Opinion

Special Issue: Induced biogenic volatile organic compounds from plants

Induced BVOCs: how to bug our models?

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Climate–herbivory interactions have been largely debated vis-à-vis ecosystem carbon sequestration. However, invertebrate herbivores also modify emissions of plant biogenic volatile organic compounds (BVOCs). Over the shorter term, they do this by the induction of *de novo* synthesis of a plethora of compounds; but invertebrates also affect the relative proportions of constitutively BVOCs-emitting plants. Thus, invertebrate–BVOCs interactions have potentially important implications for air quality and climate. Insect outbreaks are expected to increase with warmer climate, but quantitative understanding of BVOCs–invertebrate ecology, climate connections and atmospheric feedback remain as yet elusive. Examination of these interactions requires a description of outbreaks in ecosystem models, combined with quantitative observations on leaf and ecosystem level. We review here recent advances and propose a strategy for inclusion of invertebrate–BVOCs relationships in terrestrial ecosystem models.

Dynamic vegetation models and BVOCs

Plant-generated volatile organic compounds, especially isoprene and monoterpenes, are the chief constraints on tropospheric levels of ozone [1] and secondary organic aerosol (SOA; see Glossary) [2]. Tropospheric ozone is a potent greenhouse gas and toxic pollutant, and SOA contributes to the substantial, but highly uncertain negative radiative forcing by aerosols [1,2]. Thus, these emissions have important impacts on air quality and climate, and are crucial for accurate prediction at regional and global levels. A number of different emission algorithms have been proposed and increasingly are being applied within dynamic vegetation models (DVMs) to study interactions between vegetation, atmospheric composition and climate change [3]. So far, these models have concentrated exclusively on constitutive emissions [3,4]. However, every plant species can be triggered to emit BVOCs by environmental and, in particular, biotic stresses [5]. These induced emissions include a broader range of BVOCs such as oxygenated compounds from the lipoxygenase pathway, volatile sesquiterpenes and novel monoterpene species. Induced BVOCs have a crucial ecological role, especially as induced defence compounds against herbivory, and for plant–plant and plant–animal signalling [6,7]. Two factors taken together stimulate questions as to whether induced BVOCs affect regional or even global atmospheric chemistry to a degree worthy of consideration in chemistry–climate simulations:

(i) the sheer dimension of the area affected by invertebrate outbreaks, and the potential of stress-induced BVOCs to form particles [8,9], and (ii) increasing evidence of a substantial number of BVOCs “missing” for closure of atmospheric chemistry simulations [10,11].

Disturbance events can profoundly modify ecosystem development and function [12], but so far only certain DVMs include disturbance events, and even in these models, fire is the sole episodic disturbance agent [13]. The interest in fire is clear, as it affects carbon cycling, atmospheric chemistry and habitat diversity to a substantial degree in nearly all natural environments, and it is greatly influenced by humans via ignition and suppression [14]. By contrast, large scale invertebrate herbivore outbreaks have so far escaped the attention of global terrestrial modellers despite their demonstrated relevance for carbon cycling [15]. In some regions, the area affected by insect attacks can be several-fold larger than the area

Glossary

BVOCs: biogenic volatile organic compounds, synthesised by living organisms, mainly living plants. Their production and emission can be constitutive (e.g., in response to abiotic drivers such as light or temperature) or induced (e.g., in response to stress such as wounding)
D(G)VM: Dynamic (global) vegetation model, simulates dynamic changes in vegetation cover (represented by plant functional units, plant functional types (PFTs)), and terrestrial water and carbon cycles in response to changes in climate and atmospheric CO_2 concentration. Many DVMs also contain subroutines to estimate constitutive BVOCs emissions, generally those of isoprene and monoterpenes
Diapause: stage of dormancy during development, normally in insects. Release from diapause is triggered by defined environmental conditions
Eddy covariance technique: micrometeorological technique to measure directly the exchange of energy or a substance between the surface and the atmosphere. The flux is directly proportional to the time-averaged (i.e., 30 or 60 minutes) covariance between the fluctuation in vertical wind speed and the compound of interest (i.e., CO_2, or a BVOC)
Herbivory: consumption of plant material
Oviposition: laying of eggs (oviparous animals)
Poikilotherm: an organism whose body temperature co-varies with the outside temperature
Secondary organic aerosol, SOA: carbon-containing particulate matter that is formed in the atmosphere from anthropogenic or biogenic precursors. BVOCs and their oxidation products are a major source for the latter.
Univoltine: lifecycle-completion within one year

