

Language of plants: Where is the word?

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Abstract Plants emit biogenic volatile organic compounds (BVOCs) causing transcriptomic, metabolomic and behavioral responses in receiver organisms. Volatiles involved in such responses are often called “plant language”. Arthropods having sensitive chemoreceptors can recognize language released by plants. Insect herbivores, pollinators and natural enemies respond to composition of volatiles from plants with specialized receptors responding to different types of compounds. In contrast, the mechanism of how plants “hear” volatiles has remained obscured. In a plant-plant communication, several individually emitted compounds are known to prime defense response in receiver plants with a specific manner according to the chemical structure of each

volatile compound. Further, composition and ratio of volatile compounds in the plant-released plume is important in plant-insect and plant-plant interactions mediated by plant volatiles. Studies on volatile-mediated plant-plant signaling indicate that the signaling distances are rather short, usually not longer than one meter. Volatile communication from plants to insects such as pollinators could be across distances of hundreds of meters. As many of the herbivore induced VOCs have rather short atmospheric life times, we suggest that in long-distant communications with plant volatiles, reaction products in the original emitted compounds may have additional information value of the distance to emission source together with the original plant-emitted compounds.

Keywords: Green leaf volatiles; plant-insect communication; plant language; semiochemicals; volatiles

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Invited Expert Review

INTRODUCTION

Plants are chemical factories. They contain compounds originating from primary as well as from secondary metabolism. Secondary metabolites are defined as plant chemicals with no role yet found in growth, photosynthesis (Pn), reproduction or other primary functions. Primary metabolic processes are relatively well characterized in contrast to the secondary counterparts. Biogenic volatile organic compounds (BVOCs) are major secondary metabolites in plants. Plant physiological status, availability of light and other metabolic processes may affect significantly the distribution and the emission rates of BVOCs from different parts of plant canopy (Šimpraga et al. 2013).

An increasing number of secondary metabolites are identified to be signal molecules, antioxidants or compounds having other ecological functions. Especially, BVOCs are present in our everyday life perfuming the air around us. The typical pine smell (α -pinene and β -pinene), lemon scent (limonene), black pepper spiciness (sabinene) and eucalyptus smell (cineole) are some familiar examples of BVOCs from plants. Major BVOC subgroups are benzenoids, isoprene, mono-, and sesquiterpenoids. Besides being

present in plants and animals, they also occur in bacteria and fungi.

Volatile organic compounds emitted from plants can be semiochemicals (Greek “semeion” is a mark or a signal) representing volatile signals of plants and they function as mediators in communication between plants and other organisms and between plants (Peñuelas et al. 1995). BVOC biosynthesis depends on the carbon, nitrogen and sulfur availability as well as energy from the primary metabolism (Dudareva et al. 2013). The same authors explain that in some cases a single reaction and a single enzyme will convert a primary metabolite into a volatile compound, whereas in other cases multiple steps are required. These biosynthetic pathways are connected via a metabolic “crosstalk” mediated by yet unidentified transporter(s) (Muhlemann et al. 2014). Based on biosynthetic origin, BVOCs include multiple compound classes. Dudareva et al. (2013) classified them into four groups as terpenoids (pathway: MEP and MVA), fatty acid derivatives (pathway: Phytooxylipin), phenylpropanoids and benzenoids (pathway: Phenylpropanoid) and other amino acid derivatives. Terpenoids are the largest class of secondary metabolites with many volatile representatives. Phytooxylipin products are better known as green leaf volatiles (GLVs). They

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include C6 aldehydes, alcohols and their esters. GLVs compounds are produced when leaves are injured or suffer from biotic/abiotic stresses. GLVs are released within seconds in response to tissue damage. As they are gaseous and transported via air they can serve as a rapid within plant communication, which moves from one plant organ to the other much faster than any plant-internal compound (Heil and Bueno 2007). Finally, they have antifungal properties delaying fungal growth (Shiojiri et al. 2006).

