Leaf scale (µg g DW^{-1} h^{-1})	Canopy (µg m^{-2} h^{-1})
Crops	*Triticum* spp.	Wheat	0.01[1]		n.d.[2]	
	Zea mays	Maize	0[1]	0[3]	0.5[1]	
	Oryza spp.	Rice	n.d.[4]	3.7[5]	0.4[4]; 0.5[1]	0.15[5]
Oil palm	*Elaeis guineensis*	Oil palm	0–20[6]	12 480[a,7] 8850[a,8]	1[9,estragole]	102[a,8]; 113[a,7] 1234[a,7,estragole]; 440[9,estragole]
Woody biomass plants	*Populus* spp.	Poplar	0–50[10] 60[11] >87[a,12]	6580–9410[a,13]	0.01–8[10]	
	Salix spp.	Willow	20[14]34[11] 0.2–76[10] >61[a,12]	1000[14]	0.1–10[10]; 0.8[1]	
	Eucalyptus spp.	Eucalyptus	20[11], 15–49[15]	4000–5000[15]	3[11] 5.4[1] 0.7–5.2[15]	200–600[15]
Perennial biomass plants	*Miscanthus × giganteus*	Elephant grass	0.005[b,16]	n.d.[14]		
	Panicum virgatum	Switch grass	0.018[b,17]		0.038[17]	
	Arundo donax	Giant cane	34[18], 142[19]			

The emission potentials are for standard conditions [30 °C and photosynthetically active radiation (PAR) 1000 µmol m^{-2} s^{-1}], unless otherwise noted.

[a] Converted from µg g carbon dry weight (DW)$^{-1}$ h^{-1} to µg g matter DW^{-1} h^{-1}.

[b] Includes isoprene and other C5 compounds.

1. Karl *et al.* (2009); 2. Piesik *et al.* (2010), 22 °C, ambient light; 3. Hardacre *et al.* (2013); 4. Bao *et al.* (2008); 5. Redeker *et al.* (2003); 6. Wilkinson *et al.* (2006); 7. Fowler *et al.* (2011), ambient conditions; 8. Hewitt *et al.* (2009), 27, 9 °C and ambient light; 9. Misztal *et al.* (2010); 10. Hakola *et al.* (1998), ambient conditions; 11. Simpson *et al.* (1999); 12. Isebrands *et al.* (1999); 13. Westberg *et al.* (2000); 14. Copeland *et al.* (2012); 15. Street *et al.* (1997); 16. Crespo *et al.* (2013); 17. Eller *et al.* (2011), 30 °C and PAR 500 µmol m^{-2} s^{-1}; 18. Hewitt *et al.* (1990), measurements in 25 °C and PAR 1000 µmol m^{-2} s^{-1}; 19. Owen *et al.* (2001).

n.d., not detected.

tional 7 ppbv O_3 represents a very large change. However, the level remains too low to bring about a substantial O_3 toxicity effect on plants and thus to indirectly influence climate through reducing the biospheric C uptake (Sitch *et al.* 2007), while the direct radiative forcing from this increase would be of the order of 0.02 W m^{-2}. [Assume that the 7 ppbv increase is valid across a 1000 m depth of the atmosphere, which has an average density of 2.3×10^{19} molecules cm^{-3}. Radiative forcing is taken as 0.042 W m^{-2} DU^{-1}, where DU is Dobson Unit, a measure of integrated atmospheric O_3 column density equivalent to 2.69×10^{16} molecules O_3 cm^{-2} (Ramaswamy *et al.* 2001, section 6.5.2.2)]. Wu *et al.* (2012) also simulated a relatively substantial reduction in biogenic SOA concentration of up to 0.5 μg m^{-3}, compared with typical tropical forest aerosol concentrations (e.g. 1.5–1.6 μg m^{-3}; Hewitt *et al.* 2010; Huffman *et al.* 2012). Organics can modify aerosol reflectivity, as well as their potential to act as cloud condensation nuclei, so the ultimate climatic effect of SOA changes is not well understood, although recent work suggests that such aerosol may have a substantial cooling effect (Boucher *et al.* 2013; Paasonen *et al.* 2013).

In contrast to forest-to-crop conversion in a low NO_x environment, similar LUC under high NO_x mixing ratios are likely to yield a decrease in local tropospheric O_3 mixing ratio. Unlike the remote tropics, in the northern mid-latitudes, especially North America, Europe and Eastern China, the background atmosphere is often in a state of VOC limitation, or on the boundary between the two limitation regimes. Conversion of large forest areas to cropland would tend to decrease O_3 mixing ratios and organic aerosol concentrations in these regions (e.g. Chen *et al.* 2009; Wu *et al.* 2012). However, the current tendency for LUC in these regions is more towards afforestation or cropland abandonment (Alcantara *et al.* 2013; Erb *et al.* 2013), which has the opposite effect (analogous to the biofuel example in the section Conversion for biofuels).