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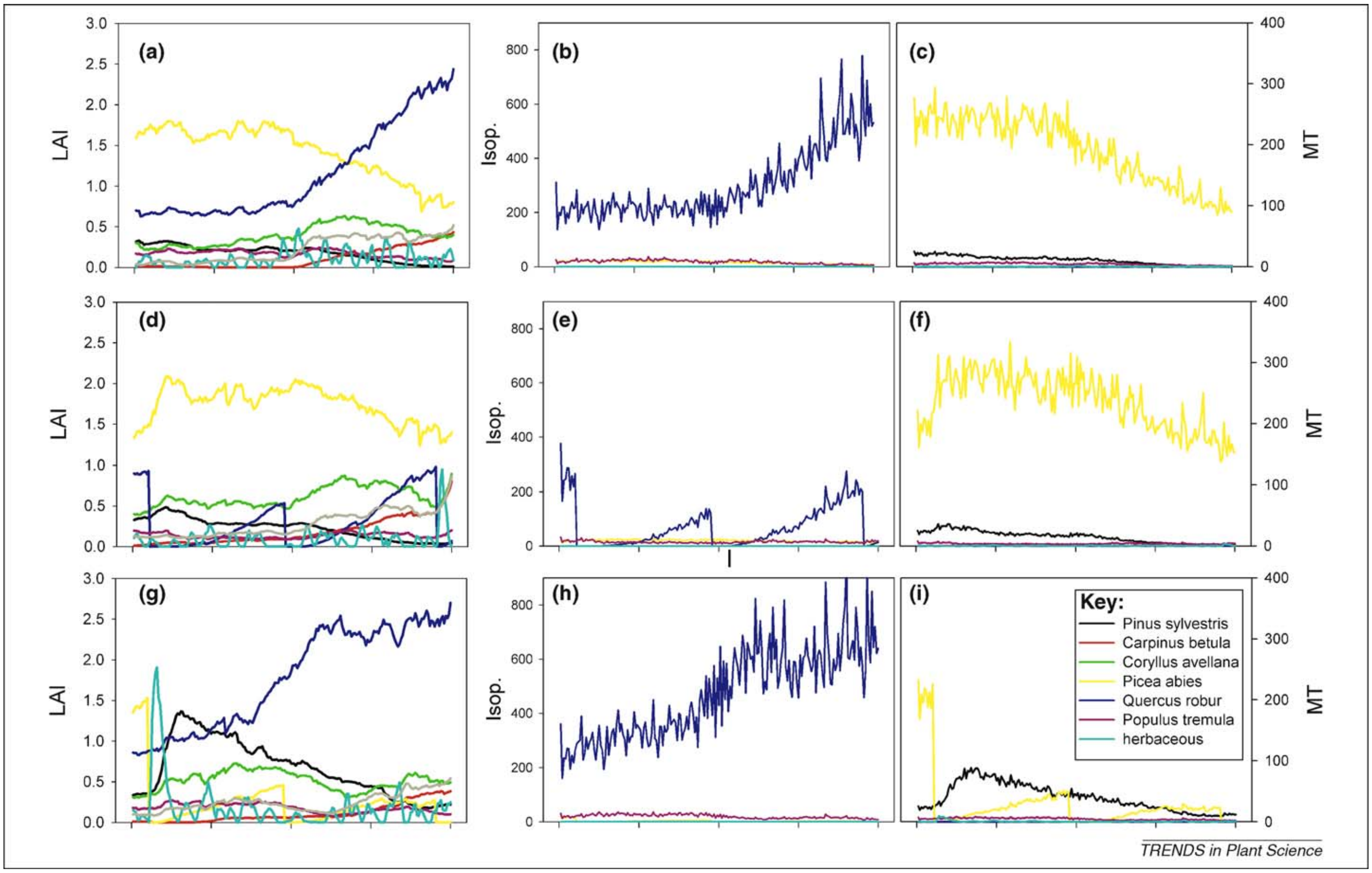


