



Review Article

Interactions Among the Plants with Different Neighbor Identities and Plant Communication (A Review)

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Abstract | It is well established that plants can communicate with each other under different stressful conditions through (signals, cues, and rhizosphere interactions). Numerous studies have been conducted to find how plants respond to different neighbors at various points of genetic affiliation. Contrasting results and lack of molecular evidence in species recognition studies have made this topic more curious and complex. Some plant species compete more vibrantly for below-ground resources when an encounter with neighboring unrelated conspecifics as compared to related conspecifics (kin recognition). Some species increase competition when interacting with related and unrelated conspecifics (niche partitioning); some species do not show any change in the above/below ground allocation pattern. In this review, we attempt to provide a research background of species recognition in plants and plant communication, the current state of knowledge, and future perspectives. It has been established that species identification and communication between plants exist through many mediums like damage induced warnings, call for predators, root secretion, and volatile signaling. We found that most of the research has been executed in a controlled environment with a continuous supply of nutrients and water; more field studies should be conducted to assess the behavior of related/ non-related conspecifics. Furthermore, not many studies have focused on kin related plant communication via volatile signals, protein interaction and cues.

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Keywords | Plant interaction, Conspecific, Heterospecific, Plant communication, Plant competition, Plant facilitation



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Introduction

Plants and animals compete for resources, resulting in two sorts of transformative processes: those that improve competitive capabilities and those that diminish competing interactions. (Schmitt *et al.*, 1995; 1999; Nardini *et al.*, 1999). Plant growth is greatly influenced by the existence or absence of neighboring competitors within close proximity. Bi-

ologists have recognized that various animal species have transformed to distinguish and collaborate with other members of the same community, especially from the kin members of that community for survival. In recent, studies it has been well established that numerous microbes/pathogens, some of the simplest creatures, are also capable of distinguishing their kin (Jaafry *et al.*, 2019; Jaafry and Fatima, 2021). So, it is not surprising that plants may also communicate and

recognize the presence of neighboring plants within close proximity. Interaction among plants is one of the key processes which can amend the composition, structure, diversity, and mechanism of plant populations (Schmitt *et al.*, 1995). Plants are immovable organisms; they are not mobile and free to move like animals so that communication between plants most likely takes place within the nearest neighbors (Milbau *et al.*, 2007). Increasing studies of plant-plant collaboration indicate that intraspecific genetic assortment may have extensive ecological consequences for interspecies interactions (Genung *et al.*, 2012) and that difference between genotypes maybe even more significant than the disparity among the different species in understanding species cohabitation (Husain Jaafray *et al.*, 2020).

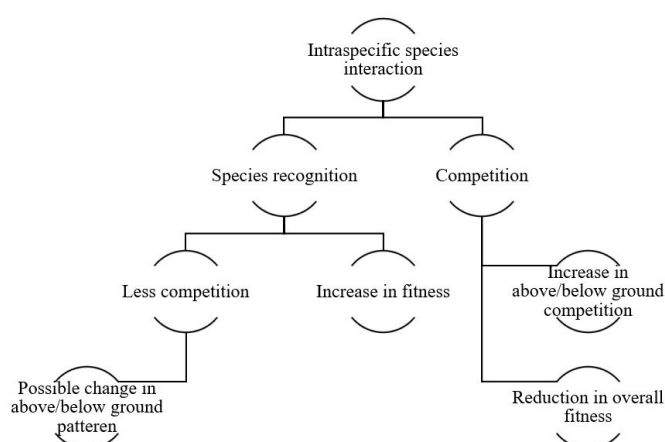


Figure 1: Intraspecific interaction of species and their possible outcomes.