Phenylpropanoids and benzenoids are common constituents of floral scent. Recently, several enzymes that catalyze the formation of floral benzenoid volatiles have been identified and characterized. A volatile benzenoid representative is MeSA (methyl salicylate). Additionally, phenylpropanoids include, for example, phenolic compounds containing hydroxyl functional group on an aromatic ring. They play several roles in plants such as defensive compounds against insect herbivores and fungi. Phenolic biosynthesis involves two pathways: Shikimic acid (higher plants) and malonic acid (fungi and bacteria) pathway. The other amino acid derivative is indole (derivative from amino acid tryptophan) produced by shikimate pathway (Erb et al 2015). Other amino acids such as alanine, methionine, valine serve as precursors for plant volatiles including aldehydes, alcohols, esters and acids. A group of volatile semiochemicals mediating plant–insect communication deserving attention are aldoximes and nitriles. They are released from several species after foliar damage (Takabayashi et al. 1991) as well as from flowers as attractants for hymenopteran parasitoids of herbivores in behavioral studies (Kugimiya et al. 2010). Compared to many GLVs or terpenoids these N-containing compounds are low in abundance. They show to be useful cues in the orientation of various parasitoid and predatory herbivore enemies. However, their biosynthesis as well as biological relevance are still unknown. Other example of N-containing volatiles, isothiocyanates attract braconid parasitoids that exploit hosts feeding on *Brassicaceae*, whose glucosinolate (S-containing metabolites) defenses are hydrolyzed on tissue damage to isothiocyanates (Murchie et al. 1997).

As BVOCs induction occurs by abiotic and biotic stresses, this may occur by human, animal or nature-induced way such as wounding, vegetation fires and light/temperature fluctuations. Herbivory induced BVOCs occur due to feeding or, for example, insect oviposition. Additionally, cut-induced such as mowing the grass, will also prime plumes of BVOCs release to the air.

PLANT LANGUAGE COMPONENTS

The term “plant language” or “talking trees” is used to describe plant signaling to neighboring plants. For example, elevated levels of phenolics and tannins in intact trees are observed when nearby trees were suffering mechanical leaf damage (Baldwin and Schultz 1983). The “plant language” is also considered to cover all communication with plants and other organisms (Peñuelas et al. 1995; Martinelli et al. 2013; Gagliano and Grimonprez 2015). The BVOC based communication of talking plants is more understandable when the receiver is an animal with wide variety chemosensors in their olfactory organs such as antennae in insects, but plants were

considered to be deaf based on the fact that no animal-like chemosensor structures for volatile signal perceptions has been described (Dicke et al. 2003).

Peñuelas et al. (1995) focused on terpenoids as plant language, because they are easily induced and emitted in response to abiotic and biotic stress factors and because terpenoids form the most diverse group of BVOCs. In their interpretation each five carbon isoprene units (C₅) of terpenoids forms a “syllable” and the sequential combination of these units in various volatile monoterpene (C₁₀) and sesquiterpene (C₁₅) compounds forms a “word”. In this analogy diverse terpenoid blends in the volatile plume emitted by a plant forms the “message”, and the “dialects” of plant language comes from the qualitative and quantitative characteristics of terpene composition in different plant species (Peñuelas et al. 1995). Indeed, Karban et al. (2014) found that within a plant species, individuals of the same chemotype communicated more effectively and experienced less herbivory than individuals of differing chemotypes, suggesting that plants may distinguish relatives from strangers. Gagliano and Grimonprez (2015) pointed out that the language of plants may also involve visual signals as gestures to complement the information transmitted by scents, and the specific chemical compound may have evolved to pass different information in different geographical areas.

RELEASE OF THE VOC SIGNALS FROM PLANT

Proton transfer reaction-time of flight (PTR-TOF) mass spectrometry has opened a new high resolution possibility for online measurement of rapid changes in plant volatile emissions rates (Brilli et al. 2011; Maja et al. 2014). Emissions GLVs (C₆ oxylipin compounds) are rapidly induced as a result of mechanical damage on plant tissue in several plant species including *Dactylis glomerata*, *Populus alba* (Brilli et al. 2011) and *Betula pendula* (Maja et al. 2014). In *B. pendula* GLVs are emitted rapidly after each feeding activity period of *Geometrid* larvae during a 2 h monitoring period (Maja et al. 2014, Figure 1). The ion mass *m/z* 81.070 (corresponding to C₆ aldehydes, e.g., (Z)-3-hexenal, (E)-3-hexenal and (E)-2-hexenal), being the compound group showing the most rapid response having the emission peak within 2–3 min from the start of feeding damage. Ions corresponding to, for example, (Z)-3-hexenol and (Z)-3-hexenyl acetate have the emission peak with 10–15 min delay and this fluctuation of emissions can be monitored even 24 h (Maja et al. 2014). Similar succession in the emission of these compounds was found by Brilli et al. (2011) after cutting a leaf with a sharp blade. Matsui et al. (2012) reported that (Z)-3-hexenal is the major product in completely disrupted *Arabidopsis* leaf tissues, while (Z)-3-hexenol and (Z)-3-hexenyl acetate were the main products formed in the intact parts of partially wounded leaves.