TRENDS in Plant Science

Figure 1. Implications of catastrophic events on long-term ecosystem dynamics. A simple model experiment was performed, applying a dynamic vegetation model framework that simulates European tree species distribution over a 200 year, 20th and 21st century model period [49,68]. For the 21st century a CO_2- and climate change scenario (HadCM3-A2) [49] was adopted. The simulation was run for a location in northern Europe (59°N) where the model projects a mixed conifer-deciduous forest, with increasing dominance of broadleaf deciduous trees in a warmer, high-CO_2 world (panel a). Three simulations were compared: **(a-c)** one with standard model set-up, **(d-f)** one with an artificial killing-event for *Quercus robur* and **(g-i)** one with an artificial killing of *Picea abies* prescribed to take place every 80–100 years. The panels show the interacting effects of climate change, increasing atmospheric CO_2 concentration and extreme disturbance on leaf area index (LAI) and constitutively emitted BVOC isoprene (isop.) and monoterpenes (MT; both in mg C m^{-2} a^{-1}), modelled as in [49,68]. Fire disturbance was excluded from the simulations. Although these simulations are based on an artificially prescribed and extreme disturbance level, they clearly demonstrate that depending on species equilibrium in a given community, and whether or not environmental conditions during recovery after disturbance are transiently changing, a community returns to given state after selective infestation and decline of a given species, but may also develop to a different community. Thus, catastrophic pest attacks can profoundly alter ecosystem function and services.

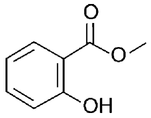
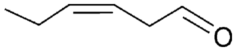
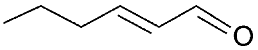
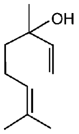
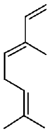
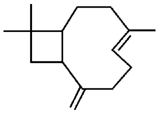
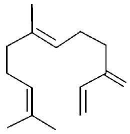
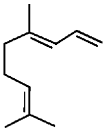
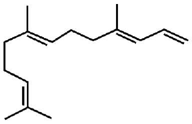
affected by fire [16]. Overall, the relative extent of disturbances caused by fire and insects varies temporally and spatially, but the disturbances are frequently causally related: for example, the accumulation of fuel following an insect outbreak might determine the extent or intensity of a subsequent fire, and in addition, fire represents a stress to the forest that predisposes its trees to subsequent attacks by insects [16,17]. As with fire, large-scale invasion by specialist herbivores can alter the species composition of plant stands [18] (Figure 1). Selective feeding on certain plant species can significantly modify the distribution of constitutively BVOCs-emitting and non-emitting vegetation and thereby also affect the constitutive emissions over long-term (Figure 1).

We argue here that quantitative herbivory-induced BVOCs emission studies can be a principal motivator for the eventual development of induced leaf emission algorithms, but to date, the number of such studies is limited, and proper experimental design is still lacking in many respects. At the same time we propose a conceptual framework that could be adopted for actual herbivory model development—discussed here in view of induced BVOCs emissions, but principally also applicable for other ecological applications, including fire–insect interactions. We restrict our discussion to large- scale insect infestations where some data on temporal and spatial patterns exist for eventual model evaluation. Although also possibly of importance, we do not consider in the current analysis the background moderate levels of biotic stresses always present in natural communities, but impossible to parameterise with present knowledge.