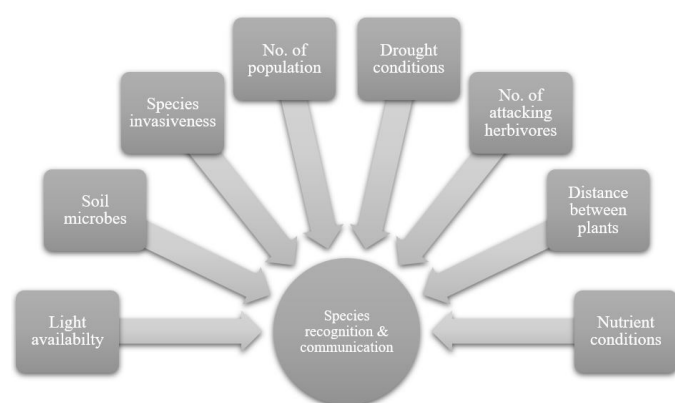


Figure 2: Factors that may affect the species recognition and plant communication.

Contrary to kin recognition in plants, classical ecological theory entails that competition is anticipated to be tougher as individuals become more alike in their resource concerns (Figure 1). In this study, a systematic review was conducted to collect evidence if plant interaction and species recognition. This study

has focused on explaining different factors that may influence plant interaction and species recognition (Figure 2).

According to recent studies on plant species recognition and competition, plants may identify neighboring plants within a close vicinity on the basis of relatedness and species identity (conspecific or heterospecific). Until now, inconsistencies and contradictory conclusions have plagued the subject of plant species recognition, with some studies supporting the kin recognition phenomenon. (Crepy and Casal, 2016), other established contrasting results (Cheplick and Kane, 2004; Lepik *et al.*, 2012; Mercer and Eppley, 2014), and some studies concluded insignificant change between sibling conspecific and non-sibling conspecific groups (Puustinen *et al.*, 2004; Husain Jaafray *et al.*, 2020). This is why the understanding of kinship and species recognition phenomenon is still ambiguous. Progress regarding molecular proofs and protein-protein interaction is not sufficiently provided for root secretions, and, to date, lesser molecular information to determine the kin recognition has been established, leaving many queries in the field unrequited. In this text review, we attempt to provide a comprehensive background to this innovative topic to inspire young researchers to do further studies to understand kin, species identification, and plant interaction mechanism in a better way.

Many studies of animal kin or species recognition have been published; however, plant kin and species recognition, as well as their reactions, has only lately piqued ecologists' interest, and many ecologists remain unconvinced that plants might have such a differentiating feature. Plants, like animals, have evolved over millions of years and are emerging under similar circumstances, such as competition for above- and below-ground resources, as well as reproduction. As a result, they have developed a lot of intricate survival and survival procedures, which we will go over in more detail later.

Species interaction and recognition in plants

Intraspecific competition may affect the overall fitness of plants through modification in above and below-ground growth patterns (Bisseling and Scheres, 2014). Previous research on different species mainly focused on interspecific competition as compared with intraspecific interaction in different ecosystems (Padilla *et al.*, 2013), and competitive indices used

to estimate interspecific competition have been reported explicitly, but it has been well established that intraspecific competition is more severe than interspecific interaction (Husain Jaafry *et al.*, 2020). However, little evidence is presented on the evaluation of the intraspecific competition in crops, clonal, and non-clonal plants. Intraspecific competition is the main factor that can influence the plant growth pattern to increase root density for capturing the below-ground resources (e.g., water and nutrients), above-ground resources (e.g., light), or both.

Before consideration of siblings or kin, specific studies, self-recognition, and non-self roots, discrimination in plants was studied. Mahall and Callaway studied the feedback of *Ambrosia dumosa* (a desert shrub). They split the roots and observed the root morphology of the exposure with self roots and compared with exposure to other plant roots belong to the same population (conspecifics). They depicted that the root growth of *A. dumosa* was quenched when it exposed to different individual's roots as compared with self roots (Mahall and Callaway 1991; 1992; 1996; Maina *et al.*, 2002). Additionally in their research, it was established that the desert shrub (*A. dumosa*) did not sense the neighboring roots from strangers (different population or heterospecific neighbors) hence, they concluded that self, a non-self distinction may only develop among siblings or genetically related plants (Callaway RM 1992; Mahall and Callaway 1996).