The order of the C₆ compound emissions after larval feeding activity may explain at least partially why *Cotesia vestalis*, a parasitoid of *Plutella xylostella*, prefers landing on damaged *Brassica* leaf tissue and first actively analyze the extension of damage, although the host larvae are available on the same leaf (Holopainen et al. 2013). It is likely that emission of hexenal compounds from a damaged area may

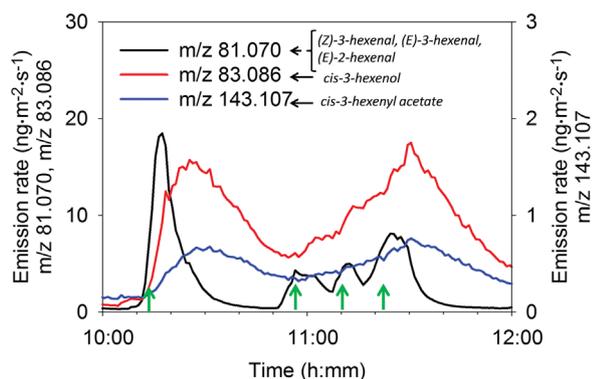


Figure 1. Example of emission of volatile organic compounds (VOCs) used in short distance communication between plant and parasitoids of herbivores

Herbivore-induced emissions of C6 green leaf volatiles from *Betula pendula* foliage were monitored by Proton transfer reaction-time of flight mass spectrometry (PTR-TOF-MS) in a series of experiments reported by Maja et al. (2014). Green arrows indicate detected feeding periods by Geometrid moth larvae.

indicate the most recent damage and presence of host larvae nearby, while emissions dominated by (Z)-3-hexenol and (Z)-3-hexenyl acetate indicate damaged leaf, but not so fresh damage, thus possibly telling the parasitoid about lower probability to find a host larva. In laboratory tests, when offered separately (E)-2-hexenal, (Z)-3-hexenol and (Z)-3-hexenyl acetate cues elicited positive response in *C. vestalis* (Reddy et al. 2002).

On the other hand, continuous 24 h mechanical damage on plant leaves with a mechanical MecWorm is sufficient to induce similar composition of oxylipins, but also emissions of typical herbivore-induced terpenoids and benzenoids (Mithöfer et al. 2005). Normally induction of these compounds is related to herbivorous insect saliva and regurgitates (Gouinguene and Turlings 2002) and therefore herbivore-induced compounds function in attraction of natural enemies of insect herbivores (Dicke et al. 2003).

LIFE TIME OF VOC SIGNALS IN THE ATMOSPHERE

Pinto et al. (2007) and Blande et al. (2010) found that in conditions of elevated tropospheric ozone (O_3) the atmospheric concentrations of many of the herbivore-induced BVOCs rapidly decreased and some compounds even disappeared. It is very well known that BVOCs have different atmospheric life time due to their reactivity with ozone, hydroxyl radicals (OH) and nitrate NO_3 radicals (Atkinson and Arey 2003). Particularly, the number of double bonds affects their reactivity. Among key BVOC groups known to act as plant signals, GLVs and some monoterpenes (MT) have slightly longer life time than sesquiterpenes (SQT), but there is huge variability. In standardized OH, O_3 or NO_3 concentration lifecycle of MT *cis/trans*-ocimene is 33, 44 and 3 min, SQT β -caryophyllene 42, 2 and 3 min and GLV

cis-3-hexenyl acetate 1.8, 7.3 and 4.5 h, respectively. The respective values are, for example, for MT β -pinene 1.8 h, 1.1 d and 27 min and for SQT longifolene 2.9 h, <33 d and 1.6 h (Atkinson and Arey 2003).