Induction of volatiles by invertebrate feeding

Induction of volatile organic emissions in response to invertebrate herbivore feeding has been demonstrated in numerous studies [5,7,19]. As the common wounding response, feeding first induces large emissions of methanol, followed by volatile products of the lipoxygenase pathway such as various C6 aldehydes [20,21]. Feeding also activates a plethora of defence genes, leading to large emissions of volatile hormones such as methyljasmonate, methylsalicylate and volatile monoterpenes linalool and trans-β-ocimene, and a variety of sesquiterpenes and homoterpenes (Table 1) [22–24], with emission compositions depending on host plant and feeding animal species [22,25]. Moreover, the odours of induced volatiles

Table 1. Typical plant volatiles induced by herbivores and their atmospheric lifetime

Compound class	Examples	Molecular structure	Atmospheric lifetime (h)[a]	Refs
Short-chained oxygenated compounds	Methanol	–OH	106	[62]
Volatile hormones	Methyl salicylate		52	[63]
Lipoxygenase (LOX) reaction products	*Cis*-3-hexenal, *Trans*-2-hexenal	 	2	[25,64]
Monoterpenes	Linalool		0.50	[62,65]
	Trans-β-ocimene		0.25	[62]
Sesquiterpenes	β-Caryophyllene		0.032	[62]
	β-Farnesene		0.24	[66,67]
Homoterpenes	DMNT		?	
Homoterpenes	TMNT		?	

[a] Atmospheric lifetime (τ) is inversely proportional to the rate of reactions scavenging the given compound, mainly through reactions with OH radicals and O_3 and was calculated as $\tau = (k_{O3})[O_3]+k_{OH}\,[OH])^{-1}$, where k_{O3} is the compound rate constant for the reaction with ozone and k_{OH} that for the reaction with OH radicals and $[O_3]$ is the ozone concentration and [OH] the hydroxyl radical concentration. Here the lifetimes were calculated for a relatively non-reactive atmosphere with O_3 concentration of 25 nmol mol^{-1} (ppb) and OH radical concentration of 0.1 pmol mol^{-1} (ppt). Data sources for the rate constants as shown in the table. No data of atmospheric lifetime are available for homoterpenes DMNT ((*E*)-4,8-dimethyl-1,3,7-nonatriene) and TMNT ((*E*,*E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene). The compounds with lower lifetime participate more actively in atmospheric chemistry and play a more important role in O_3 formation reactions and secondary aerosol formation, while compounds with longer lifetimes mainly serve as OH sinks in the atmosphere. Apart from atmospheric quality, both the formation of aerosols and reduction of OH radicals have large impacts on climate. Secondary aerosols affect solar transmission and cloud formation, and contribute to global cooling, while the reduction of OH radicals increases the atmospheric lifetime of greenhouse gas methane, thereby contributing to global warming.

have been shown to elicit defence gene expression in neighbouring plants [20,22], potentially leading to amplification and propagation of the feeding signal in the infected plant community. Although the atmospheric reaction rate constants are currently missing for some important induced volatiles (Table 1), many of the compounds induced by herbivores have been determined to have high atmospheric reactivity. Apart from the ozone-generating potential that can be assessed on the basis of the compound reaction rate constants with atmospheric oxidants (inverse of atmospheric lifetime, Table 1), there is conclusive experimental evidence of formation of organic aerosols in odour blends emitted from infected plants [8].

Induced BVOC: from what to how much

Many previous insect-feeding experiments have had the drawback that the measurements of emitted volatiles have been non-quantitative. Typically, emission composition has been measured rather than the quantity of compounds per unit enclosed plant leaf area [20,26,27]. For incorporation of herbivory into BVOCs emission models, development of quantitative relationships is crucial between the biogenic stress and the amount of volatiles emitted per unit leaf area and time. Quantitative assessment of herbivory-induced BVOCs source strength has been further complicated by the use of simple enclosures without environmental control in plant–invertebrate studies. The emissions of several induced compounds such as induced monoterpenes strongly depend on light and temperature [23]; therefore, precisely defined experimental conditions in the enclosures, as well as experiments under controlled conditions, are important to parameterize the herbivory-induced BVOCs emission models.

