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Infochemical terminology: based on cost-benefit analysis rather than origin of compounds?

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Abstract. The involvement of chemicals in interactions between individual organisms has been recognized for many years. The current terminology of these so-called semiochemicals developed over a 25 year period and the definition of each category was proposed in a specific context. As a result, the definitions of the various categories are heterogeneous.

The present definition of semiochemicals (Nordlund & Lewis, 1976) includes toxins and nutrients. We distinguish between (a) toxins and nutrients, which are *themselves* to the benefit or detriment to the interacting organisms and (b) information conveying chemicals (infochemicals). Through the *response* they elicit these latter chemicals are to the benefit or detriment of the receiving organism. Toxins and nutrients may also convey information. If so, we propose to refer to these chemicals as toxin or nutrient when poisonous or nutritious aspects are considered and as infochemical when their role as information carrier is considered.

Semiochemical terminology according to Nordlund & Lewis (1976) is based to a large extent on the origin of the compounds in specific interactions. Only those interactions are regarded where one of the interactants is the producer or emitter of the chemical. However, if an infochemical plays a role in the interaction between two individuals, it is by no means certain that either of the two is the actual producer or emitter. The producer or emitter may be a different organism from the same or even from another trophic level but is clearly associated to at least one of the

interactants. Arguments are given to eliminate the origin criterion from the terminology and to use the cost-benefit criterion as the sole determinant of infochemical subdivisions.

Introduction

The involvement of chemicals in conveying information in intra- and interspecific interactions between organisms appears to be widespread. Interactions mediated by these so-called semiochemicals (Law & Regnier, 1971; Table 1) can be found within and between vertebrates, invertebrates, plants and micro-organisms (Nordlund, Jones & Lewis, 1981; Schoonhoven, 1981; Albone, 1984; Bell & Cardé, 1984; Rhoades, 1985; Sabelis & Dicke, 1985; Sonenshine, 1985; Visser, 1986; Dicke, 1988a) in the same or different trophic levels (Price, 1981). They involve many behavioural activities or physiological responses, such as searching for food or oviposition sites, locating a mate, marking a resource area and so on.

Many terms have been proposed to describe different classes of semiochemicals (for review see Table 2.1 in Nordlund, 1981) but only a few have survived (Nordlund & Lewis, 1976). Also, the definitions of some terms have been modified. For instance, compare the definitions of allomone in Brown, Eisner & Whittaker (1970) with those in Nordlund & Lewis (1976); the latter authors modified the original definition and distinguished between allomones and synomones as two classes of the original category of allomones. Because of the many modifications in semiochemical terminology, current definitions are heterogeneous. Each definition was developed and proposed in a specific context; e.g. the term pheromone (Karlson & Lüscher, 1959; Table 1) was coined to distinguish this class of semiochemicals from hormones.

A summary of current semiochemical terminology (according to Nordlund & Lewis, 1976) is shown in Fig. 1. This structure is reasonably consistent but we think that the different definitions should be based on a more explicit and common logic to make it more coherent and less

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Table 1. Contemporary semiochemical terminology according to Nordlund & Lewis (1976).

<i>Semiochemical</i>
Chemicals involved in the chemical interactions between organisms. Nordlund & Lewis, 1976.
<i>Pheromone</i>
A substance that is secreted by an organism to the outside and causes a specific reaction in a receiving organism of the same species. Karlson & Lüscher, 1959.
<i>Allelochemic</i>
Chemical significant to an organism of a species different from its source, for other reasons than food as such. Whittaker, 1970.
<i>Allomone</i>
Chemical substance produced or acquired by an organism, which, when it contacts an individual of another species in the natural context, evokes in the receiver a behavioural or physiological reaction adaptively favourable to the emitter but not to the receiver. Nordlund & Lewis, 1976.
<i>Kairomone</i>
A substance produced or acquired by, or released as the result of the activities of an organism, which, when it contacts an individual of another species in the natural context, evokes in the receiver a behavioural or physiological reaction adaptively favourable to the receiver but not to the emitter. Nordlund & Lewis, 1976.
<i>Synomone</i>
A substance produced or acquired by an organism, which, when it contacts an individual of another species in the natural context, evokes in the receiver a behavioural or physiological reaction adaptively favourable to both receiver and emitter. Nordlund & Lewis, 1976.

ambiguous. This is the subject of the present paper.