While these examples should be broadly representative for conversions of forest to agriculture globally, at least as regards isoprene, there is considerable variation in the literature over the appropriate isoprene emission factors for generic grasses and crops. Lathière *et al.* (2006) and Ashworth *et al.* (2012) used isoprene emission factors for crops of the same order of magnitude as for broadleaf forests (5 and 16 μg g dry matter $(DM)^{-1}$ h^{-1} as, respectively). Conversely, simulations based upon more recent experimental data tend to use much lower crop emission factors, for example, Karl *et al.* (2009) and Beltman *et al.* (2013) used 0–0.5 μg g DM^{-1} h^{-1}, and Guenther *et al.* (2006) gave canopy emission factors for crops two orders of magnitude smaller than those for broadleaf trees. This variation reflects, to a large degree, the limited measurements available at the time of formulation of the widely used Guenther algorithm (Guenther *et al.* 1995). For generic crops, the balance of evidence seems to support low isoprene emission factors; however, the choice will have profound impacts on the results of LUC studies and must be taken into account when assessing past studies. For monoterpenes, there is a very wide spread in the measurements, but the typical monoterpene emission factors for crops and broadleaf trees seem to be similar (Ashworth *et al.* 2012, see also Table 1), although both are less than for typical needle-leaf species (Guenther *et al.* 1995; Karl *et al.* 2009). Clearly, species-specific emission factors should be used wherever possible in assessing the outcomes of LUC.

Conversion for biofuels

Although agricultural crops typically have low BVOC emissions relative to the forest species they replace, there are many woody 'crop' species that emit much higher levels of BVOCs than the typical natural vegetation (Table 1). Key examples are oil palm (*Elaeis guineensis*) and fast-growing tree species like poplar (*Populus* spp.), willow (*Salix* spp.) or eucalyptus (*Eucalyptus* spp.). These species are often used in plantation systems for cellulose production or more recently in SRC for bioenergy generation.

Oil palm. Oil palm is a highly important commercial crop, grown in large monoculture plantations throughout the tropics, but especially in South-East Asia. In Malaysia, 13% of land area was covered by oil palm plantations in 2009 (Hewitt *et al.* 2009). In Indonesian Borneo, the figure is currently 6%, but allowed leases cover 23%, and the potential maximum plantable area is 90% (Carlson *et al.* 2012; Warwick *et al.* 2013). The majority of these plantations replace tropical rainforest. Unlike rainforest, oil palm emits almost no monoterpenes, but its isoprene emission potential is approximately five times higher (Hewitt *et al.* 2009; Table 1). In a field study measuring isoprene fluxes above rainforest and oil palm canopies located within 60 km of each other, isoprene emissions above oil palm were on average 10 times higher than those over the rainforest (Langford *et al.* 2010; Misztal *et al.* 2011), reflecting also the higher temperatures and lower cloudiness over the oil palm plantation (Fowler *et al.* 2011).

Despite the huge increase in isoprene fluxes, the measured O_3 mixing ratio over both oil palm and rainforest landscapes was virtually identical (Hewitt *et al.* 2009, 2010). This is consistent with landscape-scale model simulations that showed a strongly NO_x-limited O_3 formation regime in Borneo (Hewitt *et al.* 2009). Increased NO_x emissions resulting from fertilization and processing plants only proved sufficient to balance the O_3 loss due to the additional BVOC. Yet the simulations also showed that an increase in NO_x mixing ratio to ca. 3–5 ppbv, typical of rural Western Europe, would result in O_3 mixing ratios exceeding 100 ppbv. Such an increase would have a substantial direct radiative forcing effect (of the order of 0.3 W m^{-2} following the previous calculations) and notably reduce the C sink potential of most plants (Sitch *et al.* 2007), as well as having considerable immediate implications for crop yields and human health.

Similarly, notwithstanding the much reduced monoterpene emissions, a small increase in organic aerosol concentrations was found over the oil palm relative to the rainforest (0.67 μg m^{-3} versus 0.48 μg m^{-3}; Hewitt *et al.* 2010). This at least partially reflects a higher contribution from isoprene to biogenic SOA (MacKenzie *et al.* 2011). Semi-volatile sesquiterpenes and phenylpropanoids may also be emitted from either/both landscapes and likely have a very high aerosol yield (Ng *et al.* 2007). Unfortunately, difficulties in their measurement have limited their assessment in the field thus far. However, emission of estragole, a volatile phenylpropanoid, which is important for attracting pollinators and for which a very high aerosol yield has been reported (Lee *et al.* 2006), was of comparable magnitude to monoterpene emissions from the rainforest (Misztal *et al.* 2010) and quite likely contributes notably to the aerosol mass. An assessment of the implications of changing land-use that only includes isoprene and monoterpenes, the most commonly considered reactive BVOCs, could therefore predict the wrong sign for aerosol concentration change.

