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Protective perfumes: the role of vegetative volatiles in plant defense against herbivores

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Herbivore damage to leaves and other vegetative tissues often stimulates the emission of volatile compounds, suggesting that these substances have a role in plant defense. In fact, ample evidence has accumulated in the last few years indicating that volatiles from vegetative plant parts can directly repel herbivores, such as ovipositing butterflies and host-seeking aphids. Volatiles have also been demonstrated to protect plants by attracting herbivore enemies, such as parasitic wasps, predatory arthropods and possibly even insectivorous birds. Even below ground herbivory results in the release of volatiles that attract herbivore enemies. However, plant volatiles are also known to attract enemies of plants. Hence, to determine the true value of these substances in defense, more research is needed especially in natural communities with non-agricultural species.

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Introduction

Among the huge variety of chemical compounds produced by plants, some are released into the surrounding atmosphere. In addition to carbon dioxide, oxygen, water vapor and the gaseous hormone ethylene, plants have been shown to emit a variety of other organic compounds. Volatiles are released not only from floral organs but also from vegetative parts, especially after herbivore damage. The two most common constituents of these volatile blends are terpenes (C_{10} monoterpenes and C_{15} sesquiterpenes) and green leaf volatiles (C_6 aldehydes, alcohols and esters derived from lipoxygenase cleavage of fatty acids that embody the typical odor of damaged leaves).

The close association of volatile release with herbivory has long suggested that these substances act in plant defense, and some fascinating lines of research provide support for this notion. Here we review recent findings on the role of vegetative volatiles in anti-herbivore defense. We summarize studies on both the direct action of volatiles against invertebrate herbivores and the role of volatiles in attracting herbivore enemies, discuss why volatile emission might not always be advantageous to plants and suggest what further work is necessary to demonstrate the defensive function of vegetative volatiles in nature.

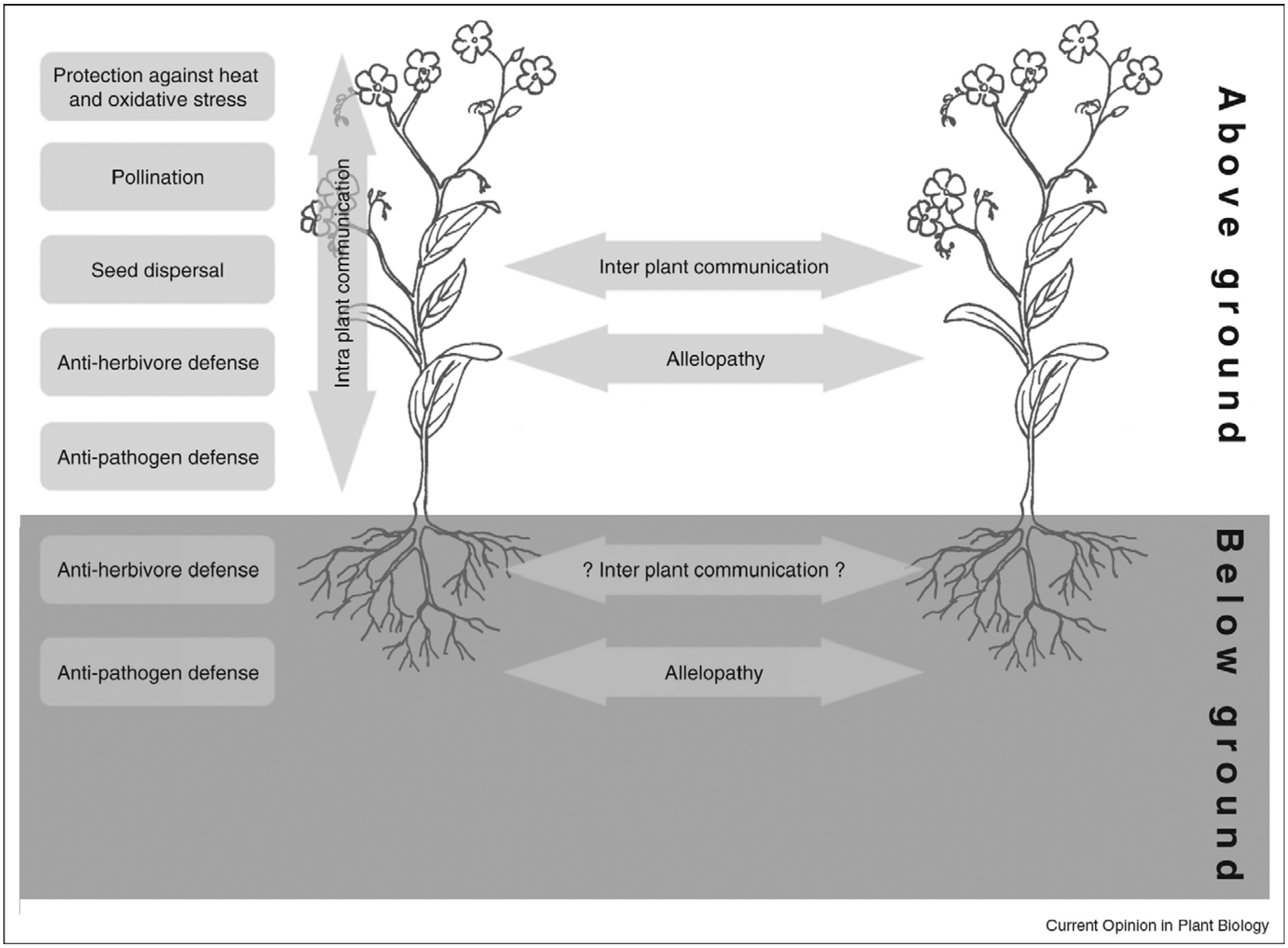
Vegetative volatiles play other intriguing roles in plants that are not covered here, including defense against pathogens, protection against heat and oxidative stress [1], signaling among plant organs [2], inter-plant communication [3] and allelopathy (Figure 1). In addition, volatile emission from herbivore-damaged plants or plant parts may not immediately trigger defense responses, but instead prepare the metabolic machinery for subsequent defense production upon further herbivore attack, a phenomenon known as priming [4]. These functions and other aspects of plant volatiles were also treated recently in an excellent general review [5].