Infochemicals, toxins and nutrients

Law & Regnier (1971) defined semiochemicals as ‘chemical signals that transmit information between individual organisms’; the essential word being ‘signals’ (Greek σημειον, semion: mark or signal). The word ‘signal’ pre-supposes that the chemical is purposefully sent to the receiver and hence that *communication* is taking place (Law & Regnier, 1971). However, the receiving organism commonly acts as an eavesdropper that uses chemicals from the emitter as a source of *information* (cf. Otte, 1974 for discussion on the terms signal, information and communication). This was recognized by Nordlund & Lewis (1976) and therefore, they (Nordlund, personal communication)

eliminated ‘signal’ from the definition, and re-defined semiochemicals as ‘chemicals involved in the (chemical) interactions between organisms’ (Nordlund & Lewis, 1976; Nordlund, 1981). Also the qualification ‘information transmitter’ has been removed. Thus, the original definition of a semiochemical (Law & Regnier, 1971) has been broadened by Nordlund & Lewis (1976) and Nordlund (1981) to include not only information-transmitting chemicals but also chemicals that function as toxins or nutrients.

Why organisms invest in producing information transmitters is an interesting question and requires a clear understanding of the benefits to the producer. The evolution of their production is less obvious than that of nutrients and toxins, that are themselves to the benefit or detriment of the receiving organism. Organisms generally perceive toxins and nutrients (but see Schoonhoven, 1981)

Fig. 1. Structure of current semiochemical terminology according to Nordlund & Lewis (1976).

Table 2. Infochemical terminology.

<i>Infochemical</i>	A chemical that, in the natural context, conveys information in an interaction between two individuals, evoking in the receiver a behavioural or physiological response that is adaptive to either one of the interactants or to both.
<i>Pheromone</i>	An infochemical that mediates an interaction between organisms of the same species whereby the benefit is to the origin-related organism ([+, −] pheromone), to the receiver ([−, +] pheromone) or to both ([+, +] pheromone).
<i>Allelochemical</i>	An infochemical that mediates an interaction between two individuals that belong to different species.
<i>Allomone</i>	An allelochemical that is pertinent to the biology of an organism (organism 1) that, when it contacts an individual of another species (organism 2), evokes in the receiver a behavioural or physiological response that is adaptively favourable to organism 2 but not to organism 1.
<i>Kairomone</i>	An allelochemical that is pertinent to the biology of an organism (organism 1) and that, when it contacts an individual of another species (organism 2), evokes in the receiver a behavioural or physiological response that is adaptively favourable to organism 1 but not to organism 2.
<i>Synomone</i>	An allelochemical that is pertinent to the biology of an organism (organism 1) that, when it contacts an individual of another species (organism 2), evokes in the receiver a behavioural or physiological response that is adaptively favourable to both organism 1 and 2.

and respond to them (e.g. Pasteels, Daloze & Rowell-Rahier, 1986). Thus, toxins and nutrients may also convey information. For these reasons we propose to classify poisonous substances as toxins and alimentary substances as nutrients when poisonous or alimentary aspects are considered respectively and as infochemicals (Table 2) when their role as information carriers is considered. Thus, a specific chemical may be both a toxin and an infochemical, depending on which aspect of the chemical is being discussed. In the remaining part of this paper we discuss infochemicals exclusively.