Larger scale chemistry-transport model studies considering the effect of a widespread expansion of oil palm plantations and associated NO_x emissions on the whole of Borneo found O_3 and biogenic SOA increases of up to 15 ppbv (70%) and 0.5 $\mu g\ m^{-3}$ (12%), respectively, in some areas, with smaller, but notable effects stretching 1000 s km downwind (Pyle *et al.* 2011; Ashworth *et al.* 2012; Warwick *et al.* 2013). However, Hardacre *et al.* (2013) calculated a non-significant impact on surface isoprene mixing ratios and chemistry when spreading oil palm production more globally rather than concentrating in South-East Asia, although the coarse scale of this analysis ($4° \times 5°$) precludes the analysis of local effects. From the standpoint of atmospheric composition, the planting of oil palms and similar high isoprene-emitting crops in the tropics should have a minimal influence so long as background NO_x mixing ratios are kept low and the BVOC emissions are not advected over a high NO_x region before becoming oxidized and dispersed.

SRC plantations and alternatives. Quite a different scenario can be drawn for SRC plantations in Europe where the high background NO_x mixing ratios facilitate increases in O_3 formation. Isoprene emissions from typical SRC species are two to six times above typical deciduous forest emission rates (Simpson *et al.* 1999). Ashworth *et al.* (2013) simulated the effect of converting all excess crop, pasture and wasteland in Europe to SRC, and found an increase in continental isoprene emissions from 11.5 to 16 Tg C a^{-1}, sufficient to give monthly mean O_3 increases of up to greater than 12 ppbv over heavily planted regions, and 6 ppbv over Eastern Europe as a whole, where the planting in the model exercise was concentrated. Using more conservative SRC planting scenarios, Beltman *et al.* (2013) and Hardacre *et al.* (2013) found comparable results. Ashworth *et al.* (2012) calculated an increase in monthly mean biogenic SOA concentration of up to 0.6 $\mu g\ m^{-3}$ in Eastern Europe due to SRC planting. Similar effects on O_3 and aerosol have been simulated for North America for both SRC and the growth of the giant cane *Arundo donax* (Wiedinmyer *et al.* 2006; Ashworth *et al.* 2012; Porter *et al.* 2012; Hardacre *et al.* 2013).

Several low BVOC-emitting crop species can function as a bioenergy source (Sims *et al.* 2006; Karl *et al.* 2009; Eller *et al.* 2011; Crespo *et al.* 2013) and may offer advantages over SRC in the polluted middle latitudes in terms of their influence on atmospheric composition. However, many of the traditional crops have less favourable biomass yield, as compared to woody bioenergy species (Aylott *et al.* 2008). Moreover, in the case of maize, the high emission of N_2O and nitrate leakage in cultivation must be weighed against the effect of low BVOC emissions (Crutzen *et al.* 2007). Switchgrass and elephant grass (*Miscanthus* × *giganteus*) are both low BVOC emitters, with an isoprene emission potential being below 0.01 μg g dry weight $(DW)^{-1}\ h^{-1}$ (Eller *et al.* 2011; Copeland *et al.* 2012; Crespo *et al.* 2013; Table 1). Both crops are good candidates for use in second-generation biofuel production, as their emission rates are much lower than those expected from eucalyptus or poplar plantations (Table 1; Eller *et al.* 2011) and the annual energy yields under a temperate climate are comparable to those of woody biomass species (McKendry 2002). Another perennial grass with potential as a biofuel source is Black bamboo (*Phyllostachys nigra*); however, the species is a strong isoprene emitter, with emission potentials (28.5 μg g $DW^{-1}\ h^{-1}$) of similar magnitude to oil palm (Crespo *et al.* 2013; Table 1).

Influence of land management processes on BVOC emissions

In addition to the effects of abiotic factors such as light intensity, temperature, atmospheric CO_2 mixing ratio and nutrition, there are a range of processes related to LUC and other human activities that are capable of altering BVOC emissions. In contrast to our understanding of environmental stresses and the possible future climate change on BVOC emissions (Holopainen & Gershenzon 2010; Loreto & Schnitzler 2010), how land management will influence the atmosphere through changes in BVOC emissions is largely unknown. Land management, for example, by harvesting, irrigation and fertilization, influences BVOC emission rates and pattern both directly and indirectly (Fares *et al.* 2008; Ibrahim *et al.* 2008; Ormeno *et al.* 2009; Malkina *et al.* 2011; Crespo *et al.* 2013; Davis *et al.* 2013).

Harvesting and post-harvesting

BVOC emissions can be induced through direct rupture of storage organs, that is, mechanical wounding, which can occur through land clearing, harvest and management. BVOC emissions from cutting can be particularly high for conifers; Haapanala *et al.* (2012) measured monoterpene emissions from a clear-felled pine forest in Finland that were more than eight times higher over the growing season than typical emissions from an intact forest. Scaled-up estimates suggested that cutting of Scots pine (*Pinus sylvestris*) in Finland increased the annual monoterpene emission from those forests by 10%. Given a typical monoterpene emission factor for Scots pine of 1.2 mg $m^{-2}\ h^{-1}$, the direct flux from harvesting is substantial, with potential to affect both biogenic SOA and O_3 loading over clear-cut areas. Although most of these emissions were believed to come from storage, Haapanala *et al*. (2012) also speculated whether microorganisms might produce additional monoterpenes from litter decay. This degradation process of plant materials might also result in substantial BVOC emissions from cut trees even when they lack a large monoterpene storage capacity.