SIGNAL PERCEPTION IN INVERTEBRATES

In the analysis of herbivorous insect host location behavior Bruce et al. (2005) suggested the ratio of volatile compounds in host-plant emitted odor plume is essential for flying insects to be able to locate their host plant. Electroantennogram measurements have shown that receptors in herbivorous insect antennae may have strong response, if the ratio of compounds in the odor is typical for this host. When the same compounds in different ratios were offered, the attraction was switched off. This means that flying insects are capable of locating their host plant on the basis of olfactory signals, although the same ubiquitous compounds are emitted by various plants in the environment. The ratio of specific compounds separates the noise from the signal.

In long distance communication by BVOCs the situation becomes more complicated. Atmospheric oxidants such as ozone, OH and NO_3 radicals may degrade some plant emitted VOCs at a substantially higher rate than other compounds in the same plume (Atkinson and Arey 2003, Holopainen and Gershenson 2010). This means that the original ratio of compounds emitted by the host plant do not exist in the longer distances, e.g., 100–200 m from the emitting plant in the ambient air of an industrial era (McFrederick et al. 2009). The same authors suggested that insect may suffer from the loss of reliable plant signals, but the evidence of behavioral tests with parasitoids and predators in ozone-rich atmospheres does not give very strong support to this hypothesis (Pinto et al. 2007). Pinto et al. (2007) suggested that signal value loss of original plant emitted VOCs by atmospheric reactions could be compensated with increased number of reaction products of the parent VOCs and these may also have signaling value for insects. However, recent BVOC analyses and behavioral tests with *Brassica nigra* flower volatiles and bumblebees at ozone-polluted atmosphere (120 ppb O_3) revealed that monoterpenes, anisaldehyde and alkylbenzene *p*-cymene concentrations in floral scent was reduced approximately 20% at a 3 m distance and 30% at a 4.5 m distance from the inflorescence and scent attractiveness to pollinator was significantly reduced over a 4.5 m distance when compared to original scent (Farré-Armengol et al. 2016).

What are the breakdown products of BVOCs? In general, atmospheric reactions of BVOCs are complicated, and, ozonolysis reaction products of a common monoterpene limonene may yield more than 1,200 chemical compounds that may be semivolatiles or solid particles (Kundu et al. 2012). Reaction chamber experiments have shown that O_3 mostly affects C=C bonds OH and NO_3 radicals C=C and C-H bonds of BVOC molecules. Alkyl radicals are often the early stage reaction products (Atkinson and Arey 2003). Therefore, we propose (Figure 2) that some of the breakdown products of plant VOCs such as C2–C6 fragments of C10 monoterpenes or oxidized forms of emitted BVOCs (Lee et al. 2006) may have signaling value together with the original compound released

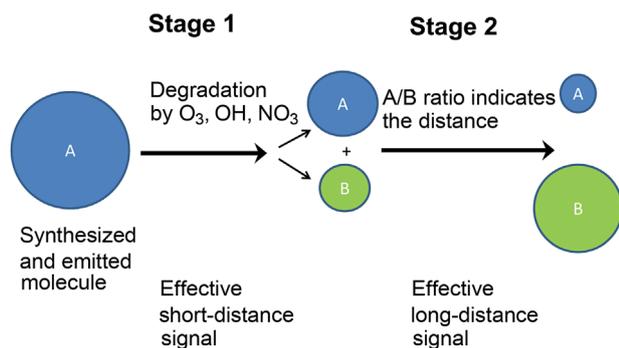


Figure 2. Suggested process of long-distance communication by combination of herbivore-induced volatile organic compounds (VOCs) and their reaction products in reactions with ozone, OH and NO₃ radicals.

by plants in long-term communication. Their proportion and ratio to original compound in the volatile plume could even be an indicative “odometer” for orientating insects. So far, olfactory sensors in parasitoid antennae and their functions are still relatively poorly known, although the importance of herbivore-induced volatiles blend are known to be more important attractants than a single compound causing orientation towards herbivore-damaged plants (Mann et al. 2012; Nishimura et al. 2012; Aksenov et al. 2014). Some of the breakdown products are less volatile than the original emitted BVOCs and this change of volatility may cause stickiness, better absorbance on receiver plant surface and possibly influence at least associational resistance in the neighborhood of emitter plants (Blande et al. 2014).