A number of quantitative measurements on the importance of insect-induced BVOCs have been conducted recently. These studies demonstrate that in constitutively isoprene- and monoterpene- emitting species, induced compounds might add up to a large fraction of total emissions, comparable to the constitutive amount [23,28,29]. In addition to the novel compounds induced by herbivores, the constitutive emissions can also be elevated after insect attacks, especially in monoterpene-emitting species with large storage pools [30,31], possibly reflecting the release from damaged resin ducts. However, enhanced 'constitutive' monoterpene emissions have also been observed in infested plants lacking such extensive storage pools [28,32]. Elevated isoprene emission in isoprene-emitting species has also been demonstrated as an immediate wounding response [33], and longer-term experiments with insect-feeding have indicated reduction of isoprene emission in damaged leaves [23]. These studies collectively indicate that in addition to induction of novel compounds, herbivory has an important impact on volatile isoprenoids considered to be emitted constitutively. In light of this evidence, the 'constitutive' BVOCs emission models also need revision to incorporate biotic effects.

Stress-induced BVOCs at the ecosystem level: towards quantification of the atmospheric importance

In addition to quantitative, controlled laboratory experiments, leaf- and ecosystem-level observations under field conditions, covering seasonal changes, are required to support the development and verification of induced-emission algorithms. BVOCs canopy fluxes can be measured by a number of micrometeorological techniques, in particular eddy covariance based on rapid measurements of fluctuations in vertical wind velocity and BVOCs concentration. Currently, a proton reaction mass spectrometer (PTR-MS) is used as the fast BVOCs sensor [34]. Flux measurements have concentrated on forest isoprene- and monoterpene-emissions [35,36] and their short-term or seasonal controls. Information on canopy-scale volatile emission responses to physical disturbance is available only from a few relatively short measurement campaigns investigating the effects of mowing on crops and agricultural grasslands [37–39]. In these studies, fluxes of several oxygenated BVOCs increased substantially directly after cutting; in particular, fluxes of typical wounding-induced compounds such as acetaldehyde and Z-3-hexenol were enhanced.

Box 1. How to elucidate BVOCs stress response on canopy scale

Karl *et al.* [40] measured monoterpene (MT) and methylsalicylate (MeSA) fluxes above a walnut (*Juglans california X J. regia*) canopy using a canopy concentration profile technique, combining GC-MS and PTR-MS sampling. Canopy fluxes were derived using an inverse Lagrangian transport model applied to the measured canopy mixing-ratio profiles. Over a circa 30-day period in summer, measurements indicated average MeSA and MT fluxes of the same order of magnitude (up to *c.* 0.2 – 0.25 mg m^{-2} h^{-1}). Daily fluxes of MeSA correlated best with the temperature difference (ΔT) between previous-night minimum and present-day maximum temperature, and were highest when this ΔT was large following a cool night. Minimum or maximum temperatures alone were not a sufficient explanatory factor. No effect of oxidative stress (e.g., O_3 response) on the fluxes was discernible. MeSA is also released during herbivore attacks but during the period of measurements no insect damage was apparent in this managed orchard and MeSA fluxes did not change significantly before and after application of insecticide. The correlation of MeSA with ΔT was stronger before than after onset of irrigation indicating a combined T- and water-stress response, acting via the leaf energy balance and enhanced leaf temperatures under conditions of low stomata conductance. The observed MeSA flux patterns could be interpreted as possible stress response to chilling injury, which was supported by the detection of lipid-derived typical wound VOC on days with high MeSA emissions (e.g., Z-hexenal). This study is the first on canopy scale to demonstrate substantial VOC emissions in stress response and puts forward a strong argument for these to be an important component of total BVOCs budget.

The sole example to date of the induction of BVOCs emissions in response to a canopy stress-response comes from measurements of the plant stress hormone methylsalicylate (MeSA) above a walnut (*Juglans californica* x *Juglans regia*) orchard (Box 1) [40]. Average daytime MeSA correlated strongly with the temperature difference between previous-night minimum and measurement-day maximum temperature, indicative of the plant response to temperature stress. This study clearly demonstrated that induced emissions can be of the same order of magnitude as constitutive emissions.