Large relative increases in sesquiterpene emissions following cutting have been observed in heathland ecosystems (Rinnan *et al*. 2013). However, the total sesquiterpene fluxes were relatively small, peaking at around 0.1 mg m^{-2} h^{-1} on the day of cutting, and declining rapidly thereafter. In the Eastern US, harvesting of forests was shown to increase isoprene but decrease monoterpene emissions (Purves *et al*. 2004). Other examples from Europe showed that hay harvesting in the alps could influence the local AQ on a short-term basis (Karl *et al*. 2001) with short-term total BVOC fluxes up to 8.7 mg C m^{-2} h^{-1} (Ruuskanen *et al*. 2011). In general, it appears, however, that harvesting of non-woody ecosystems is not a major, long-term source of reactive BVOCs.

In addition to the impact of harvesting itself, different post-harvesting procedures can influence BVOC emissions. Emissions from freshly cut and shredded leaves and wood of eucalypts, for example, were ca. 2.35 mg C g DW^{-1} from leaf mulch and wood chips integrated over 48 h with the highest emission rate occurring directly after cutting (Kim *et al*. 2011). Ghirardo and colleagues (personal communication) measured a total BVOC-released C loss from poplar wood chips of ca. 0.028% (of DW C) during 6 weeks of storage. Lower temperatures decreased BVOC emissions by almost one-third but did not impair the drying process, suggesting that proper management can optimize the drying for minimal BVOC release. Post-harvesting processes of cereals also release BVOCs; Malkina *et al*. (2011) reported 80 different volatile compounds, predominantly short-chain alcohols, released from maize, alfalfa (*Medicago sativa*), wheat and oat (*Avena sativa*) grain silages. Beside the post-harvesting treatment itself, the seasonal stage at the time of harvesting can affect the release of BVOCs (Crespo *et al*. 2013).

Fertilization

Nitrogen fertilization can, in general, be expected to increase isoprenoid emissions by increasing leaf photosynthetic capacity and thus enabling higher isoprenoid biosynthesis (Blanch *et al*. 2007; Ormeno *et al*. 2009). In maize, BVOC emissions from unfertilized or little-fertilized maize were minimal in comparison to heavily fertilized plants (Gouinguene & Turlings 2002). Isoprenoid production in pine trees also increases due to higher N availability (McCullough & Kulman 1991; Ormeno *et al*. 2009), although opposite results also exist (Blanch *et al*. 2007). However, such interactions with N are complex as N fertilization might be expected to affect the oxidation of BVOCs in the lower atmosphere by increasing NO_x emission from the soil (see also the sections The role of BVOCs in the climate system and Regional aspect of LUC-AQ-climate interactions).

Phosphorus levels can also influence isoprene emission rates. Fares *et al*. (2008) showed lower isoprene emission under higher concentrations of phosphorus in the soil. Interestingly, and so far unexplained, isoprene emission was uncoupled from photosynthetic rate under high phosphorus concentrations (Fares *et al*. 2008).

Besides constitutive emissions, the plant nutritional status also influences pest-induced BVOC emissions (Ibrahim *et al*. 2008). Oilseed rape plants grown at high soil nutrient levels showed higher emissions of several different BVOCs in comparison with infested plants at a low soil nutrient level. Moreover, compared with wild cultivars, sesquiterpene (α-farnesene) and homoterpene [(E)-4,8-dimethyl-1,3,7-nonatriene (DMNT)] emissions from infested transgenic *Bt*-oilseed rape (expressing the cry1Ac endotoxin gene from *Bacillus thuringiensis*) were more sensitive to the fertilization level (Ibrahim *et al*. 2008). This may have complex implications as DMNT and α-farnesene are important cues in plant–herbivore interactions (Kappers *et al*. 2005; Ghirardo *et al*. 2012).

Irrigation

Irrigation *per se* is a little studied topic in the context of BVOCs, and at present, no clear answer can be given in which direction land management by irrigation alters BVOC emissions. A few observations have shown that monoterpene and isoprene emissions in oaks and isoprene emission in poplar are diminished by severe drought stress (Brüggemann & Schnitzler 2002; Fortunati *et al*. 2008; Peñuelas *et al*. 2009) and that emission levels recovered by re-irrigation (Fortunati *et al*. 2008; Peñuelas *et al*. 2009). Generally, it seems that isoprene and monoterpene emission potentials of trees become impaired only under severe, long-term drought conditions, while moderate water limitations have no influence on emission potentials (Loreto & Schnitzler 2010).