SIGNAL PERCEPTION IN PLANTS

Lack of known chemosensor organs with their odor-binding proteins in plant has limited the understanding of plant to plant communication (Dicke et al. 2003). However, plants can uptake various gaseous compounds including CO₂ and BVOCs through their stomata and after taking up BVOCs can enter into anabolic or catabolic pathways of plants (Niinemets et al. 2014). A precursor of one of the phytohormones MeSA is one of the best known plant-to-plant signaling molecules inducing response in neighboring plants (Shulaev et al. 1997). MeSA is hydrolyzed to generate the active form of salicylic acid (SA) (Forouhar et al. 2005), which induces defense responses against pathogens (Kumar and Klessig 2003). MeJA is also well-known plant-plant signaling molecule. Recently several SA-binding proteins have been described in plants (Manohar et al. 2015) which could be related to MeSA signal perception. Exogenously applied methyl jasmonate is hydrolyzed by esterases to yield free jasmonic acid (Wu et al. 2008). In *Arabidopsis*, free jasmonic acid would be further converted into jasmonoyl-l-isoleucine (Staswick and Tiryaki 2004, Fonseca et al. 2009).

Priming of genes related to several pathways in plant has been described when plants are exposed to volatiles from neighboring plants (Arimura et al. 2000, Yoneya and Takabayashi 2014). Monoterpene β -ocimene and

homoterpenes DMNT and TMTT, but not the monoterpene alcohol linalool, primed defense genes in lima bean (Arimura et al. 2000). Benzenoid indole is an important priming volatile compound in corn (Erb et al. 2015). It should be also noted that plants are capable of sensing the volatiles emitted by their potential antagonist such as herbivorous insects. Helms et al. (2013) found that when Goldenrod plants were exposed to male sex pheromones (spiroacetals) of the gall-inducing fly *Eurosta solidaginis* production of defense hormone jasmonic acid was enhanced in herbivore damaged plants. However, *E. solidaginis* sex pheromones did not prime defense response in maize or beans suggesting that plant can “eavesdrop” only communication between coevolved herbivores (Helms et al. 2013).

Kishimoto et al. (2005) monitored expression profiles of the genes involved in defense responses upon exposing *Arabidopsis thaliana* to GLVs ((*E*)-2-hexenal, (*Z*)-3-hexenal and (*Z*)-3-hexenol). Among the genes investigated, chalcone synthase (CHS), caffeic acid-O-methyltransferase (COMT), diacylglycerol kinase1 (DGK1), glutathione-S-transferase1 (GST1) and lipoxygenase2 (LOX2) were shown to be induced with (*E*)-2-hexenal, (*Z*)-3-hexenal, (*Z*)-3-hexenol. A salicylic acid-responsive gene, pathogenesis-related protein 2 (PR2), was not induced by the volatiles. Detailed analyses of the expression profiles showed that the manner of induction varied depending on either the gene monitored or the volatile used, indicating that plants could recognize the chemical structure. With a jasmonate-insensitive mutant (*jar1*), the induction by the volatiles was mostly suppressed; however, that of LOX2 was unaltered. It was suggested that both the jasmonate-dependent and -independent pathways were operative upon perception of the volatiles.

Kikuta et al. (2011) showed that wound-induced VOCs from artificially damaged *Chrysanthemum cinerariaefolium* plant induced the biosynthesis of pyrethrins in volatile-exposed neighboring plants. In this plant-plant signaling, a blend of five compounds ((*Z*)-3-hexenal, (*E*)-2-hexenal, (*Z*)-3-hexenol, (*Z*)-3-hexenyl acetate and (*E*)- β -farnesene) at specific concentrations is essential for the pyrethrin biosynthesis in receiver plants. Thus, in this system, a specific blend of volatile compounds is a sentence indicating the forthcoming danger.