How to model invertebrate herbivory?

In addition to quantitative induced-BVOCs algorithms, the representation of insect or other invertebrate herbivory in DVMs is a cardinal premise for estimation of regional and global herbivory induced BVOCs source strength, and for assessment of the responses of these emissions to changing environment. We propose here a generic modelling template adopting a framework (Figure 2) synonymous to that used by state-of-the art fire models in DVMs (Thonicke *et al.*, unpublished) focussing initially on insect outbreaks in temperate and boreal forests. Ours is a first-order approach aiming to reproduce large-scale patterns based on generic representation of functional types and processes as the starting point. This requires simplifications, and we recognise that many aspects of known ecological significance, *sensu* all that is species-specific, cannot be included on such a scale. As for all model developments, once initial efforts have shown to be fruitful, improvement and adaptation of frameworks will be an ongoing, iterative process. This will include adaptation of generic frameworks to specific studies, including advanced representation of biological variability.

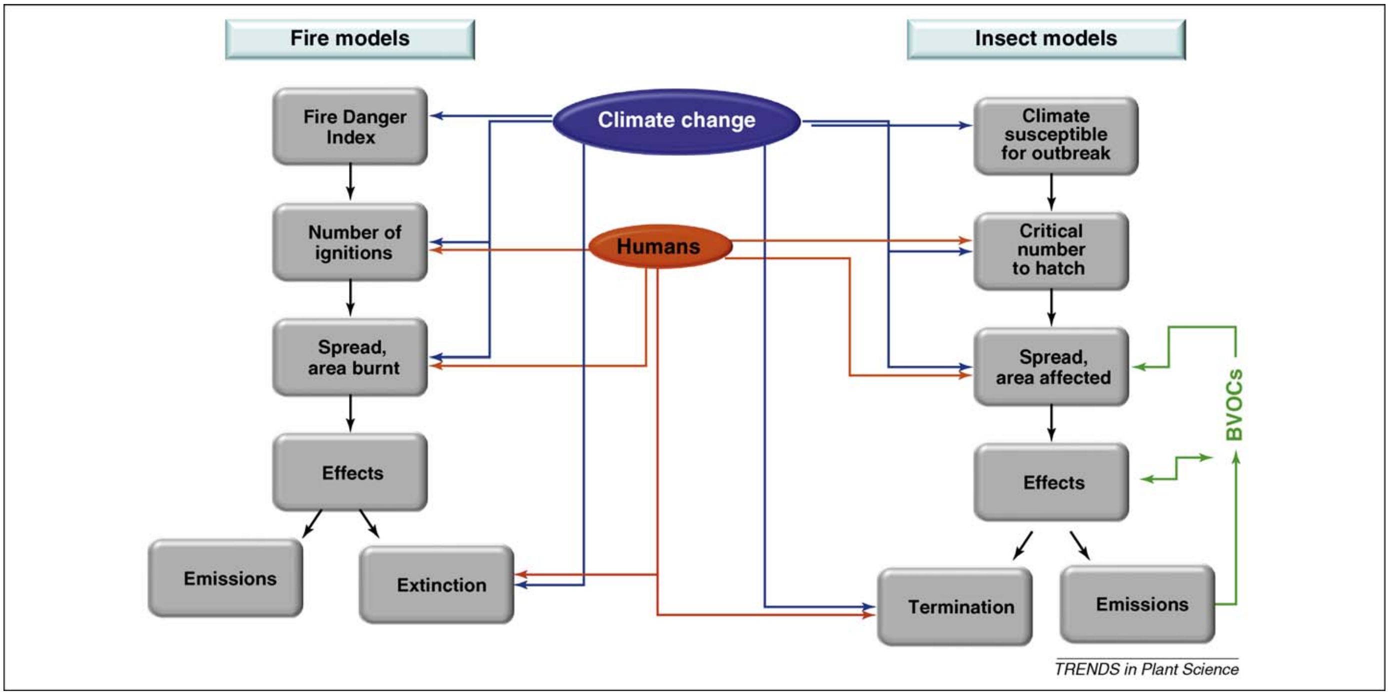


Figure 2. Episodic events in dynamic vegetation models. Proposed framework for modelling insect herbivory, analogue to state-of-the art fire models (Thonicke *et al.*, unpublished). Blue and red arrows indicate where climate and human-induced changes will have most effects; green arrows indicate interactions between processes related to insects (and invertebrate herbivores in general) and emissions of plant volatiles.

Climate conditions susceptible for range and outbreak

Temperature is the ultimate control on range, life-cycle completion and survival in poikilothermic organisms, particularly in seasonal environments. In DVMs, set bioclimatic limits define establishment and survival of plant functional types (PFT) [41] and in the same way determine also the presence or absence of food sources for possible analogous functional classes of invertebrates (BFT, bug functional type; e.g., broadleaf or evergreen defoliators or bark borers; see also *Spread, area affected,* below). Accumulated temperature sums have been successfully applied to reproduce insect developmental stages and infestation patterns [42], in a similar way to that used in many leaf phenology models [43], including those within DVMs. A more advanced method, closer to actual process understanding, is to explicitly model the temperature-dependent growth rate during various developmental stages [44].

Critical number to hatch