BVOC, LUC AND CLIMATE CHANGE MITIGATION AND ADAPTATION

Breeding and phenotyping to decrease constitutive and induced BVOC emissions

Awareness that BVOC emissions from different species and cultivars can vary greatly is maybe the simplest starting point for species selection to manage BVOCs and hence their AQ and climate impacts. For several species and hybrids of *Populus* spp., a large number of genotypes have been analysed to allow the cultivation of appropriate plants under different climatic conditions (Calfapietra *et al*. 2010). Biomass production rates from poplar are highly variable according to the clone, climate and other environmental constrains, with woody biomass production often around 8–12 Mg DM ha^{-1} $year^{-1}$ (Monclus *et al*. 2006; Calfapietra *et al*. 2010). *Populus* and *Salix* are relatively easy systems to breed and the BVOC emission potentials of poplar genotypes are very different (Isebrands *et al*. 1999). Eller *et al*. (2012) quantified the differences in isoprene, methanol and monoterpene emissions from 30 hybrid poplar genotypes.

They were able to explain about 40–50% of the variation in isoprene emission potential across these genotypes by a combination of instantaneous photosynthesis rate and seasonal aboveground growth. Both genotype and parental cross were significant predictors of isoprene and monoterpene emissions (Eller *et al*. 2012). The authors of that study observed a threefold range in isoprene emission rates across all 30 genotypes, with a positive trend between isoprene emission and plant productivity. This trade-off between growth and isoprene emission potential may make it challenging to mitigate the BVOC emissions of poplar plantations through selection (Eller *et al*. 2012). However, Guidolotti *et al*. (2011) showed no clear association between isoprene emission and photosynthesis within different poplar genotypes grown in a common garden experiment. The photosynthetic C lost as isoprene and isoprene emission showed a linear correlation, suggesting a constant proportion of photosynthetic C directed to isoprene emission (Guidolotti *et al*. 2011). According to these results, isoprene emission rate might be related to the final plant productivity but not to the photosynthetic capacity of poplar.

Before phenotyping for choosing future cultivars with specifically altered BVOC emissions can be realized, the plant performance under various climate scenarios and co-occurring biotic stresses must be understood. In general, BVOC emissions by stressed plants are higher than that by healthy, undamaged plants (Degenhardt *et al*. 2003; Loreto & Schnitzler 2010; Holopainen 2011). In addition to pests and pathogens (Pichersky & Gershenzon 2002; Mumm & Dicke 2010), high temperature (Monson *et al*. 1992; Loreto *et al*. 2006; Behnke *et al*. 2007), limited water availability (Sharkey & Loreto 1993; Brüggemann & Schnitzler 2002; Gouinguene & Turlings 2002; Fortunati *et al*. 2008; Blanch *et al*. 2009), O_3 (Loreto & Velikova 2001; Loreto *et al*. 2004; Velikova *et al*. 2005; Vickers *et al*. 2009), UV-B radiation (Tiiva *et al*. 2007) or physical stresses such as wind or forest fires (Maleknia *et al*. 2009; Haapanala *et al*. 2012; Kivimäenpää *et al*. 2012) affect plant VOC emissions in contrasting ways.

This complicates the characterization of BVOC emission potentials from field observations. For example, while untreated soybean do not release high amount of BVOCs, in plants attacked by insect pests, large emissions of individual compounds [100–200 ng g fresh weight $(FW)^{-1}$ h^{-1} α-farnesene and indole] were reported (Winter & Rostás 2008). Similarly, even if healthy wheat shows almost no BVOC emissions, under environmental stress, emission rates of up to 20–400 ng plant FW^{-1} h^{-1} (Piesik *et al*. 2010) were reported. The large variety in the possible induced combinations of BVOCs, and in the emission quantities, makes it difficult to accurately characterize BVOC emissions from stressed plants. For example, when wheat, oat and barley plants were either mechanically injured, attacked by two different beetle species (*Oulema* spp.) or infected by three different fungal species (*Fusarium* spp.), the result in all cases was a plant- and pest-specific induction of BVOC emissions (Piesik *et al*. 2011). Moreover, combination of abiotic and biotic stresses is likely to further modify the emission potential. Like for crops, environmental stress conditions modify BVOC emissions from trees to a large degree. Even a small temperature increase (1 °C) leads to notable changes in monoterpene and green leaf volatile (GLV) emission of poplar cultivars (Hartikainen *et al*. 2009). Pollution by O_3 has also been shown to induce BVOC emissions. Isoprene and monoterpene emissions, for example, can be induced by very high O_3 doses (for review, see Loreto & Schnitzler 2010). Further, O_3 air pollution can stimulate the emission of stress-inducible low-volatility BVOCs, which may result in additional SOA formation. Such aerosols may change volatile BVOC emissions by modifying photosynthetically active radiation (PAR) incident on the canopy and, consequently, feedback on O_3 mixing ratios.