Pheromones and allelochemicals

Pheromones, as originally defined by Karlson & Lüscher (1959), are substances that are secreted by an organism to the outside and cause a specific reaction in a receiving organism of the same species. Originally the words ‘to the outside’ were the most important part of this definition, to distinguish these chemicals from hormones. To date, for distinguishing pheromones from allelochemicals the last four words of the pheromone definition (‘of the same species’) are the most important. According to current terminology, a pheromone mediates an interaction in which the emitter and the receiver are conspecific, whereas in the case of an allelochemical the ‘source’ and receiver belong to different species (Table 1). Allelochemicals can be subdivided into three

categories: allomones, kairomones and synomones (Nordlund & Lewis, 1976). According to the current definitions, these chemicals are produced or acquired by the source organism (the ‘emitter’). The distinction between the three categories is made according to which organism benefits in the interaction: the emitter (allomone), the receiver (kairomone) or both (synomone). In agreement with Weldon (1980), we feel that this is a useful criterion as knowledge of an organism’s response to an infochemical necessarily evokes questions about cost-benefit aspects.

Allomones

The term allomone has been used widely and without question. However, we feel that in many cases the substances described are toxins and not infochemicals: e.g. Nordlund (1981) who regarded venoms used by rattlesnakes in capturing prey as allomones and Duffey (1976) whose review on allomones deals exclusively with toxins.

Often allomones are described as repellants but they may also serve as attractants of prey organisms (Eberhard, 1977; Balan & Gerber, 1972; Jansson & Nordbring-Hertz, 1979).

Kairomones

There have been many discussions on the usefulness of the term kairomone (Blum, 1974; Weldon, 1980; Pasteels, 1982) but it is used widely. The main criticism has been that a chemical mediating

an interaction that is detrimental to the emitter will be selected against. However, the evolutionary persistence of a kairomone depends on the benefit the emitter obtains in other interactions mediated by this chemical, relative to the detriment suffered when it acts as a kairomone (Nordlund & Lewis, 1976; Weldon, 1980). For instance, the aggregation pheromone of bark beetles may function in interspecific interactions as a kairomone that attracts predators (Wood, 1982).

The term kairomone has mainly been used for chemicals mediating interactions between predators/parasites and their prey/host (e.g. Nordlund *et al.*, 1981). Unfortunately, infochemicals mediating interactions between herbivores and their host plants have not generally been referred to as kairomones (for exceptions see e.g. Metcalf, Metcalf & Rhodes, 1980; Price, 1981; Schoonhoven, 1981; Lanier, 1983; Andersen & Wilkin, 1986; Dicke, 1986).

Synomones

Whittaker & Feeny (1971) classified allelochemicals that benefit the receiver as well as the emitter as both kairomones and allomones (see Table 1 in their publication). Nordlund & Lewis (1976) ended this confusion and introduced the term synomone for such allelochemicals. This was a valuable contribution to the terminology. However, application of the term has not been satisfactory to date. Many authors who describe synomones do not use this word (e.g. Eisner & Grant, 1981; Camazin, 1985). Others erroneously use the repellency criterion to classify compounds as allomones that are in fact synomones. For instance, Schoonhoven (1981) reviews plant chemicals that repel herbivorous insects and classifies these compounds as allomones. However, as these allelochemicals not only benefit the plant in reducing damage but also benefit the insect by avoiding intake of toxins, they should be classified as synomones.

Criteria in the present terminology

The present terminology (Nordlund & Lewis, 1976) uses two criteria for classification: (1) whether the organism that is the origin of the compound ('the secreting organism' in the pheromone definition or 'the source' in the allelochemical definition; Table 1) and the receiver are conspecific or not; (2) whether the emitter ('producer or acquirer'), the receiver or both benefit from the interaction that is mediated by the compound; this cost-benefit criterion has only

been applied to allelochemicals. The origin of the compound is of central importance in this terminology. However, in the distinction that depends on the origin criterion (between pheromones and allelochemicals) ambiguous terms are used, such as 'secreted to the outside' or 'source'. These terms do not clarify whether the origin produces or emits the compound. Moreover, apart from confusion about the identity of the origin, the mere inclusion of the origin in the distinction may lead to ambiguities. This is illustrated below.