Adaptive seasonality describes the phenomena of synchronous emergence of feeding insects at a certain time of the year [44,45], and models based on this feature are clearly promising representatives for dynamically varying outbreak patterns in DVMs. Their *modus operandi* considers the developmental rate at a particular life stage which is inversely proportional to the time required to complete this particular stage [44]. An outbreak occurs when a combination of environmental conditions allows a sequence of ovipositional dates that yield the same, one year long life-cycle and hence a univoltine population with synchronised emergence. Effects of too low or too high temperatures during periods critical for completion of the entire life cycle (e.g., cold-hardened instars must be produced once the cold season approaches) can be investigated; this is an important facet of investigating effects of climate change. Regrettably, this concept is probably not universally applicable (e.g., in cases of obligatory diapause). Overall, in insect herbivores with cyclic population dynamics, the period length is strongly linked to the longevity of food plant species [46], providing an important connection to key features of plant functional types.

Spread, area affected

Just as a successful ignition is not in itself sufficient to develop a fire, the availability of suitable climate conditions and the synchronous emergence of a large number of invertebrates are not intrinsically sufficient cause for a major infestation event. Crucial additional requirements include suitable environmental conditions for survival after hatching, host presence and synchronicity with host phenology, mandatory for food supply [47]. Matching host phenology or cohort age is important, especially in cases of feeders on deciduous trees, or those that target a specific canopy size class. With our current knowledge, representing species diversity can only be achieved with highly parameterized models. This can only work for relatively small regions where the necessary data for parameterisation are available; it is computationally expensive, and because of the need for extensive empiricism, such types of models are difficult to apply using future or past environmental conditions. Some advanced DVMs not only calculate PFT distribution and phenology but also include forest gap-model elements. These DVMs can resolve canopy structure into functionally different age- (and hence size-) cohorts, even to tree species level (Figure 1) [48,49], as the basis for resolving insect–host interactions built on targeted food sources [50]. The geographic resolution of DVMs is normally determined by the available climate input, which is typically at a horizontal resolution of ten minutes to 0.5 degrees. For first generation 'insect-enabled' DVMs we do not consider it of prime importance to explicitly account for the movement of insect populations across grid-cells. Appropriate environmental and vegetation conditions for existence and survival in neighbouring grid-cells should be sufficient in the first instance to estimate the total area affected, although it will be necessary to test whether this results in an infestation area that becomes too large, too fast. Adopting an explicit description of population spread becomes of importance, however, when considering mass-migrating species such as locusts [51].