Vegetative volatiles deter herbivory

Evidence that vegetative volatile compounds function to directly repel herbivores has begun to accumulate in the last decade [6,7]. For example, the monoterpene volatiles of *Chrysanthemum morifolium* were recently reported to repel ovipositing females of the diamondback moth (*Plutella xylostella*). This lepidopteran does not normally lay eggs on *C. morifolium*, and the repellence of the monoterpene volatiles may help explain why [8]. However, diamondback moth females that had prior experience with these volatiles were not necessarily repelled. Volatiles may not only chase away adult lepidopterans but also deter caterpillars from feeding. The common C_5 volatile, isoprene (Figure 2), previously implicated in plant protection against temperature and oxidative stress [1], was shown surprisingly to deter tobacco hornworm (*Manduca sexta*) caterpillars from feeding on isoprene-releasing transgenic tobacco lines and on isoprene-emitting artificial diet [9••].

Vegetative volatiles have also been shown to repel other insect groups, such as aphids [10–12]. In one instance, this appears to result from outright deception. The sesquiterpene, (*E*)-β-farnesene (Figure 2) is a common aphid alarm pheromone that is released by attacked aphids and causes other aphids in the vicinity to stop feeding and move away. The same compound is also present in some

Figure 1



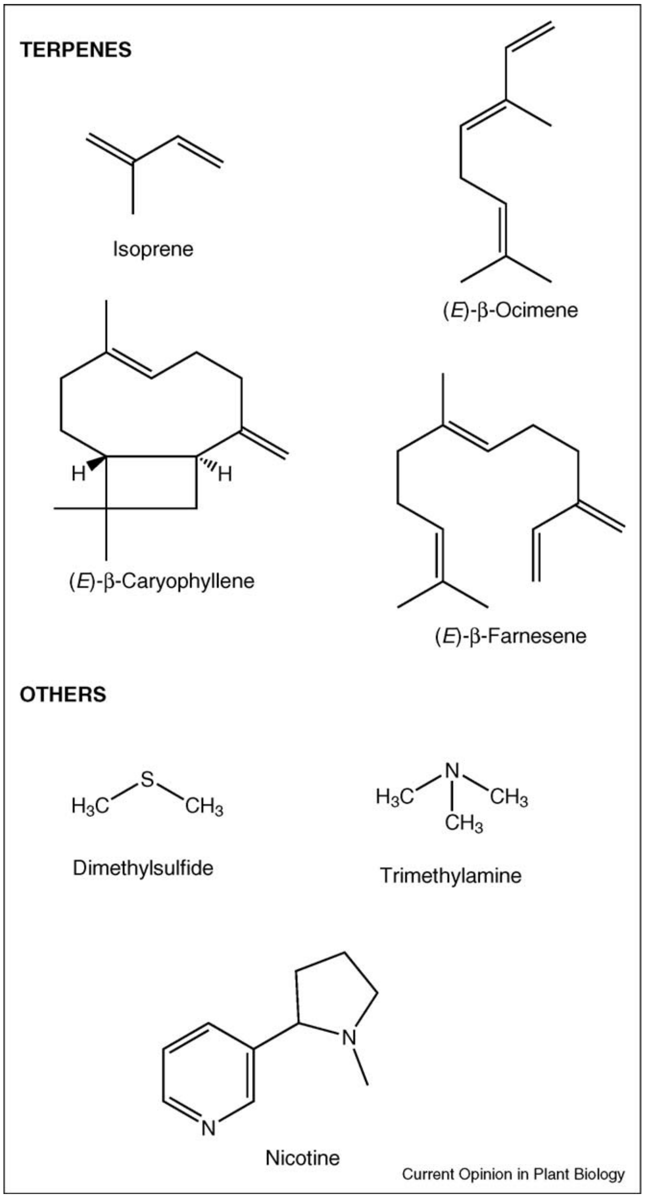
Volatiles play many diverse roles in the lives of plants. This review focuses on their role in anti-herbivore defense.

plant volatile mixtures. Volatiles from *Arabidopsis thaliana* engineered to emit (*E*)-β-farnesene repelled the green peach aphid (*Myzus persicae*) in comparison to volatiles from non-emitting control lines [13]. However, volatile blends containing mixtures of (*E*)-β-farnesene and other sesquiterpenes are not necessarily repellent [14], so the ability of this sesquiterpene to function as a natural aphid repellent requires further investigation. In addition to aphids, another piercing-sucking insect, the western flower thrips (*Frankliniella occidentalis*), was repelled from oviposition by volatile nicotine (Figure 2) [15•].

In the marine environment, volatile plant defenses have also been recently documented. The brown alga, *Dictyota dichotoma*, releases trimethylamine and dimethylsulfide (Figure 2) after wounding, which in combination with a non-volatile compound, acrylate, inhibited feeding by a marine amphipod [16•]. Dimethylsulfide and acrylate are derived upon wounding from dimethylsulfoniopropionate, a compound found in a variety of algal species [17]. Interestingly, other sulfur volatiles, dimethyldisulfide and dimethyltrisulfide, were emitted from the roots of *Brassica nigra* upon feeding by the cabbage root fly (*Delia radicum*) [18••]. These substances were previously described as insect neurotoxins [19] and so could also act in direct defense.

To date, little information is available on how plant volatiles might actually cause herbivore repulsion or inhibit feeding. One may speculate that volatiles could function as good markers of a species identity and so repel herbivores from non-hosts. Additionally, herbivore-induced volatiles may serve as reliable signals to other herbivores regarding the presence of competitors or the danger of herbivore enemies. These compounds could also indicate that a prospective host has increased its defenses due to prior herbivore attack. Furthermore, volatiles could have direct toxic action on herbivores,

Figure 2



Chemical structures of selected vegetative volatiles that function in repelling herbivores and attracting herbivore enemies. Although most vegetative volatiles identified to date are either terpenes or green leaf volatiles, some of the latest studies report the involvement of alkaloids, sulfur compounds or amines in repelling herbivores.

but this possibility needs to be tested under biologically realistic conditions with appropriate concentrations of chemical compounds, which are mostly emitted at rates of nanograms or micrograms per hour per gram of leaf tissue.

