

Signaling and Communication in Plants

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Plant Communication from an Ecological Perspective

 Springer

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Preface

Since the concept of allelopathy was introduced almost 100 years ago, research has led to an understanding that plants are involved in complex communicative interactions. They use a battery of different signals that convey plant-relevant information within plant individuals as well as between plants of the same species or different species. The 13 chapters of this volume discuss all these topics from an ecological perspective. Communication between plants allows them to share physiological and ecological information relevant for their survival and fitness. It is obvious that in these very early days of ecological plant communication research we are illuminating only the 'tip of iceberg' of the communicative nature of higher plants. Nevertheless, knowledge on the identity and informative value of volatiles used by plants for communication is increasing with breath-taking speed. Among the most spectacular examples are situations where plant emitters warn neighbours about a danger, increasing their innate immunity, or when herbivore-attacked plants attract the enemies of the herbivores ('cry for help' and 'plant bodyguards' concepts). It is becoming obvious that plants use not only volatile signals but also diverse water soluble molecules, in the case of plant roots, to safeguard their evolutionary success and accomplish self/non-self kin recognition. Importantly, as with all the examples of biocommunication, irrespective of whether signals and signs are transmitted via physical or chemical pathways, plant communication is a rule-governed and sign-mediated process.

The previous volumes focused on signalling molecules and pathways, as well as on communication related to plant sensory biology underlying the emerging concept of plant behaviour. Here, individual chapters deal with diverse aspects of plant communication such as evolution of plant signals and toxins, chemical signals in plant photobiology and 'arms-races' in pathogen defence, allelopathy of exotic plant invasion, volatile chemical interactions between undamaged plants and their effects at higher trophic levels, chemical communication in plant-ant symbioses, as well as effects of global atmospheric changes on plants and their trophic interactions. Finally, two chapters deal with the perspective of exploiting the chemical signals of plant communication for sustainable agriculture, and the technological

possibility of monitoring plant volatile signals to obtain information about plant health status in greenhouses.

For many years, plants were placed outside of the communicative and even the sensitive living domain. Immanuel Kant even went so far as to place plants outside the living realm. The vocal-based physical (acoustic) language of humans depends on air vibrations that are decoded in the ears. The volatile-based chemical language of plants is communicated by volatiles decoded via diverse receptors (most of them still unknown). Plants are unique and differ greatly from animals. This makes it very difficult for us, biased by the human-centric perspective of our world-view, to grasp their whole communicative complexity and to understand the true nature of their communications. The sessile nature of plants and the dual character of plant bodies, with the above-ground autotrophic shoots and the below-ground heterotrophic roots, are further phenomena obscuring the real nature of plant communication. In science, one should try to keep a neutral unbiased position and not exclude any possibility. We can look forward to witnessing the next wave of surprising discoveries.

Bonn, April 2010
Uppsala, April 2010

František Baluška
Velemir Ninkovic

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Evolutionary Ecology of Plant Signals and Toxins: A Conceptual Framework

H. Jochen Schenk and Eric W. Seabloom

Abstract Plants are capable of acquiring information from other plants, but are they able to send signals and communicate with them? Evolutionary biologists define biological communication as information transmission that is fashioned or maintained by natural selection and signals as traits whose value to the signaler is that they convey information to receivers. Plants, then, can be said to communicate if the signaling plant derives a fitness benefit from conveying information to other plants. Examples for interplant communication that fit these definitions potentially include territorial root communications, self/non-self recognition between roots and associated with self-incompatibility, volatile signals that induce defenses against herbivores, signals from ovules to mother plants, signals associated with root graft formation, and male to female signals during pollen competition. Natural selection would favor signals that are costly to the signaler and therefore are likely to convey reliable information because they cannot be easily faked. Toxins in low concentrations may commonly act as signals between plants rather than as inhibitory allelochemicals. This explains why toxic concentrations of plant allelochemicals are rarely found in natural coevolved systems.

1 Introduction

Do plants communicate with other plants? To many readers, this would appear to be a redundant question in a volume devoted to plant communication from an ecological perspective. However, anyone even vaguely familiar with the voluminous

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literature on human communication (e.g., Littlejohn and Foss 2008; Watzlawick et al. 1967) and animal communication (e.g., Dawkins and Krebs 1978; Maynard Smith and Harper 2003; Otte 1974; Searcy and Nowicki 2005; Zahavi and Zahavi 1997) will know that this is by no means an easy question to answer, the answer depending very much on one's definition of biological communication. The purpose of this chapter is to review the pertinent biological communications literature and apply it to communication between plants.

2 What Is Communication?

The Merriam–Webster dictionary defines communication as *a process by which information is exchanged between individuals through a common system of symbols, signs, or behavior*. For biological communication, this definition would have to be expanded to include information exchanges between any kind of signaler and receiver, e.g., within organisms, among organs, or cells. (To avoid confusion, we will use the terms signaler and receiver throughout this chapter instead of the synonymous terms emitter, agent, actor, source, or sender on one side and target, reactor, and recipient on the other.) Following common usage in biological sciences, it is also useful to replace the terms *symbols, signs, or behavior* with *signal*, which Webster's defines as *a detectable physical quantity or impulse by which messages or information can be transmitted*. This gives us the following general definition: *Communication is a process by which information is exchanged between a signaler and a receiver through a common system of signals*. Definitions similar to this one have been widely used in studies of human communications (Watzlawick et al. 1967).