Effects

Herbivores consume a certain amount of plant production, either in the form of leaf biomass or as phloem-sap. The effect on the plant is a reduction in potential growth and competitiveness, and possibly death, if overall plant carbon balance becomes negative over a sufficiently long time period. Empirical stand-damage relationships [52] or more functional ones between insect dry matter consumption and their growth rate obtained from laboratory studies [53] can be adopted. These vary with food quality as the total intake must match the requirements to sustain growth [53]. As DVMs begin to account for ecosystem nitrogen flows [41], dynamically changing leaf carbon to nitrogen ratios can serve as indicators for food quality. In fertiliser experiments, increased as well as decreased consumption rates as a function of foliar nitrogen have been found [54] and these initial data provide a starting point for empirical algorithms in DVMs. Eventually, induced defence, as one of the links between herbivory and BVOCs (Figure 2), could be captured by accounting for variable leaf monoterpene storage in DVM-BVOCs models [55,56], but the quantitative understanding necessary to do so is currently lacking (see *Emissions* below).

Termination

Outbreaks are typically terminated by food limitation or by climate conditions that directly cause insect mortality. Thresholds such as late spring frosts that can damage newly developing foliage, and hence food supply can serve as the simple modelling means [57] to achieve this. Abbott *et al.* [47] proposed a more comprehensive framework to study synergistic effects between consumption and population dynamics but their equations need to be simplified, omitting empirical representation of processes that are computed in a process-based way within a DVM framework.

Emissions

Production and emission of BVOCs in response to an outbreak (Figure 2) will affect spread of invertebrate attack and food consumption. Because of a lack of quantitative information on leaf level interactions between feeding and emissions, it seems premature to suggest concrete ways forward. But because insect models first need to be incorporated into DVMs, this field will mature and information to parameterise processes and algorithms will become available. In further model development, complex tritrophic interactions (plants–herbivore, invertebrates–parasitoid, and carnivore–invertebrates) will need consideration, in particular because many herbivore invertebrate induced BVOCs serve as volatile clues to attract parasitoids and carnivorous insects, thereby suppressing the populations of herbivores [6,58].

Conclusions and outlook

Two chief premises must be fulfilled for linking (herbivory) induced BVOCs emissions to chemistry-climate models. Quantitative information on leaf, plant and ecosystem scale must become available to foster development of suitable induced-BVOCs algorithms to be included into large-scale models, and for evaluation of model output. At the same time, the large-scale models initially need to represent invertebrate herbivory. We argue here, that the community should be in a good position to pursue herbivory modelling and put forward a conceptual framework. During the development, testing and maturing of the insect-herbivory models, time should be spent to ensure that quantitative information on induced volatiles are available when the ecosystem modelling community is ready.

Although extreme events might be rare, they can profoundly shape the ecosystem in terms of species composition, induced and constitutive BVOCs emissions, and their interactions with climate. Current evidence suggests that several global change drivers such as elevated CO_2 and ozone concentration also affect both constitutive and herbivore-induced BVOCs production [29,59–61]. Any model used to predict invertebrate–plant interactions on longer time-scales needs to consider the modification of these interactions by global change. This is a complex task but initial models will at least provide a quantitative assessment of the potential significance of induced BVOCs source strength and role in atmospheric chemistry and climate. They are unlikely to reliably predict the exact timing or location of high induced BVOCs episodes. In further model development, higher order trophic interactions and feedback (e.g., herbivore insects versus parasitoid insects), modified through induced BVOCs emissions, can be taken into account as more information becomes available, allowing a more reliable prediction of the invertebrate outbreak patterns.

Disclosure statement

The authors declare they have no conflict of interest.

Acknowledgments

The authors acknowledge discussions at the 2009 ESF VOCBAS science meeting in Taagpeera, Estonia. AA was supported by the Swedish Research Councils Vetenskapsrådet and Formas, and ÜN by the Estonian Science Foundation (Grant 7645) and the Estonian Ministry of Education and Science (grant SF1090065s07).

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