1 Ambiguity of the origin concept causes confusion: an example of beetle pheromones produced by associated micro-organisms.

Bark beetles aggregate on trees, where they feed and breed on host tissues just under bark. The interindividual interactions in which these beetles take part are mediated by many infochemicals (Wood, 1982; Birch, 1984). Bark beetles that singly attack a tree may die because of resin production by the tree. By attacking a tree communally the beetles are more likely to overwhelm the tree's defense and colonize it. After pioneer beetles attack a tree, conspecifics are attracted by a mixture of beetle-released compounds and host tree compounds (see Birch, 1984, for review). However, in some cases the beetle-released compounds are produced by symbiotic fungi living in the beetle's mycangium (Brand *et al.*, 1975, 1976). Therefore, not all components are pheromones (*sensu stricto*). However, although it is known that bark-beetle pheromones may not be produced by the beetles but by micro-organisms, the fact that the interaction is between conspecific beetles has been the decisive factor for classifying non-beetle compounds as beetle pheromones.

A similar situation exists in the beetle *Costelytra zealandica* (White) in which a volatile sex pheromone (phenol) is produced by bacteria in the colleterial glands of the females (Henzell, 1970; Henzell & Lowe, 1970; Hoyt, Osborne & Mulcock, 1971).

2 Ambiguities resulting from the inclusion of the origin criterion in the terminology: plant-related origin of spider-mite kairomone and spider-mite pheromone.

Spider mites feed on plants. They insert their stylets into the plant tissue, inject saliva (Storms, 1971) and consume the predigested plant-cell contents (Helle & Sabelis, 1985). During this process, volatile chemicals are emitted from the plant-mite complex, which are used as infochemicals in prey searching by spider-mite predators from the acarine family Phytoseiidae (Sabelis & Dicke, 1985). These volatile allelochemicals are

Fig. 2. Illustration of 3 possible infochemical emitting pathways.
E = Emitter
P = Producer
A = Acquirer
I = Inducer
R = Receiver

spider-mite species specific and have been referred to as kairomones (Sabelis & Van de Baan, 1983; Dicke & Groeneveld, 1986). The cost/benefit analysis was the criterion for that classification. Application of the origin criterion is far from clear cut as the origin of the compounds is still poorly understood; they are present on/in the host-plant leaf and in the spider mites and their faeces (Sabelis, Afman & Slim, 1984). Previously infested leaves from which all spider mites are removed are highly attractive to the predators but it is unknown in what way the leaf gets contaminated with the kairomone. The faeces on the leaf are not sufficient to explain the attraction of previously infested leaves (Sabelis, Afman & Slim, 1984). Presumably part of the compounds is emitted from the host plant but only after spider-mite damage. This mechanism, that will be called induction, is an alternative to production or acquisition of an allelochemical (cf. definitions of allomones, kairomones and synomones in Nordlund & Lewis, 1976). Induction is a process where the actual producer of the infochemical may not be one of the interactants but an organism that is closely associated to one of them (Fig. 2). In this process the inducer affects the production of the infochemical. The spider mite may be involved actively (nutritious compounds are metabolized by the spider mite and the waste products emanate from the plant) or passively (the plant 'recognizes' spider-mite damage and responds by producing the specific allelochemical). Research directed to elucidating the source of the kairomone will be of great value in better understanding the role of the

spider mite and the host plant in kairomone production/induction.

From comparison of data of Dabrowski & Rodriguez (1971), Dicke (1986) and Dicke (1988b) it can be deduced that at least one of the kairomone components is also a component of a volatile dispersing pheromone of the prey mite. This means that an infochemical that is emitted from the host plant mediates the interaction between individual conspecific spider mites. Because of its origin, this infochemical would not be classified as a pheromone (emitter and receiver are not conspecific) but when the interacting organisms are taken into account it is.