2.1 What Is Information?

If communication is information exchange, what exactly is information? That turns out to be a surprisingly difficult question to answer, and interested readers are referred to the voluminous literature on information theory starting with Shannon (1948) and Wiener (1948). The most helpful and most memorable definition was offered by Gregory Bateson (2000, p. 381): *Information is any difference which makes a difference in some later event*. Information comes in the form of answers to binary questions such as self or non-self, male or female. Continuous information can be expressed as a series of binary choices. This means that the amount of information can be measured in bits (Bradbury and Vehrencamp 1998).

2.2 What Is Biological Communication?

The definition of communication as information exchange, however, is not the one used by most evolutionary biologists, for whom it is important to adopt a pragmatic

view that distinguishes between evolved functions and incidental effects. Pragmatic definitions of the terms *signal* and *communication* in evolutionary biology, then, should be restricted to behavioral, physiological, or morphological information transmission that is fashioned or maintained by natural selection (Dicke and Sabelis 1988; Maynard Smith and Harper 2003; Otte 1974). Otte (1974) suggested using the term *cue* for information exchanges that have not been under selection to inform, and this usage, which is widely accepted in animal communication studies (Bradbury and Vehrencamp 1998; Maynard Smith and Harper 2003), will be adopted in this chapter. For example, a plant detecting the presence of a neighbor through alterations in the red/far-red light ratio is considered to have received a cue rather than a signal.

2.3 What Is a Signal?

Unfortunately, there are several colloquial meanings of the word *signal*, referring either to the physical quantity or impulse being transmitted – such as quanta of light or molecules –, the signal’s meaning, or to the emitting source, such as a pattern of skin pigments, a vibrating vocal cord, or the biochemical pathway that creates a signaling molecule. Most animal communication researchers adopt the third usage and define signals as genetically encoded traits that are under natural selection (Maynard Smith and Harper 2003; Otte 1974; Wilson 1975; Zahavi and Zahavi 1997). There is almost universal agreement that a biological signal benefits the sender (i.e., increases its fitness) by altering the likelihood that the receiver will respond in a certain way (Bradbury and Vehrencamp 1998; Dawkins and Krebs 1978). Some have argued that the receiver has to benefit from the information for “true communication” to occur (Dusenbery 1992; Marler 1977). This, however, would exclude deceptive signaling from biological communication, and few biologists appear to have adopted this very restrictive definition (Bradbury and Vehrencamp 1998). A receiver has to benefit, on the average, from responding to a certain type of signal in a certain way. For example, a male insect benefits from responding to a pheromonal signal that is most likely to originate from a female, even though it may be tricked occasionally into responding this way by an orchid that mimics the signal. For the remainder of this chapter we will adopt the pragmatic definition of biological signals from Zahavi and Zahavi (1997): “Signals are traits whose value to the signaler is that they convey information to those who receive them,” which is a more generalized version of an earlier definition by Otte (1974). As customary in evolutionary biology, terms such as “value” and “benefit” are understood to mean adaptive value or benefit, on average, a positive effect on fitness.

Pragmatic definitions of biological communication focus on the evolutionary aspects of communication and sidestep other aspects of communication, such as the nature of information transmission (syntactics) and of meaning (semantics) (Watzlawick et al. 1967). The downside of the evolutionary approach, of course, is that we do not actually know whether most traits are under natural selection (Gould

and Lewontin 1979). In many cases, it will be relatively easy to determine whether signaler and/or receiver on average benefit from a signal transmission, but in many other cases this will be less apparent. Consider, for example, altruistic signal exchange, that appears to benefit only the receiver or even a group of receivers. Even in more clear-cut cases of signal exchange between two individuals, the advantage to sender or receiver must often be assumed to exist rather than empirically demonstrated (Slater 1983). Defining a process by its supposed function can invite adaptationist reasoning when natural selection has not in fact been involved in the shaping of the process (Gould and Lewontin 1979). It is important to keep in mind that whenever we speak of biological communication we are in fact formulating a hypothesis about the adaptiveness of a process (see chapter “Volatile Interaction between Undamaged Plants: A Short Cut to Coexistence”).

Plants have innumerable ways of gathering information from cues received from their environment, including from other plants, but, as the discussion above has made clear, information gathering from incidental cues, while immensely important to organisms, is not considered biological signaling or communication (Bradbury and Vehrencamp 1998; Maynard Smith and Harper 2003; Otte 1974) and therefore is not further discussed here.