Vegetative volatiles attract herbivore enemies

Since the earliest studies on herbivore-induced volatiles by Dicke, Turlings and others [20,21], researchers have been captivated by the idea that volatiles could attract arthropod predators and parasitoids of herbivores and thus reduce plant damage [22]. This phenomenon, which is known as indirect defense, has been extended recently to vertebrate predators of herbivores. When *Betula pubescens* trees were heavily infested with caterpillars of the autumnal moth (*Epirrita autumnata*), artificial caterpillars attached to branches were more frequently attacked by passerine birds than artificial caterpillars on trees without autumnal moth infestation. The amount of bird attacks was directly correlated to the emission of several terpenes, including (*E*)-β-ocimene (Figure 2), linalool and DMNT, indicating that these volatiles could attract birds to herbivore-infested trees [23•].

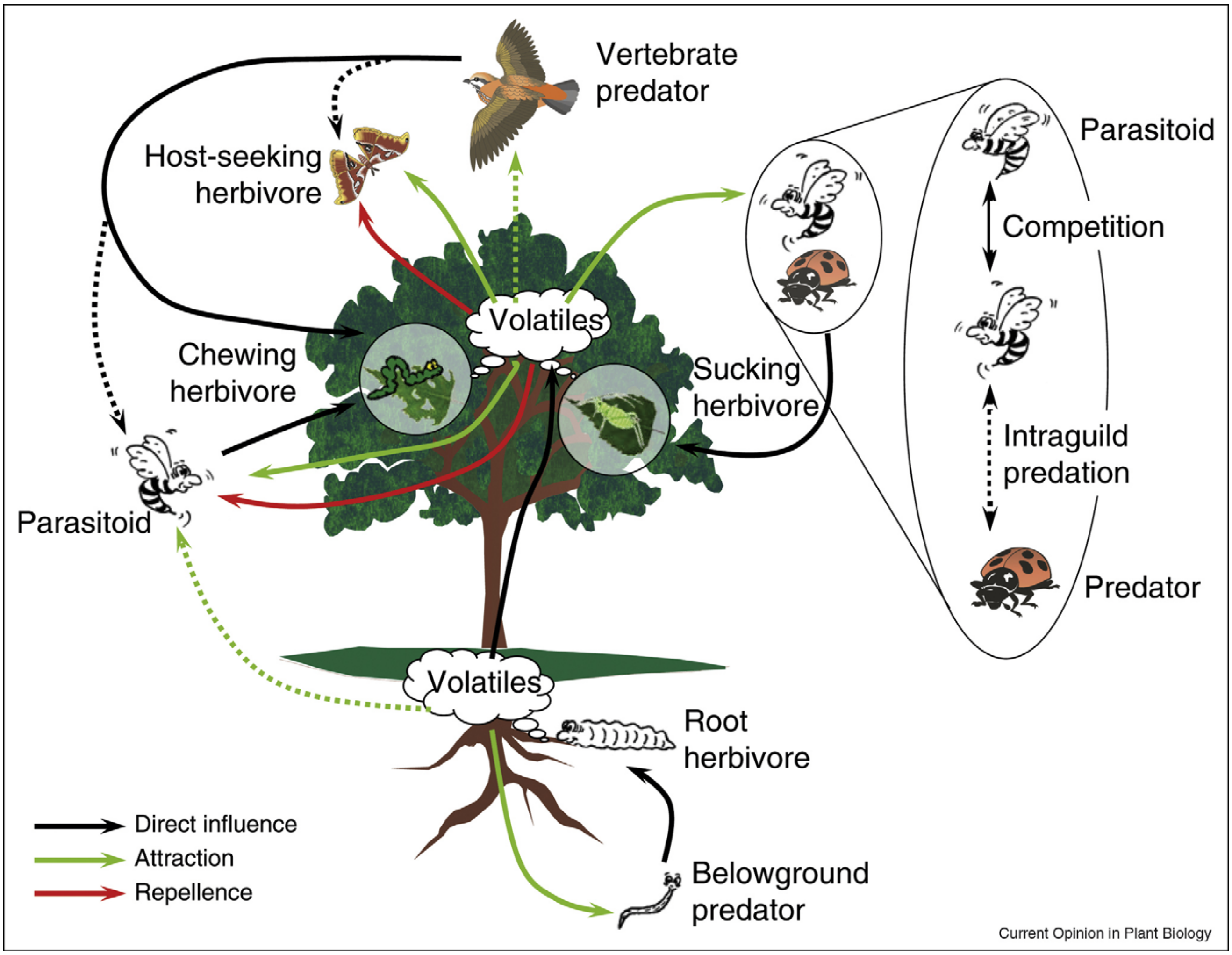
The vast majority of studies investigating the role of volatiles in attracting herbivore enemies have been performed with a very restricted group of plant species of agronomic importance (e.g. [24–28]). These species belong principally to four plant families, the Poaceae (maize, wheat), the Fabaceae (lima bean, cowpea, soybean), the Brassicaceae (cabbage, black mustard) and the Solanaceae (tomato, potato). In contrast, the number of contributions where non-crop-species have been investigated for volatile-based indirect defense is comparatively small (e.g. [29,30]). A study by Kessler and Baldwin [7] on the wild tobacco species, *Nicotiana attenuata*, in the desert of the southwestern United States was the first to demonstrate that herbivore-induced volatiles attract herbivore enemies in a natural community. More recently, some remarkable field studies by Heil and Kost on wild lima bean growing in Mexico showed that plant volatiles primed plants to increase their production of extrafloral nectar, which functions as a reward for carnivorous arthropods, such as ants, that attack herbivores [31,32].