At the moment, available data on plant ability to cope with stressful factors elicited by various environmental conditions are still rather scarce (Monclus *et al*. 2006; Bidart-Bouzat & Imeh-Nathaniel 2008; Long & Ort 2010). Moreover, climate change will significantly change production conditions in the forthcoming years (White Paper of the European Commission 2009, p. 147); changes in temperature and precipitation will clearly alter land suitability for agricultural use as well as yield (Schmidhuber & Tubiello 2007; Long & Ort 2010). Abiotic stresses generally inhibit photosynthesis (Flexas *et al*. 2006; Wahid *et al*. 2007), and plant's defence against various environmental stressors has direct consequences on plant biomass production. For example, it has been shown (Brilli *et al*. 2007; Teuber *et al*. 2008) that under abiotic (e.g. drought and salinity) stress, the percentage of photosynthetically fixed C emitted as VOCs increases dramatically. To be able to characterize the yields and BVOC emissions for breeding purposes under future conditions, more information on plant performance under multiple stresses must be collected (Holopainen & Gershenzon 2010).

Modifying and utilizing BVOC profiles for climate-friendly cultivars

Genetic modification of BVOC emission

In order to identify the best-suited cultivars for different conditions, molecular biological tools are a useful addition to silvicultural, biochemical and ecophysiological methods (Neale & Kremer 2011). Genetic engineering enables the transfer of desired characteristics into plants, or the knockout of specific traits, when it is not possible through conventional plant breeding. The first results using genetically modified organisms (GMOs) to assess the role of individual BVOCs in different stresses are very promising (Kappers *et al*. 2005; Behnke *et al*. 2007; Laothawornkitkul *et al*. 2008; Vickers *et al*. 2009). Plants with either silenced or up-regulated isoprenoid synthesis are not only excellent tools to dissect the functional role of individual plant VOCs but also offers the opportunity to create 'VOC-silent plantations' or, alternatively, introduce effective volatile defence compounds helping plants to mitigate abiotic and biotic stresses (Bouwmeester 2006; Chang & Keasling 2006). From the perspective of AQ in areas with high NO_x mixing ratios, low or non-isoprene-emitting biomass plants are desirable. Several studies exist in which isoprenoid emission has been induced or brought into a non-emitting plant (Kappers *et al.* 2005; Loivamäki *et al.* 2007; Vickers *et al.* 2009; Lee *et al.* 2010) but only a few studies have tried to create non-emitting plants. The bioenergy species poplar and willow display several characteristics (rapid growth and seed development, simple clonal propagation, established transformation and *in vitro* propagation protocols) that make the integration of modern genomic tools with conventional techniques possible (Neale & Kremer 2011). Behnke *et al.* (2007) used these characteristics to create GM poplars with almost fully repressed isoprene biosynthesis. It was hypothesized that losing the trait of isoprene emission causes negative effects on plant productivity, fitness and pest resistance (Loreto & Schnitzler 2010). Such disadvantages were, however, not observed in semi-natural conditions (Behnke *et al.* 2012). More detailed analyses of these lines proved that poplars are able to replace the benefits of isoprene production by other biochemical means under certain conditions (Way *et al.* 2013; Kaling *et al.* 2014). However, more long-term field trials are needed (and already started; Schnitzler *et al.*, unpublished data) to clarify whether non-isoprene-emitting bioenergy plants can prevent negative atmospheric impacts of large-scale plantations under various environmental conditions.

Moreover, even if volatile isoprenoids are associated with plant defence properties, the down-regulation of emission may sometimes also reduce the susceptibility to pests, as seen for poplar where the isoprene non-emitting lines are less susceptible against a typical fungal pest (Behnke *et al.* 2012). Similarly, in orange trees, the down-regulation of D-limonene increased the resistance against the fungus *Penicillium digitatum* (Rodriguez *et al.* 2014). Thus, in some cases, not only fewer isoprenoids are released into the atmosphere but also higher resistance may be achieved. Hewitt *et al.* (2009) suggested that the biotechnological down-regulation of isoprene emission in oil palm, similarly to that carried out for poplar, would be essential to extinguish isoprene emissions and thus avoid the potential implications discussed in the section Conversion for biofuels.