2.4 What Is Allelopathy?

For most of its history, botany has had its own concepts and terms that often were quite different from those used in other areas of biology. A good example is the term allelopathy, coined by Hans Molisch (1937) to refer to “the influence of one plant on another,” i.e., *all kinds* of stimulatory and inhibitory interactions between plants. Allelopathy today is normally used in a much more restricted meaning to denote chemical inhibition - an understanding that may have originated from translating the two Greek words that make up the term, *allelōn* as “one another other” and *pathē* as “suffering.” In fact, *pathē* also has a more general meaning, “subject to, experience,” and this is obviously what Molisch (1937) had in mind, because his research in allelopathy largely concerned the volatile plant hormone ethylene, not a toxin at concentrations normally found in plants. Rice (1984) and Einhellig (1995) used the term allelopathy in a slightly narrower meaning to include only *chemical* interactions: communication, as well as inhibitory and stimulatory (e.g., nutritional) ones. Because these are very different kinds of interactions, none of which are unique to plants, there is really no reason, other than deference to history, to retain this broad concept of allelopathy. Previously, accepting the current usage of terms, we adopted the view that chemical communication should be distinguished from allelopathy, which would be defined as chemical interactions that involve toxic allelochemicals (Schenk et al. 1999). However, as we will see, it is often extremely difficult to determine whether chemicals act as toxins, signals, or both. Moreover, words are powerful in directing thoughts, and retaining the word allelopathy for plants brings with it the powerful suggestion that chemical

interactions in plants are somehow fundamentally different from those in bacteria, fungi, protists, or animals. For these reasons, the term allelopathy has outlived its usefulness and, in the interest of integrating general concepts across all of biology, should be retired (Schenk 2006).

2.5 *What Is the Difference Between a Toxin and a Signal?*

The distinction between transmission of energy and transmission of information is vital in studies of organismal interactions (Dawkins and Krebs 1978; Dicke and Sabelis 1988; Dusenbery 1992; Wiley 1994). Expenditure of energy on aggressive interactions is costly and surprisingly rare in animals which have evolved communication mechanisms. Probabilistic information about the fighting ability of an adversary allows many organisms to exchange signals and avoid the costly fight. Calls and songs of birds, insects, frogs, and toads all around us attest to the evolutionary power of signaling over aggression (Krebs and Davies 1997; Wilson 1975). Obviously aggressive behavior can contain important information, but conceptually the information contained in a blow to the head of a rival male bighorn sheep is quite distinct from the damage or backward movement caused by the blow. The distinction between energy and information exchange was reflected in Wiley's (1994) definition of biological communication (which did not include criteria of adaptation): "A signal is any pattern of energy or matter produced by one individual (the signaler) and altering some property of another (the receiver) *without providing the power to produce the entire response* (p. 162, author's italics)."

An important difference between signaling and energy exchange is that the receiver has full physiological control over its response; it can respond or ignore the signal depending on the circumstances or the nature of the signal (Dusenbery 1992). In the case of energy transmission (including toxins), the energy source has the physiological control over the response and the receiver does not have the option of ignoring the transmission. Obviously, the ability to potentially ignore a signal will usually be an advantage for a receiver. For example, it was found that male mice of low body weight tend to avoid territories scent-marked by another male, while heavy mice with higher competitive ability are more likely to ignore such signals (Gosling et al. 1996). Larger frogs and toads are more likely to ignore high-frequency calls from smaller competitors than low-frequency calls from larger ones (Arak 1983; Wagner 1989). Similarly, in plants, the ability to ignore root signals from a competitor (Schenk 2006; Schenk et al. 1999) may be an advantage for a strong competitor, while an inefficient competitor, such as a seedling, may benefit from avoiding soil volume occupied by other roots. Signalers can also benefit from the receivers' ability to ignore their signals, as indiscriminate responses from all potential receivers are unlikely to benefit a signaler. In contrast, a powerful toxin could potentially harm a large variety of other organisms, including some that could be beneficial to the emitter of the toxin.

It clearly is important for organisms to be able to ignore a signal, but this ability brings up an interesting conundrum for researchers. It is universally agreed upon that for pragmatic reasons biological communication can only be said to have occurred when a response of the receiver is observed (Searcy and Nowicki 2005). Yet, in the case of a potential receiver that does not respond to a signal it is often impossible to know if the signal was received. In the case of acoustic communication, as in the frog and toad studies mentioned above (Arak 1983; Wagner 1989), it may be safe to assume that receivers heard a call, but in the case of chemical communication the distinction between not perceiving or ignoring a signal will be almost impossible to make. This creates a special problem for plant researchers, who typically face signals that are difficult to observe.

2.6 Differences Between Plant and Animal Communication

So far, much of our discussion has been about animal communication. The idea that plants may possibly communicate was controversial until quite recently. Reports in the early 1980s of pheromonal signal exchange among trees (Baldwin and Schultz 1983; Rhoades 1985) were much debated, heavily criticized on methodological and analytical grounds, and ridiculed as “talking trees” (Fowler and Lawton 1985). Silvertown and Gordon (1989) stated that visual and olfactory signals transmitted from plants are exclusively directed at animals. Since then, a wealth of information on signal exchange and chemical interactions among plants, and among plants and other organisms, including microbes, fungi, and animals has accumulated, forcing a re-evaluation of the nature of plant interactions (Baluška 2009; Baluška and Mancuso 2009b, this volume). Already it seems hard to believe that plants used to be singled out as the only group of organisms not thought to be able to exchange chemical signals – an ability easily acceded to bacteria, fungi, protists, and animals. The book by Zahavi and Zahavi (1997) on biological signaling, for example, did not include a single reference to plants, even though one of the authors was a plant physiologist. Plant communications research clearly has come a long way since then. However, the question remains: are there important or even fundamental differences between communication in plants and in other groups of organisms?