Sugimoto et al. (2014) reported that undamaged tomato plants that had been exposed to volatile from tomato plants infested by common cutworms (CCW) (exposed plants) became more defensive against CCWs than those exposed to volatiles from uninfested conspecifics (control plants) in a constant airflow system under laboratory conditions. The amount of (*Z*)-3-hexenylvicinioside (HexVic) was detected to be higher in exposed plants than that in control plants, and this compound negatively affected the performance of common cutworms when added to an artificial diet. The aglycon of HexVic, (*Z*)-3-hexenol, was originated from the neighboring infested plant volatiles. These data suggest that glycosidation is one of the mechanisms involved in the volatile reception in plants.

PATHOGEN INFECTION INDUCES AND/OR ALTERS VOC PRODUCTION

Beside having an impact on plant transpiration (increase), plant respiration (increase) and Pn (decrease), pathogens and

plants communicate by means of volatiles by inducing or altering them. Pathogenic bacteria are capable of producing a large variety of volatile metabolites (Bos et al. 2013). Pathogenic fungi as well as pathogenic bacteria do have a distinct metabolism. A great deal of progress has been made in understanding the role and mechanisms of bacteria (or fungi)-specific BVOCs release. Pathogen-induced plant responses include changes in both volatile and non-volatile secondary metabolites (Huang et al. 2003). It has been documented that pathogen infections alter BVOC profiles making infected plants more attractive to specific vector. This way, transmitted pathogens potentially aid pathogen propagation (Aksenov et al. 2014). Additionally, by altering BVOC production volatiles influence plant morphology and plant chemistry (Mann et al. 2012).

Pathogens induce chemical release from plants that benefit their survival and suppresses plant defense responses (Mann et al. 2012) as, for example, *Candidatus phytoplasma mali* apple infection induces release of β -caryophyllene attracting apple phylloids (*Cacopsylla picta*). This way volatiles facilitate pathogen spreading. White mold (*Sclerotium rolfsii*) infected peanut plants emitted a mixture of lipoxygenase products, terpenoids, indole, and MeSA, which were both quantitatively and qualitatively different from volatiles collected from healthy plants (Huang et al. 2003). Mann et al. (2012) explained that different virus-infected plants (viruses such as CMV, PLRV and BYDV) are more attractive to their aphid vectors (such as *Aphis gossypii*, *Myzus persicae* and *Rhopalosiphum padi*) than to non-infected plants. The reason lies in the induced production of volatiles as a result of infection (Mann et al. 2012). Pepper plants exposed to different bacteria emitted distinct blends of compounds consisting of monoterpenes, homoterpenes, lipoxygenase products, linalool, MeSA and cis-jasmone (Cardoza and Tumilson 2006). This has been reported in several crop and plant systems, including maize, citrus, potato, peanuts and tobacco plants (Huang et al. 2003; Aksenov et al. 2014). Finally, the idea of implementing these semiochemicals for pathogen management is becoming common, however, these pathogen-plant volatile interactions are not within the scope of this mini review.

CONCLUSIONS AND FUTURE CHALLENGES

We conclude that there is evidence of different kind of chemical “words” on the volatile communication by plants. In very short range communication the C6 GLV compounds may have important roles to guide parasitoids to actual feeding sites of herbivores in the plant foliage. GLVs act also in within-plant and between-plant communications. Reports of volatile plant-plant communication indicate rather short, usually not longer than one meter distances in signaling. Signal perception in plants is not as sensitive as chemoreception by insects. Therefore, it is obvious that BVOC sensing by plants is more prone to atmospheric disturbances and BVOC reactions with atmospheric oxidants may lead to even shorter signaling distances (Blande et al. 2010). This observation suggests that response in receiver plant needs rather high concentration of signaling compounds and the atmospheric

reaction products of BVOC might not have signaling value for receiver plants.

Reduction in concentration or total loss of the herbivore-induced compounds in ozone-rich air does not eliminate BVOC signals for insects and other arthropods (Pinto et al. 2007). This is supporting our suggestion in this review that a combination of original plant emitted compound and the reaction product may have signaling value for orientating insects. Electroantennogram experiments with some known reaction products of known signaling VOCs are needed for testing this hypothesis.

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AUTHOR CONTRIBUTIONS

M.S., J.T. and J.K.H. drafted the manuscript together, M.S. wrote the manuscript and J.T. and J.K.H. commented and revised the manuscript.

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