Volatile attraction of herbivore enemies is not restricted to the aerial parts of plants. Rasmann *et al.* [33] discovered that insect-induced (*E*)-β-caryophyllene (Figure 2) emission from maize roots attracts nematodes that prey on the attacking insect larvae. Subsequent studies have investigated the combined effects of above and below ground herbivory, and demonstrated that herbivory in both locations reduces volatile emissions and predator and parasitoid attraction in maize and other species [18••,34,35••]. For example, the parasitic wasp *Cotesia glomerata* was attracted preferentially to caterpillars of the large cabbage white butterfly (*Pieris brassicae*) feeding on black mustard with undamaged roots as compared to cabbage white caterpillars feeding on plants whose roots were simultaneously infested by the cabbage root fly [18••].

The extension of studies on plant volatiles, herbivores and herbivore enemies to include multiple herbivores is a welcome development since this may more closely reflect natural conditions. Plants face a diversity of biotic and abiotic stresses in their natural environments that could modify volatile emission and indirect defense [36]. Concerning abiotic stresses, the increasing attention to global climate change has prompted some researchers to investigate whether increases in ambient levels of CO_2 or ozone in the atmosphere have any influence on the attraction of herbivore enemies. Some herbivore-induced volatile compounds are highly reactive with ozone, and elevated ozone concentrations were found to degrade most of the terpenes and green leaf volatiles emitted from both *Brassica oleracea* and *Phaseolus lunatus* after herbivore damage [37,38]. Nevertheless, herbivore enemies still oriented towards damaged plants after ozone treatment suggesting that ozone-stable volatile compounds, such as methyl salicylate and benzyl cyanide, might serve as sufficient signals for the enemies investigated in this study, the predatory mite *Phytoseiulus persimilis* and the parasitic wasp *Cotesia plutella* [37].