The main trait that sets plants apart from other organisms is the rigid cellulose cell wall that restricts their movement to relatively slow rates. The modular nature of plants is not unique to them, but it certainly sets them apart from unitary animals. Does either of these traits affect the abilities of plants to communicate? The modular nature of all plants and the clonal nature of about 40% of all plants (Tiffney and Niklas 1985) certainly has interesting implications for the evolution of plant signals through individual selection (more on that below). Rigid cell walls generally do not allow plants to send and perceive signals that require rapid movement of organs or cells. However, plants clearly emit and perceive visual cues, better called radiational cues, as plants do not have eyes, and nobody seriously disputes the ability of plants to produce and perceive chemical cues. Plants also create and

respond to electrical fields (Baluška and Mancuso 2009a; Davies 2004; Fromm and Lautner 2007; Lund 1947), and are able to perceive tactile information (Chehab et al. 2009). As far as we know, plants do not appear to have evolved the ability to produce or perceive sound, but this statement has to be qualified by noting that outside pseudoscientific, unreplicated experiments (Retallack 1973), reactions of plants to sound do not appear to have been studied, and that plants are known to produce sounds in the acoustic and ultrasonic range as byproducts of physiological processes (Ritman and Milburn 1988; Zweifel and Zeugin 2008). Thus, the main difference between plant and animal communication is that plants lack complex sensory organs and signals that require rapid movement. Most communication between plants is likely to be chemical or possibly electrochemical – unfortunately the most difficult types of communication to observe.

Thus, other than in animals, where many signals such as calls or visual displays are easily observed, the study of plant signals typically requires specialized equipment and complex analytical procedures. Frequently, the existence of signals is only inferred from observations of a plant's response to a neighbor, and the actual signal may never be identified (e.g., Mahall and Callaway 1991, 1996). This of course makes it impossible to determine whether a signal was received when no response is observed. Thus plant communication is much more difficult to study than animal communication, and this likely has been the reason for the long-held, tacit assumption that plants do not communicate.

3 How Can Communication Between Plants Evolve?

Research on plant communication is still in its infancy compared to animal communication, and an evolutionary biology of plant signals is still lacking. The key evolutionary question that must be asked about any hypothesized communication between organisms is: Who benefits from the interaction? Individual selection is the major driving force of evolution, so a signal exchange that does not benefit the signaler would seem to be impossible to evolve (Dawkins and Krebs 1978). However, individuality in plants is a much less clear concept than it is in unitary animals. All plant ancestors were clonal, all plants are modular, and about 40% of all plants today are still clonal (Tiffney and Niklas 1985). Adding to that the observation that many plant species have poor long-distance dispersal abilities, one has to conclude that a sizable proportion of plants, perhaps even the majority, will have some long-term neighbors, which are either genetically identical or closely related. This would suggest that evolutionary pathways of traits involved in plant interactions may differ substantially from those in unitary animals, and that evolution of cooperative signaling that benefits a conspecific neighbor may not be unusual in plants. Moreover, plants tend to live in extraordinary stable groups of neighbors, which create conditions that allow for group selected traits to evolve under certain circumstances (Dudley and File 2007; Goodnight 1985; Tuomi and Vuorisalo 1989; Wilson and Sober 1994; Wilson 1987).

3.1 Evolution of Signaling Through Individual Selection

Signal reliability has been the major focus of biological signaling theory for the last three decades (Searcy and Nowicki 2005), but with the exception of deceptive plant signaling to pollinators, the topic has not received much attention by researchers who study signaling between plants. Yet the subject is of vital importance, because signals that provide false information about the signaler are not evolutionarily stable unless the deception only occurs in a small proportion of instances (Searcy and Nowicki 2005). Thus, receivers will respond only in a fashion that, on the average, benefits the signaler if the signal has a high probability of being reliable (Zahavi and Zahavi 1997). After much initial debate and controversy, the theory that signals have to be costly to the signaler (Zahavi 1975, 1977; Zahavi and Zahavi 1997) has been largely supported by the evidence from a multitude of studies, both modeling and experimental (Bradbury and Vehrencamp 1998; Grafen 1990; Johnstone 1997; Searcy and Nowicki 2005). Signal costs may include direct and indirect costs, such as the metabolic energy to produce a toxin and the costs for the biochemical machinery to prevent autotoxicity, as well as ultimately the fitness costs for producing the signal (Searcy and Nowicki 2005). Costly signals are unlikely to be faked and therefore will tend to be reliable (Zahavi and Zahavi 1997). Some researchers continue to maintain that there is a separate category of signals that are inherently reliable and come at no cost to the signaler (Maynard Smith and Harper 2003). An example would be claw marks made by an animal in the bark of a tree that indicate the true height of the animal. However, in practice it turns out that there are hardly any kinds of signals that are truly impossible to fake – imaging an animal jumping up the tree to make the claw marks – (Searcy and Nowicki 2005), which suggests that the handicap principle (Zahavi and Zahavi 1997) of high signal cost is essentially the only way through which signaling can evolve by individual selection. Unless it is in their own benefit to respond, receivers would not continue to respond to a signal that comes with little cost to the signaler and therefore is easily faked.