In the study of Dudley and File (2007), they examined the structure of the roots of sea rocket (*Cakile edentula*). When *C. edentula* has placed with strangers, it allocated more biomass in roots as compared when it has grown with the close relatives (*i.e.* same mother plants). Based on this research, Biedrzycki *et al.* (2010) investigated kin recognition in *Arabidopsis thaliana*. They grew *A. thaliana* plants in individual either exposing to kin and strangers conspecific roots secretions. (Biedrzycki and Bais, 2010). Their findings were similar to those of Dudley and File (2007). Plants treated with stranger secretions produced more slanted roots than those planted with kin root excretion (Biedrzycki *et al.*, 2014). This change in the root allocation pattern in response to neighbor relatedness supports the idea that, in any case, some plants are capable of sensing and categorizing their relatedness-related neighbors in the same population.

Another study regarding species recognition and fa-

cilitation shown *Centaurea stoebe* an exotic herb may transform its defensive approach in response to different neighboring plants, either conspecific or heterospecific (Broz *et al.*, 2010). While grown with conspecific (same species) neighbor, *C. stoebe*, a grown-up with other *C. stoebe*, plants changed their defense response in comparison to the interaction with heterospecific (different species) neighbors. These findings implied that an individual *C. stoebe* plant might alter its defensive mechanism based on the identity of different neighboring individuals. This approach is likely to have significant value for individual and community success. The recent studies stimulated the ecologists to figure out the defensive characteristics among the plants, which indicated that the plant species grown in a conspecific population might be more tolerant to pathogen/aphid attacks as compared to those grown in a heterospecific environment. Despite the conspecific population of *C. stoebe* were not taken as related conspecifics (siblings), it would be interesting to establish if the defense and biochemical mechanism of plants may change in kin versus conspecific environment. All of the previous results implied that invasive plants have evolved strategies to cope with its neighbors and utilized the territory and available resources (above/below-ground) more efficiently compared with normal plants (Broz *et al.*, 2010).

In the study of Murphy and Dudley (2009), they observed kin acknowledgement and competition response in *Impatiens pallida*. Inconsistent to the prior studies, which indicated that neighboring roots responded to kin or strangers by changing the growth pattern, this experiment showed that below ground kin or stranger acquaintances could also modify the above-ground growth pattern. *I. pallida* augmented allocation in the above-ground rather than to below ground by increasing stem height and number of branches when exposed with strangers versus being grown with kin (Murphy and Dudley, 2009).

Glycine max and *Sorghum vulgare* either grown with a sibling or a stranger, both did not show any differences in above-ground biomass. *G. max* did not differ among siblings and stranger groups in below-ground biomass, but *S. vulgare* grown with siblings showed lower below-ground biomass compared with strangers group (Zhang *et al.*, 2016). Conversely, *G. max* took up more nitrogen in the sibling group as compared to strangers without changing root allocation. It implies that resource uptake capacity and root competition

Table 1: *Plant interaction brief summary.*

Plant-plant communication	Outcome	Reference
Plant VOCs released differently when spider mite introduced to damaged lima beans and normal leaves	Spider mite behavior changed under different VOCs exposure from damaged and normal leaves	(Dicke, 1986)
Plant VOCs signaling, which also leads to 'snoop' on surrounding plants	Willow (<i>Salix sitchensis</i>), induced natural resistance against herbivory to their immediate neighbours	(Baldwin and Schultz, 1983)
VOCs triggered predatory insect attraction against herbivory	Herbivore-mediated VOCs stimulate a defensive response in undamaged neighbor plants of lima beans (<i>Phaseolus lunatus</i>) against herbivory damage	(Heil and Silva Bueno, 2007)
Pollinator attraction due to VOCs	Native tobacco (<i>Nicotiana attenuata</i>) attracted pollinators due to plant VOCs	(Halitschke <i>et al.</i> , 2008)
Attraction to predator insects induced by VOCs	<i>Nicotiana attenuata</i> showed resistance to three herbivore insects, by attracting predators	(Kessler, 2001)
Change in diurnal and nocturnal VOCs release due to herbivory	Tobacco plants (<i>Nicotiana tabacum</i>), numerous chemical airborne cues excreted extensively at night found highly obnoxious to female moths (<i>Heliothis virescens</i>).	(De Moraes <i>et al.</i> , 2011)
GLVs and terpenoids released to attract predators after leaf damage	Transgenic <i>Nicotiana attenuata</i> attracted predators with volatile signals, to reduce the load of herbivore	(Halitschke <i>et al.</i> , 2008)
Predatory attraction due to VOCs against insect damage	<i>Salicylic acid</i> and protein kinase stimulated by <i>Manduca sexta</i> attack and mediated damage induced caution in <i>Nicotiana attenuata</i> .	(Steppuhn <i>et al.</i> , 2004; Meldau <i>et al.</i> , 2009)
Herbivore specific VOCs	VOCs released from damaged plants specifically depend upon the nature of leaf wounding and its age, abundance of neighboring plants	(Clavijo McCormick <i>et al.</i> , 2012)