Some pesticide co-formulants are volatile and can contribute to ground-level O_3 formation. In a study by Zeinali *et al.* (2011), the O_3 forming potential of pesticides ranged from 0.1 to 3.1 g O_3 g^{-1} product. Thus, and due to other disadvantages pesticides have, not only non-emitting plants but also plants with specific inducible BVOC emissions will be effective tools to pave the way for more sustainable agriculture. Plants under herbivore attack synthesize defensive volatile compounds that directly or indirectly affect herbivore performance and mediate other interactions with the community (Penaflor & Bento 2013). The attraction of herbivore enemies by herbivore-induced plant volatiles (HIPVs) is well documented [Loreto *et al.* (2014) and articles within this special issue of *Plant, Cell & Environment*]. The discovery of the BVOC-driven network of ecological relationships has motivated further interest into BVOCs, particularly aiming at their possible exploitation for bio-control of pests and pathogens in agriculture and forestry. Several examples demonstrate that introduction of a specific terpene synthase gene led to higher resistance against herbivores or fungal pathogens (Schnee *et al.* 2006; Brillada *et al.* 2013; Dixit *et al.* 2013). In maize, a single gene (*tps10*) was sufficient to mediate the indirect defence against herbivore attack (Schnee *et al.* 2006). Moreover, linalool-emitting GM rice was more resistant to its enemy, rice bacterial blight (*Xanthomonas oryzae*) (Taniguchi *et al.* 2014). Sometimes, however, it seems difficult to manipulate isoprenoid emissions due to the very tight regulation of the biosynthetic pathways. In such cases, multiple manipulation acts might be necessary to override the plants' own regulation (Wu *et al.* 2006; Rosenkranz & Schnitzler 2013).

Some other biotechnological approaches directed to decrease herbivore damage by non-volatile compounds were shown to indirectly reduce BVOC emissions. For example, maize, which synthesizes *Bt* (*B. thuringiensis*) toxins, is less sensitive to herbivore feeding and consequently emits less HIPVs (Dean & De Moraes 2006). Some GM plants might even be useful for 'atmospheric phytoremediation' by directly removing air pollutants; Doty *et al.* (2007) have developed GM poplars with greatly increased rates of metabolism which remove small pollutants through the overexpression of cytochrome P450 2E1. These plants are able to successfully remove chloroform and benzene from the air.

Innovative, non-GM techniques to use BVOC emissions in smart agriculture

In addition to genetic manipulation, application of priming agents, so-called elicitors, or use of plant varieties that emit volatiles attractive to natural enemies is possible (Penaflor & Bento 2013; Fig. 3). In the future, it is likely that BVOCs can be induced, for example, by application of natural elicitors or hormone-like substances, like cis-jasmonate, to switch on defence pathways (Pickett *et al.* 2007) and to directly reduce the development of pests, diseases and weeds (Moraes *et al.* 2008). Cis-jasmonate is shown to induce defence by the up-regulation of secondary metabolites in wheat (Moraes *et al.* 2008), maize (Oluwafemi *et al.* 2013) and barley (Delaney *et al.* 2013). Methyl jasmonate (MeJA) is another potential priming agent; in rapeseed, MeJA spraying increased BVOC emissions (Loivamäki *et al.* 2004) and MeJA-treated (E)-β-caryophyllene overexpressing rice plants attracted more parasitoid wasps than the wild type (Cheng *et al.* 2007).

Creating co-cultures of different species and different emitter types can also be a strategy in sustainable agriculture (Ninkovic *et al.* 2013). Plant-to-plant signalling by volatiles is a general mechanism priming indirect defence in densely populated plant communities, such as an agricultural field (Heil & Silva Bueno 2007). Plants are able to decipher the odour profile of the neighbouring plants and thus optimize their own fitness in advance of biogenic stress. For example, diverse mixtures of wheat genotypes supported lower aphid populations compared with monocultures. Moreover, the mixtures were equally or, in the absence of aphids, more productive than monocultures (Shoffner & Tooker 2013). Similarly, Ninkovic *et al.* (2013) demonstrated that potato plants