It is surprising to note that to date only a single paper on the subject of signaling between plants (Zhang and Jiang 2000) – a modeling study of sibling rivalry among ovules – appears to have invoked the handicap principle. The idea of signaling cost still appears to be foreign to the debate about plant communication. This puts the field at a huge disadvantage, because signaling systems continue to be proposed without reference to whether or not they benefit the signaler and convey reliable information to a receiver and thus could possibly evolve. An example will help to make the point (see Box 1): roots of the desert shrub *Ambrosia dumosa* have been found to cease growth after contact with other roots belonging to conspecifics of the same population (Mahall and Callaway 1991, 1992, 1996). This has been attributed to signals received from the neighbor's roots. It seems intuitively clear in this example that the hypothesized signaler would benefit from the self-curtailling behavior of a potential competitor, but why would the receiver respond in this fashion? A modeling study (see Box 1) of root competition for water between plants with *Ambrosia*-type behavior suggests that plants could benefit from sensing the

presence of competing roots and reallocating root growth to parts of the soil that are not occupied by competing roots. However, this would only be true for root competition for relatively immobile resources. Allowing higher rates of soil water conductivity eliminated the advantage of root territoriality (Box 1, Fig. 1f). Moreover, the advantage of intraspecific root territoriality also disappears in the presence of a nonterritorial competitor (Box 1, Fig. 1e), such as desert annuals that normally compete with *Ambrosia dumosa* shrubs (Holzapfel and Mahall 1999). And here lies the problem: root signals that are produced by a signaler regardless of whether soil resources are depleted or available do not provide reliable information to receiver roots and therefore would appear to be unlikely to evolve. The alternative, evolution of such signals by kin or group selection is discussed below.

To take this example further, *Ambrosia dumosa* roots have also been found to cease growth when approaching roots of the much larger desert shrub *Larrea tridentata* (Mahall and Callaway 1991, 1992), with which *A. dumosa* is co-dominant over huge areas of the Sonoran and Mojave Deserts of North America. In this case, kin or group selection cannot be invoked to explain the existence of a signaling system, which suggests that *Ambrosia* roots either respond to a costly and reliable root signal from *Larrea* or that *Larrea* roots exude an unidentified toxin that cannot be ignored (Schenk et al. 1999). *Larrea* roots also cease growth when approaching other *Larrea* roots (Mahall and Callaway 1991, 1992). The modeling study presented in Box 1 found that the self-curtailing root behavior of an *Ambrosia*-like plant in competition with a *Larrea*-like plant could also benefit the “*Ambrosia*” if soil resources were immobile (Box 1, Fig. 1e) and if therefore the presence of the competitor’s root reliably indicated local resource depletion. However, in nature, *Larrea* roots are just as unlikely as *Ambrosia* roots to deplete local soil resources continuously to such an extent that the mere presence of a *Larrea* root would reliably indicate resource depletion (Box 1). Interestingly, in the modeling study, *Larrea*-type plants only benefited from self-curtailing root behavior of competitors when these competitors also behaved like *Larrea* roots (Box 1, Fig. 1e). These examples show that benefits and costs for signalers and receivers of root signals are not easily determined, thereby leaving it open to question how they could evolve.

The alternative idea that *Larrea* produces root toxins in sufficient quantities to poison the roots of a coevolved competitor seems exceedingly unlikely. In fact, there are rather few documented cases of toxic root exudates that are exuded in such large quantities that they can affect competing roots before being absorbed by soil particles or broken down by oxidation or by microbes (Cheng 1995; Newman 1978). Yet toxic root exudates undoubtedly exist (Inderjit and Weston 2003).

So why would plants produce root toxins that cannot poison the roots of their neighbors? An answer to this puzzling question is provided by Zahavi’s handicap principle (Zahavi and Zahavi 1997): a toxin is a powerful and reliable signal because it comes at a substantial cost to the signaler for production and autotoxicity prevention. If only the most active fine roots produced it then the toxin would be a reliable signal to roots of coevolved competitors of the presence of an active root that belongs to a competitor strong enough to produce such a costly signal. Thus in

Box 1 A Cellular Automaton Model of Root Territoriality

This model (Fig. 1) was developed to explore the potential benefits to plants of root signaling systems associated with root territoriality (Schenk et al. 1999). The spatially-explicit root model is run within a 100 by 100 cell two-dimensional grid, in which each cell represents 1 cm³ of soil. Simulations are run for 50 time steps of 4 days each (200 days total). All carbon costs are converted to a common currency of water units (375 mg H₂O/mg C) for production (60 mg H₂O cm⁻¹) and maintenance of roots (0.75 mg H₂O cm⁻¹ day⁻¹), for associated shoots (2.5 shoot/root ratio), and production of root signals (1.75 mg H₂O cm⁻¹ day⁻¹). Each cell in the grid is initialized with 150 mg of H₂O, with no replenishment, as might occur in a desert following a saturating rain. Initially ten plants are placed randomly in the grid, each starting with enough resources to produce four initial root nodes. During each time step, the following actions are applied in random order to each plant in the grid:

1. Pay maintenance costs in water for the total roots system
2. Extract up to 15 mg of water units per day from each cell of soil contacted by the roots
3. Produce a new root growing in a random direction starting at a node, the location where growth stops at the end of the previous time step

Roots may grow into any unoccupied cell of the nine grid cells adjacent to a node, and each new root can grow up to 1 cm per day. Root growth continues in a straight line within a time step until the plant is out of resources, the root encounters a root that it cannot cross, as determined by its territorial behavior (see below), or the root is 4 cm long. Following root growth, all water in the system diffuses to neighboring cells based on an exponential probability density function. The model outputs total root length and water uptake of each plant at each step in the simulation, produces maps of roots and water content of each cell in the grid.

Root behavior is determined by two variables that determine whether a root can cross another root of the same species or of another species. No roots are allowed to cross their own roots. We set combinations of these two variables to establish three species with different territorial behaviors: “Non-territorial” (no inter- or intraspecific root territories), *Ambrosia*-type (intraspecific root territories only), and *Larrea*-type (intra- and interspecific root territories).

In our simulations, we ran a full factorial combination of all six unique pairs of the three species (including monocultures) at each of two water conductivities ($\phi = 1$ cm and $\phi = 80$ cm) for a total of 12 unique treatments. All treatments were replicated ten times for a total of 120 simulations. Note that in the high conductivity treatment, water is redistributed nearly evenly across the entire grid, as the mean diffusion distance (80 cm) is nearly the maximum grid dimension (100 cm).

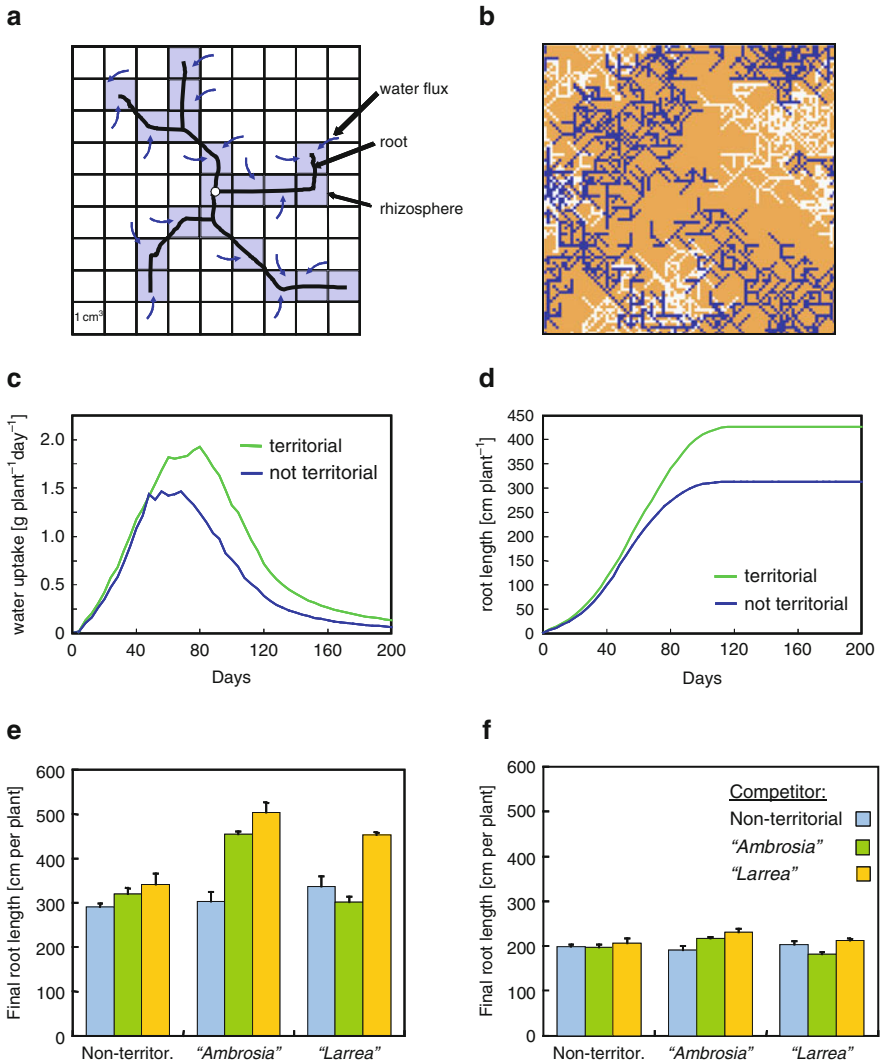


Fig. 1 (a) Basic structure of the cellular automaton model. (b) A root map at the end of a 200 day simulation. (c) Mean water uptake per plant for non-territorial and territorial plants. (d) Total root length per plant for non-territorial and territorial plants. Because of the structure of the model, cumulative water uptake is closely correlated with cumulative root length. (e) Final root lengths per plant at the end of ten 200 day simulations at low soil water conductivity. (f) Final root lengths per plant at the end of ten 200 day simulations at high soil water conductivity