3 Application of the origin criterion limits the number of interactions considered.

In the current terminology (Nordlund & Lewis, 1976) the cost-benefit analysis determines whether an allelochemical is an allomone, kairomone or synomone. In a few instances, a definite classification has not been made because the costs/benefits of the chemical to the emitter were not understood (Carton, 1976; Greany *et al.*, 1977; Dicke *et al.*, 1984). In these cases, fermentation products of the microbial food of dipteran larvae are involved in host-habitat location by larval parasites. For classification of these infochemicals the interaction between the microbes and the wasps has been taken into account. Because nothing is known about the costs and benefits of the allelochemical (emitter and receiver belong to different species) no further classification can be made in the interaction between microbe and parasitic wasp. However, when the origin criterion is abandoned, another interaction can be considered: that between the microbivore and the parasitic wasp. This interaction is mediated by the microbial infochemicals, which are pertinent to the biology of the microbivore, and therefore a cost-benefit analysis for this interaction is appropriate. This analysis leads to the conclusion that here the allelochemical is a kairomone.

Value of the origin criterion

For most infochemicals the exact origin (producer) has not been investigated. However, in one case micro-organisms have been implicated as the producers of an insect pheromone (Henzell, 1970; Henzell & Lowe, 1970; Hoyt, Osborne & Mulcock, 1971; Brand *et al.*, 1975, 1976), and in another the evidence suggests that a plant is involved in production of a spider-mite pheromone and a spider-mite kairomone (Dicke, 1986; Dicke

1988b). In our opinion the origin of an infochemical is not important for classification of the compound. From an evolutionary point of view the mere fact that an interaction is mediated by the infochemical invites a cost-benefit analysis for both interactants. We propose to eliminate the origin criterion. Thereby, the role of organisms, other than the producer/emitter or receiver, in the production of the infochemical is included. This has often been overlooked, especially when micro-organisms are involved in the production of an infochemical that mediates an interaction between two other organisms. Micro-organisms are involved in infochemical production in many different interactions (for review, see Dicke, 1988a). With the increase in our knowledge of the involvement of micro-organisms in interactions between other organisms (e.g. Jones, 1984), more mediations by microbes are likely to be discovered. When micro-organisms are involved in production of infochemicals that mediate interactions between other organisms, the origin criterion of infochemical terminology would complicate classification because of the intermediate microbial trophic level. In our classification every interaction mediated by an infochemical deserves a cost-benefit analysis but only if the infochemical is pertinent to the biology of one of the interactants.

New definitions of pheromone, allelochemical, allomone, kairomone and synomone

Pheromone

Concurrent with elimination of the origin criterion we propose to include a cost-benefit criterion. To date, no cost-benefit criterion exists for pheromones, although 'benefit-to-the-species' terms have been employed. However, natural selection does not act on the species level but on that of genes or individuals. Therefore, the cost-benefit analysis should be applied to the latter. Interacting individuals of the same species are selected for contributing a maximum genetic output to the next generation. Therefore, pheromones may not always benefit both emitter and receiver, both because of asymmetric intraspecific interactions and because of the existence of individual or kin pheromones (e.g. Greenberg, 1979; Beauchamp, Yamazaki & Boyse, 1985; Blaustein & O'Hara, 1986; Linsenmair, 1985; Sherman & Holmes, 1985). This was recognized by Rutowski (1981) who suggested restricting the term pheromone to intraspecific interactions where both emitter and receiver benefit. However, he did not suggest