A hallmark of herbivore-induced volatile blends is their complexity, but until recently it has been difficult to determine which components of a blend are required for attraction of herbivore enemies. However, the use of transgenic plants with altered volatile emission profiles has allowed the identification of specific terpenes that are involved in indirect defense [39]. For example, a recent study used transgenic *A. thaliana* overexpressing the sesquiterpene products of a maize terpene synthase enzyme induced by caterpillars of the Egyptian armyworm (*Spodoptera littoralis*) [40]. The authors showed that the parasitic wasp, *Cotesia marginiventris*, which parasitizes *S. littoralis* caterpillars, is attracted to these sesquiterpenes (chiefly (*E*)-β-farnesene (Figure 2) and (*E*)-α-bergamotene). However, the wasps must first be exposed to these volatiles in association with their hosts. Transgenic terpene-emitting *A. thaliana* plants were also used to

Figure 3



Volatile-mediated interactions among plants, herbivores and herbivore enemies. The diagram depicts some of the direct and indirect effects of plant volatiles on various types of organisms and indicates where there are influences among the organisms. Solid arrows indicate verified interactions and dashed arrows indicate proposed interactions for which the evidence is not yet strong.

demonstrate that another parasitic wasp, *Diadegma semiclausum*, a natural enemy of the diamondback moth (*P. xylostella*), is repelled by isoprene (Figure 2). Since isoprene is not released by any natural host plant of the diamondback moth, this compound appears to serve as a negative cue for host seeking *D. semiclausum* [41••].

Costs and trade-offs of vegetative volatile emission

Vegetative volatiles may not always lead to increased plant fitness when release incurs costs that outweigh the benefits of emission. For example, the production of volatiles requires energy and nutrients that could otherwise be allocated to growth or reproduction [42]. Volatile emission may also incur ecological costs since herbivores as well as herbivore enemies can exploit induced volatile cues to find their hosts. Halitschke *et al.* [43] showed in a field study that green leaf volatiles emitted by the wild tobacco (*N. attenuata*) are important for the attraction of the herbivorous flea beetle, *Epitrix hirtipennis*. In addition to herbivores, other plant enemies, such as the parasitic plant, *Cuscuta pentagona*, employ plant volatiles in host finding [44]. Herbivores can also exploit volatiles to change their behavior in a way that is detrimental to plants. Thus the nocturnal-feeding caterpillar, *Mythimna separata*, uses the diurnal rhythm of the herbivore-induced volatiles of its host plant to regulate its own activity rhythm and so avoid the diurnally-active parasitic wasp, *Cotesia kariyai* [45••].

Volatile-mediated attraction of natural enemies may also have negative consequences if too many enemies are attracted at once. A high abundance of herbivore enemies could lead to increased intraspecific competition among plant benefiting insects [46•] or to increased intra-guild predation. Attraction of insectivorous birds to plant volatiles may reduce the population of insect herbivores [23], but may also lead to declines in insect species that are herbivore enemies.

When more than one herbivore species attacks the plant simultaneously (a likely scenario under natural conditions), the beneficial effects of volatiles for indirect defense may be diminished or even eliminated. For example, Tooker *et al.* [48] demonstrated that a goldenrod (*Solidago altissima*) attacked simultaneously by a lepidopteran species and a gall inducing tephritid fly was less attractive to herbivore enemies than goldenrod attacked only by the lepidopteran. Similarly, tomato plants attacked simultaneously by *Spodoptera exigua* caterpillars and the parasitic plant *Cuscuta pentagona* reduced their volatile production compared to tomato attacked only by *S. exigua* [49•]. The detrimental effects of below ground herbivory on volatile emission induced by simultaneous above ground attack have already been mentioned [18••,35••]. Due to these mitigating factors, the release of volatiles may not always result in an increase in plant fitness.

Conclusions

Our survey of the recent literature supports the proposition that vegetative volatiles play an important role in plant defense, either by direct repulsion of herbivores or attraction of herbivore enemies (Figure 3). Nevertheless, a full evaluation of the defensive significance of plant volatiles in nature awaits more field-based research. The effect of volatiles on plant fitness must be accurately assessed under natural conditions with multiple herbivores and consideration needs to be given to the interaction of herbivores and herbivore enemies with abiotic stresses and other trophic levels, including hyperparasitoids, pathogens, mutualists, and competing plants. Ultimately, such studies might be able to explain why herbivore-induced volatile blends are typically made up of complex mixtures rather than one or two substances [50,51]. If this chemical complexity reflects the complexity of interactions mediated by volatiles, we may have just begun to sniff the exciting world of plant volatiles.

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