are two different factors that may vary according to the species. This inconsistency in competitive behavior and how species endorse erratically to kin and strangers according to the given conditions may not be specified. Wild soya bean *Glycine soja* and commercial soya bean *Glycine max* changed their leaf pattern when grown with closely related conspecifics as compared to unrelated neighbors (Murphy *et al.*, 2017).

Furthermore, according to another study, plants have the aptitude to gather evidence about their surroundings as well as nutrients. According to Cahill *et al.*, (2010), an annual plant, *Abutilon theophrasti*, displayed a distinct strategy in response to the presence of a competitor and uneven resource distributions. Rooting was reduced in plants that sensed and responded to their neighbors and were cultivated in soil with uniform nutrients. Contrary, plants with competitors and heterogeneous resource distributions abridged their belowground growth only moderately (Cahill *et al.*, 2010). While these findings are inconsistent with the data from Broz *et al.* (2010), which specified those plant responses towards its neighbors may greatly be controlled by the soil resource availability. From the previous examples of plant-plant interactions, it is obvious that plants actively contribute to the shaping of their communities. These interactions may be harmful

to one or favorable to both plants and, given the variety of these communications, it is more complex and challenging to establish that plants may always be interacting explicitly with their kin. For example, pea (*Pisum sativum* L.) did not recognize their kin. It showed lower competition with the interspecific neighbor as compared to intraspecific kin (Jacob *et al.*, 2017).

So far, identity and kin recognition has not yet become the attraction for crop breeders (Chen *et al.*, 2012); not solid pieces of evidence could be found for kinship mechanism in crop species. Fang *et al.* (2013) revealed that the root behavior pattern of seedlings of rice from the same genotype grown in close space tended to overlap more and grow closer to each other than seedlings from strangers (Fang *et al.*, 2013). Likewise, results of Fang *et al.* (2011) showed when intercropping with the same genotype, roots of maize or soybean overlapped to each other, in contrast, maize GZ1 intercropped with soybean HX3, roots pattern was reversed and tended to avoid each other (Fang *et al.*, 2011). Investigating critically, both studies targeted on the interface between the same or different genotypes, comparatively kin or non-kin, and how to root morphology affected by competition in plants and fitness consequences were also not examined (Table 1).

Evidence of VOC and molecular communication in plants

Plants are rooted and stationary, unlike mammals. Plants are unable to move around in search of food or reproduction, or to protect themselves against predators, despite the fact that their development is oriented toward the sun and may bend due to gravity. To ensure their survival in the nature, plants have created intricate tactics. Internal chemical transmission is used by both plants and animals to govern the shape and mechanism of different portions of the same individual, according to numerous research. (Henriksson, 2001). Plant chemical communication, *i.e.*, VOCs emission, plays an essential part in the rhizosphere and greater ecological perspectives. Plants have evolved extremely sophisticated and intricate sensing processes that enable them to persist in their ever-changing environments, as has been well documented (Pierik and De Wit, 2014). Undeniably, plants may sense and retort to variations in their surroundings, by collecting and evaluating disparate information and then modify their physiological, morphological and characteristics accordingly (Gundel *et al.*, 2014; Kessler, 2015).