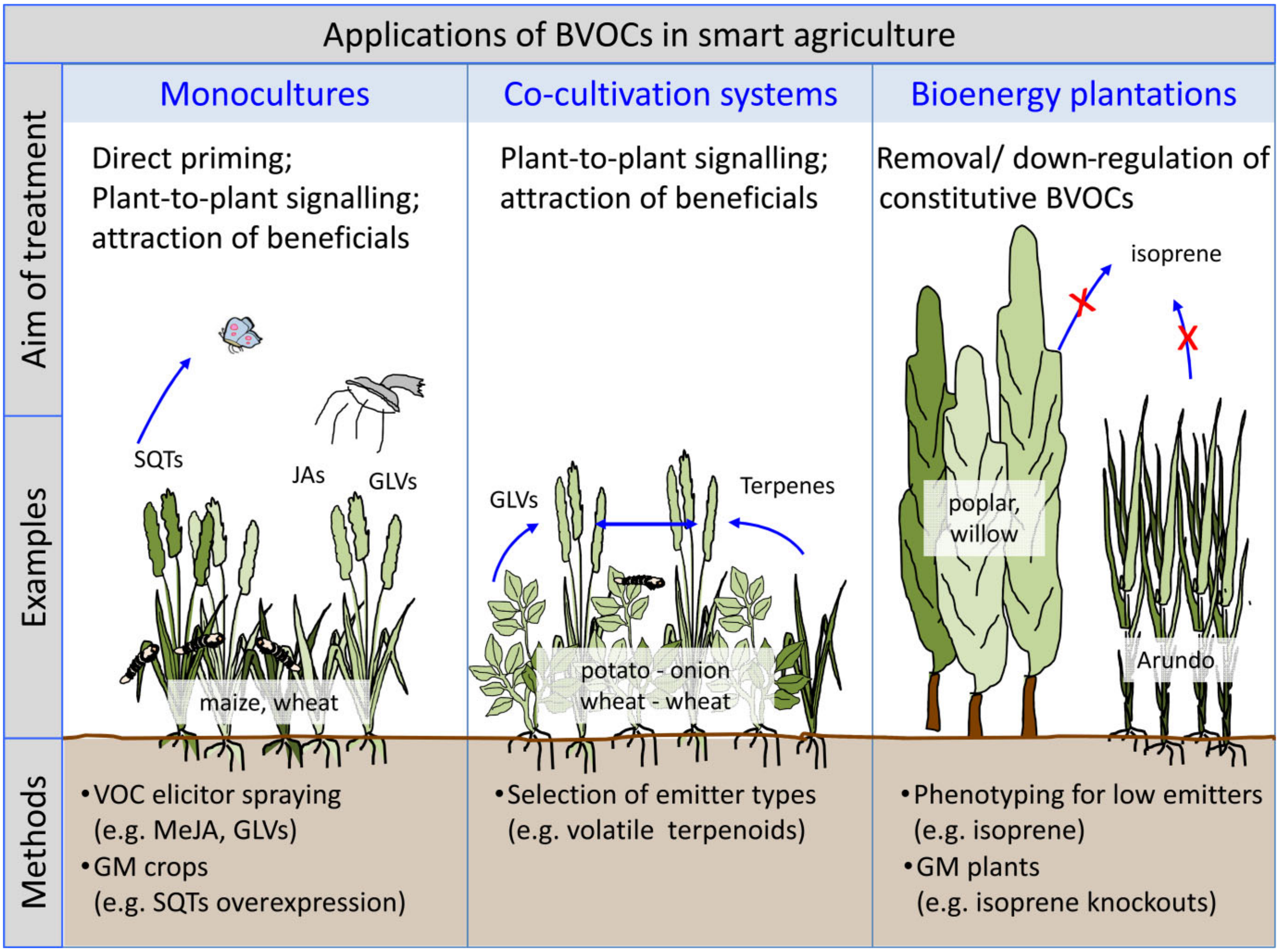


Figure 3. Schematic summary of possible applications of BVOCs in smart agriculture. GLV, green leaf volatiles; GM, gene modified; JA, jasmonates; MeJA, methyl jasmonate; SQT, sesquiterpenes.

exposed to the odour profile of undamaged onion plants in their neighbourhood were less attractive to their herbivores. Thus, mixed cultures with different BVOC emission potentials might be interesting to achieve the best possible natural degree of plant protection (Ninkovic *et al*. 2013; Fig. 3). In the study of Shoffner & Tooker (2013), however, heterocultures also emitted higher amounts of BVOCs to the atmosphere.

The increase in the understanding of the roles of BVOC in direct and indirect defence (Dicke & Loreto 2010; Loreto *et al*. 2014) allows the development of new techniques, for example, to use BVOCs for monitoring the early stages of plant diseases or microbial infection. BVOC-based profiling of plant diseases could provide early information on crop health and disease propagation, and thus facilitate pest control through proper management strategies (Sankaran *et al*. 2010). Jansen *et al*. (2010) recommended focusing upon the detection of methyl salicylate to indicate *Botrytis cinerea* infections in large-scale tomato production. Some methods to detect *Fusarium* spp. by BVOC profiles from wheat plantations are also very promising (Girotti *et al*. 2010).

CONCLUDING REMARKS

From a system's perspective, BVOC emissions *per se* are not necessarily only negative and something to avoid in agricultural systems. Rather, the challenge will be to reduce potentially negative (health or climate) atmospheric effects while enhancing the potential for stress protection. To maintain sustainable agriculture and biomass production in the future, it may be possible to make use of the differences in BVOC emissions both of different cultivars/species and under different environmental conditions, depending upon local requirements. Modern biological and chemical techniques can be used to lower isoprene emission in large-scale biomass plantations, stimulate plant-innate immunity, and trigger plant–plant or plant–herbivore communications for applications in weed control or biological pest control. Further, they can be of use in early diagnosis of abiotic or biotic stresses, or even as additives for functional food preparations. All these applications can be envisioned based upon current knowledge (Fig. 3). However, large efforts are still needed to transfer these examples into practice, for example, in breeding and phenotyping programmes of crops and bioenergy plants, biocontrol procedures or novel co-cultivation systems of species or cultivars. Similarly, simulation experiments of BVOC effects on the atmosphere under a changing environment need to place much more focus not only on the effects of land cover change but also land management. For once, modellers do not yet 'race ahead' (Monson *et al*. 2007) of observational evidence and knowledge. In particular, in view of stress responses, there is still a lot of 'catching up' with respect to implementing emerging understanding into model analyses.

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