names for pheromones benefiting only one of the interactants. As the term pheromone has been widely accepted we suggest that its use be continued but that it should be qualified with '(+, -)', '(-, +)' or '(+, +)' where respectively the origin-related organism, the receivers or both benefit. Therefore, we propose the following definitions of a pheromone: an infochemical that mediates an interaction between organisms of the same species in which the benefit is to the origin-related organism ([+, -] pheromone), to the receiver ([-, +] pheromone) or to both ([+, +] pheromone). An example can be found in the cannibalistic snail *Fasciolaria tulipa* L. (Snyder & Snyder, 1971). This predator produces a pheromone that may be used to distinguish different sizes of conspecifics. A snail moves towards conspecifics with a size smaller than its own and away from conspecifics with a size larger than its own. For a large receiver snail the infochemical involved is a (-, +) pheromone, as is the case for an interaction where the large snail is the emitter and a small one the receiver.

The pheromone subdivisions proposed here, based on cost-benefit analysis at the individual level, complement previous subdivisions that were made on the basis of the kind of interactions being mediated (e.g. marking, sex attraction). Thus, it is possible to distinguish (+, +), (+, -) and (-, +) marking pheromones. However, it should be noted that many of these classifications suggest that natural selection acts at the species level. For instance, the term anti-aggregation pheromone in bark beetles suggests that the colonizing bark beetles emit an anti-aggregation signal. However, this denies the selection pressure present on individual beetles and therefore is evolutionarily inconceivable. The colonizing beetles convey information about the present beetle density. Beetles that receive this information may then decide to settle despite the emission of the pheromone or to leave in search of another tree. Their response is determined over evolutionary time by the prospects for reproduction of these alternatives (Alcock, 1982).

Allelochemical, allomone, kairomone, synomone

Analogous to the new definition of pheromones, an allelochemical is defined as an infochemical that mediates an interaction between two individuals that belong to different species. By eliminating the origin criterion and maintaining the cost-benefit analysis criterion we propose the

Fig. 3. Structure of infochemical terminology.

following definitions for the allelochemical sub-categories:

Allomone: an allelochemical that is pertinent to the biology of an organism (organism 1) and that, when it contacts an individual of another species (organism 2), evokes in the receiver a behavioural and/or physiological response that is adaptively favourable to organism 1 but not to organism 2.

Kairomone: an allelochemical that is pertinent to the biology of an organism (organism 1) and that, when it contacts an individual of another species (organism 2), evokes in the receiver a behavioural and/or physiological response that is adaptively favourable to organism 2 but not to organism 1.

Synomone: an allelochemical that is pertinent to the biology of an organism (organism 1) and that, when it contacts an individual of another species (organism 2), evokes in the receiver a behavioural and/or physiological response that is adaptively favourable to both organism 1 and 2.

Nordlund and Lewis (1976) distinguished a fourth category of allelochemicals: apneumones. These are substances emitted by non-living material that evoke in the receiver a behavioural or physiological response that is adaptively favourable to a receiving organism but detrimental to an organism of another species that may be found in or on the non-living material. This category has not been used since it was proposed, possibly because it is difficult to distinguish apneumones from allelochemicals that are produced by micro-organisms on the non-living material (Dicke, 1988a). However, when the origin criterion is omitted from the terminology, this class becomes superfluous. These allelochemicals will be classified as kairomones based on the cost-benefit analysis for the interactants: the receiving organism and the organism that may be found on or in the non-living material. Therefore, we exclude apneumones from our classification (Fig. 3)

In all interactions mediated by infochemicals that are known to us, one of the interactants is benefited. However, it is not inconceivable that interactions exist where neither of the two interactants benefit. However, a term for these interactions should await their discovery.

Conclusion

The infochemical terminology that has developed to date has aided discussion of these substances. However, phenomena are being discovered that cannot easily be classified using current terminology. Therefore, we have proposed an alternative terminology that abandons the origin criterion (cf. Nordlund & Lewis, 1976) because this criterion excludes ecologically-significant interactions where the producer/emitter is not one of the interacting organisms. Instead we classify infochemicals on the basis of the costs and benefits of the interaction for both interactants.

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