Plants communicate with countless organisms surrounding them, *i.e.*, insects/aphids and animals that help them to pollinate and disperse their seeds for sexual reproduction, call for predator and parasitic insects that exterminate the attacking herbivorous insects, and microorganisms that support the nutrient procurement or induce resistance to disease and herbivores (Jaafray and Fatima, 2021). Due to these capabilities, plants are allowed to broaden and protect their territory. Furthermore, plants can distinguish themselves and communicate with one another, by warning them through above and below ground release of chemical signals neighboring conspecific or heterospecific plants (Farmer, 2001; Heil and Karban, 2010). Normally this form of plant communication occurs volatile chemicals transmission through the air (Karbon *et al.*, 2011) or via soluble compounds excreted by roots and mycelial networks (root exudates) in the rhizosphere (Johnson and Gilbert, 2015), although in some cases possibly alternative routes, for example, through sound (Husain Jaafray *et al.*, 2020; Jaafray and Fatima, 2021).

Plants also make changes at molecular level and release different kinds of proteins after stressful conditions and herbivore attack (Meents and Mithöfer, 2020; Jaafray and Fatima, 2021). Despite of molecu-

lar variations chemical response of the plants during stressful periods has been studied enormously due to active of VOCs release in the plants. Though primarily discouraged critically, the phenomenon of plant-plant collaboration via airborne signaling is now extensively acknowledged and has been tested in agriculture to improve agricultural practices to enhance the crops protection against pests (Blande *et al.*, 2014; Pierik *et al.*, 2014). Plant communication or plant-plant signaling also triggered more effectively after herbivore damage and caused plants to emit volatile cues that neighboring plants (Karbon *et al.*, 2014).

Future Directions

Regardless of criticism, the method of kin selection and the effect of neighbor's identity between plant species is one of the key aspects that ecologists can use to better understand plant interactions. (Klemens, 2008). Soil microorganisms may play an important role in the outcome of competitive interactions among related conspecifics, non-kin members, and communication with neighboring plants. Negative interaction (allelopathy) and positive interaction (volatile communication) between the plants may be better understood by investigating the chemical traits of the plants.

One of the most important examples of the chemical effects among the plants is garlic mustard (*Alliaria petiolata*), an invasive herbaceous flower in North American forests. Garlic mustard discharges benzyl isothiocyanate in the soil, which prevents the growth of mycorrhizal fungi that benefit tree diversity (Wolfe *et al.*, 2008). Research also proposed that exotic plants, such as Canada goldenrod (*Solidago canadensis*), *Centaurea stoebe*, and narrow-leaf cattail (*Typha angustifolia*), may secrete allelochemicals in the soil that precisely suppress the growth of native plants. By these examples, it can be assumed that the variation in plant growth of specific genotypes may be due to the influence of the identity of their neighbors and community composition of soil microorganisms.

In the rhizosphere, numerous reactions occur and may influence plant-plant communication with changing the surrounding environment. For better results interacting siblings versus non-siblings conspecifics and heterospecific must belong to a similar environment and size symmetry. There are several environmental aspects concerning kin and species recognition, and

plant communication has not been fully considered. Furthermore, comparative research should be conducted in the field and controlled condition as well, to figure out the main differences among plant response in species recognition and volatile communications. Crop species with the capability to distinguish kin related stronger and beneficial chemical communication may somehow protect the species for further herbivore attack.

More research into the processes and signaling components included in kin identification, such as root excretions and volatile cue emanations and protein interaction will be required, with implications for multitrophic plant relationships. Plants' reactions to adjacent related conspecifics are just as important, and the differential in reactivity between related and unrelated conspecifics is one of the most significant aspects of plant-plant communication. Upcoming research should focus on interactions between plants from the same and other genera, as this could bring new insights into the field of plant interaction and species reactions to a variety of neighbors. To assist make this expanding field of study more visible and understandable, further research and investigations focused on kin and species relationships are needed.

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Novelty Statement

The review article provides evidence regarding plant interaction and species recognition which would be beneficial for new researchers to understand the mechanism of species recognition.

Author's Contribution

Syed Wajahat Husain Jaafry: Manuscript preparation, core concept and relevant articles selection.

Amber Fatima: Manuscript editing, proofreading and reference management.

Conflict of interest

The authors have declared no conflict of interest.

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