coevolved systems one would not expect to find production of root toxins at levels high enough to actually poison a neighbor’s roots. However, toxin-producing plant species outside their native range can encounter new neighbors that do not recognize the signal. In that case, natural selection would either favor elimination

of the signal or an increase in its production to a level where it actually does poison neighbors' roots. The latter case is exactly what was found with the spotted knapweed, *Centaurea maculosa*, which is invasive in western North America. In its nonnative range, the species was found to produce the phytotoxin (\pm)-catechin in the field at high concentrations that inhibit native species' growth and germination, but soil concentrations of the phytotoxin in *Centaurea maculosa* populations in its native range in Europe were much lower (Bais et al. 2003). Callaway et al. (2005) found evidence for rapid natural selection for tolerance of (\pm)-catechin in competitors of *Centaurea maculosa*, which further supports the hypothesis that poisoning neighbors is not an evolutionary stable strategy. The handicap principle, on the other hand, can explain why toxic substances, including reactive oxygen species (del R o and Puppo 2009) and nitric oxide (Tuteja and Sopory 2008), are common signaling molecules both within and between plants.

3.2 *Evolution of Signaling Through Kin or Group Selection*

Evolution of signaling between a signaler and a receiver can be explained without recourse to the handicap principle, if the interests of both participants overlap and both benefit from the information exchange. Unfortunately, the history of biological communications research is rife with examples of studies where common interests have been assumed rather than tested (Dawkins and Krebs 1978). Because plants appear to lack social behavior, cases of common interests between individual plants are likely to be restricted to interactions between genetically identical or related plants and potentially to close mutualistic associations between plant species. Because many plants are clonal and/or lack long-distance dispersal mechanisms, they are likely to interact with genetically related neighbors, and this would create conditions in which "true communication" can evolve that benefits both signaler and receiver. The purported signaling mechanism by which the desert shrub *Ambrosia dumosa* reduces intraspecific root competition (Box 1) would appear to fall into this category. *Ambrosia dumosa* is a clonal shrub that normally fragments into separate ramets as it matures (Espino and Schenk 2009; Jones and Lord 1982; Schenk 1999), and competition among these ramets would create costs with no benefits to the genetic individual. Interestingly, *Ambrosia dumosa* ramets segregate their root systems only when they are disconnected from each other and they also segregate root systems from those of other ramets from the same population (Mahall and Callaway 1996). This suggests that root communication that leads to root segregation in this species may have evolved by a combination of individual, kin, and group selection, which may not be uncommon in plants (Goodnight 1985; Tuomi and Vuorisalo 1989).

Volatile "alarm calls" between conspecific plants in response to herbivore attack may offer other examples for kin- or group-selected signaling systems (Baldwin and Schultz 1983; Dolch and Tschardtke 2000; Farmer and Ryan 1990), but in clonal plants these could also evolve by individual selection (Karban et al. 2006; Shiojiri and Karban 2006, 2008). The common interest between communication

partners in this case could be the use of induced chemical defenses to deter herbivores from a whole plant neighborhood and thereby reduce the risk of further attack for all plants in that neighborhood. An alternative explanation for “alarm calls” is that they evolve through individual selection and are directed at predators (Zahavi and Zahavi 1997), informing them of defense induction or that they are directed at a predator’s predator (Kessler and Baldwin 2001).

The animal communications literature holds many examples for communication between related organisms, some of which may also occur in plants. For example, begging for food from a parent is a common behavior in birds and many other animals with parental care. The plant equivalent for this type of sibling rivalry is signaling associated with competition between ovules for resources from the maternal plant. Interestingly, research in plants has focused mostly on the maternal regulation of ovule abortion in plants (Bañuelos and Obeso 2003; Ganeshiah and Shaanker 1988; Korbecka et al. 2002; Shaanker et al. 1996), but the animal literature suggests that offspring may be more likely to affect the outcome of sibling rivalry than the mother (Mock and Parker 1998; Searcy and Nowicki 2005). Conflicts between selfish interests of ovules and interests of the mother plant were addressed in a modeling study by Zhang and Jiang (2000) that explicitly included the costs of signals produced by ovules.

Although there are many examples for positive interactions between plants (Callaway 2007), there is little evidence for mutualistic associations between plant species that are so close that signaling may be involved in forming the association. Graft formation between root systems (Graham and Bormann 1966) may fall into this category, as graft formation involves signaling between the graft partners (Pina and Errea 2005; Yeoman 1984). However, the costs and benefits of natural root grafts are poorly understood, and it remains to be seen whether they can be truly mutualistic (Loehle and Jones 1990).

3.3 Evolution of Signaling Through Sexual Selection

Sexual signaling in plants has been thought to be directed exclusively at animal pollinators (Silvertown and Gordon 1989), but a wealth of recent information on pollen competition and pollen-pistil interactions (Aizen and Harder 2007; Cruzan 1993; Erbar 2003; Herrero and Hormaza 1996; Lankinen et al. 2009; Nakamura and Wheeler 1992; Ruane 2009; Snow and Spira 1991) forces a re-evaluation of this view. Sexual selection associated with mate choice involves an abundance and variety of conspicuous signaling systems in animals (Wilson 1975), and there is no *a priori* reason to think that processes that are such powerful selective forces in animals would not be equally powerful in plants. Sexual signaling between males and females involves diverging interests between signaler and receiver, including high fitness benefits to females if they can detect high-quality males and high fitness benefits to low-quality males if they can deceive females into mating with them

(Searcy and Nowicki 2005). Male gametophytes in plants would appear to lack the resources for a plant equivalent to the male peacock's tail. Instead, male competition (Ruane 2009; Snow and Spira 1991) and female choice (Cruzan 1993; Herrero and Hormaza 1996) take place hidden from sight at the stigmatic surface or in the pollen-tube transmitting tissue (Erbar 2003). Signaling between males and females associated with sexual selection in plants has been discussed in great detail by Skogsmyr and Lankinen (2002), and readers are referred to that review.

4 A Conceptual Framework for the Evolutionary Ecology of Plant Signals

In plant literature, the term signaling has mostly been used for plant-internal signals (Baluška and Mancuso 2009b) or for interactions between plants and their environment (Baluška 2009). Consistency in terminology with other scientific literature in biology would exclude from signaling any information gathering from the abiotic or biotic environment that does not benefit a signaler. While acknowledging the separate traditions, we argue that there is much to be gained from adopting consistent terms and concepts across all of biology. Plant biology can benefit from the accumulated knowledge of many decades of research on communications in other organisms by looking for similarities and differences between communication in plants and communication in animals, bacteria, protists, and fungi. Certain categories of interactions among individuals – including territorial defense, mate choice, parent-offspring, and kin interactions – have produced a wealth of signaling systems in other organisms and are likely to have produced signaling in plants as well. Evolution of biological signals is likely to differ greatly between systems where the interests of signalers and receivers overlap, diverge, or oppose (Searcy and Nowicki 2005). Table 1 presents a conceptual framework of plant signals grouped into these three categories and further divided into specific types of interactions.

5 Conclusions

The history of animal communications research provides some useful lessons to researchers engaged in the emerging field of plant communications research. For some of the last three decades, progress in the understanding of animal communications had been hampered by conflicting uses of concepts and terms and by fundamental disagreements about the processes that underlie the evolution of animal signals. Conflicts and disagreements are important parts of the scientific process, but it is even more important for that process to learn both from past mistakes and advances in understanding. There is now an emerging consensus that

Table 1 Different types of biological communication that have been observed to occur or could potentially occur between plants, grouped by the relationship between the interests of signaler and receiver. Interest here refers to potential fitness benefits resulting from the signal exchange. References cited are only meant to cite examples and more citations may be found in the text

Relationship between signaler and receiver	Roles of signaler and receiver	Examples in plants
Interests oppose	Competitors	Territorial root communications (Schenk 2006; Schenk et al. 1999)
	Host and parasite	Signals from potential hosts that warn off parasites?
Interests overlap	Male and female gametes of the same plant	Self/non-self recognition during self-incompatibility (Haring et al. 1990; Rea and Nasrallah 2008)
	Ramets	Self/non-self recognition in roots (Falik et al. 2003; Holzapfel and Alpert 2003); “Alarm calls”: volatile signals that induce defenses against herbivores (Karban et al. 2006)
	Kin	“Begging calls”: Sibling rivalry between ovules (Bañuelos and Obeso 2003; Ganeshaiiah and Shaanker 1988); “Alarm calls”: volatile signals that induce defenses against herbivores (Farmer and Ryan 1990)
Interests diverge	Mutualists	Root graft formation? (Loehle and Jones 1990)
	Male and female gametes of different plants	Pollen competition (Ruane 2009; Snow and Spira 1991); “Female choice” of pollen (Cruzan 1993; Herrero and Hormaza 1996)
“Signaler” has no interest in signal exchange	Various	This is not biological communication and signaling, but information gathering from cues. Examples too numerous to list.

signaling costs are vital for the evolution of many, if not most, biological signaling systems. Except for communications between genetically related individuals, only costly and therefore reliable signals are likely to evolve by individual selection, and this is likely to be true also for plants.

The handicap principle that led to the understanding of the importance of signaling costs may also throw new light on the role of phytotoxins in plant interactions. The ecological roles of allelochemical toxins have been puzzling to plant ecologists for a long time, because such toxins rarely occur in concentrations large enough to actually poison a competitor. Reinterpreting toxins as costly, and therefore reliable, signals provides a new explanation for a long-standing mystery in plant ecology.

Finally, we argue that the term and concept of allelopathy are much less useful than the more consistent and integrative term and concept of plant communications. Communication and chemical inhibition are very different concepts, but molecules may commonly serve both as toxins and as signals; therefore, these two concepts cannot be relegated to separate fields of inquiry and instead should all be part of plant interactions research. Moreover, communication and inhibition are universal processes across all of biology, and maintaining separate terminologies for different biological disciplines would only serve to obscure the commonalities. Adopting

some concepts and terms from animal research will allow plant behavioral researchers to build on knowledge and understanding gained from the longer and more productive history of animal behavioral ecology and perhaps to avoid some of its pitfalls and mistakes.

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