

CHAPTER 20

FOREST ECOSYSTEMS AND ALLELOPATHY

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INTRODUCTION

A forest ecosystem is a dynamic set of living organisms: plants, animals and microorganisms, that are characterized by a predominance of trees, all interacting among themselves, with the environment in which they live (soil, climate, water and light) and ecological cycles (energy, water, carbon and nutrients) with which they are closely associated. Plants set up relations in order to compete for resources and many plants have adopted strategies of chemical usage to acquire a greater proportion of the available resources. Some of those relations involve allelopathic interactions, higher plants cannot change the location since germination, but they adapt themselves to the surrounding environment, and they are provided with different mechanisms to promote its own growth. These mechanisms have been obtained during evolution process, and here chemical substances play an important role (Nishimura and Mizutani, 1995) that vary in their relative importance depending on the ecological context in which they are studied (Hierro and Callaway, 2003): exotic plant invasion, tree regeneration, chemical information between plants, inhibition of seedling understory, impact on physico-chemical and biological characteristics of soil.

The production of chemical compounds by trees that are released in the environment, has been widely investigated in forest ecosystems (Souto et al. 1994; Souto et al. 1995; González et al. 1995; Gallet and Pellissier, 1997; Sivagurunathan et al. 1997; Peñuelas and Llusia, 1998; Rawat et al. 1998; Reigosa et al. 2000; Souto et al. 2001; Harris et al. 2003), especially when adverse impacts of understory species on tree species are suspected (Pellissier, 1993; Mallik, 1987; Mallik, 2001; Mallik, 2003)

but we will focus this review on different ecological contexts into the forest ecosystem

EXOTIC PLANT INVASION

Some examples of strong allelopathic effects can be found in the genus *Acacia*, *Ailanthus*, *Eucalyptus*, *Juglans*, *Leucaena* and some *Quercus* species. Other tree species have been studied more deeply than the previous list (*Acer*, *Kalmia*, *Picea*, *Pinus* and *Prunus*) but they produce moderate effects on other species. Most examples of allelopathy in trees are related to exotic species that act as invaders or become dominant; usually they are not as competitive at home.

Allelochemicals are secondary metabolites. The importance of the distribution and concentration of secondary components to plant relationship should not be dismissed because they are produced in plants not necessarily for competition (Berenbaum, 1995). Allelopathy was probably not developed as a specific competition mechanism between plants. If most of allelochemicals are secondary exudates from plants, they would be more likely to be effective in competition with plants outside of the native community (Rabotnov, 1982; Reigosa et al. 1999a).

Introduced species that disperse but do not fill the place of autochthonous species are thought to exploit unfilled niches in the community (Elton, 1958). Exotic species that act as aggressive plant invaders and reduce the abundance or species diversity require different explanations (Rich, 2004) and the reasons why many exotic tree species competitively exclude and eliminate their neighbors in resident communities but coexist in relative peace with neighbors in their native habitat, that usually is species-diverse system, remain one of the most important mysteries in plant ecophysiology (Hierro and Callaway, 2003).

Several hypotheses have been proposed to explain intrusiveness in plants in general (Rejmanek, 2000), all of them related to plant biology of the invader and particular characteristics of the resident community (Levine et al. 2003). The leading theory for the exceptional success of invasive plants is their escape from the natural enemies that hold them in check, freeing them to utilize their full potential for resource competition (Keane and Crawley, 2002). There are often complex interactions between the traits of the invader and resident community attributes (Shea and Chesson, 2002 and Suding et al. 2004), then could be better concur in processes responsible for plant invasions that have been tested experimentally, or are testable, using woodland species: release from natural enemies, broad tolerance limits, more efficient use of resources, hybrid vigor and allelopathic processes (Zedler and Kercher, 2004). These hypotheses are not shutting out one another. They have a good connection to exotic species released from pathogens (Mitchell and Power, 2003), predict that invasive

species have broader tolerance limits or tolerate extreme environmental conditions better than noninvasive species (Kercher and Zedler, 2004a), state that invasive species compete better because of more efficient or complete use of light, and nutrients resources (Kercher and Zedler, 2004b), focus the invasive phenomena on invaders with different species as parents (Ellstrand and Schierenbeck, 2000) and predicts that some plants become reach profit through the release of biochemical compounds that inhibit the growth and germination of species in the area of introduction (Bais et al. 2003 and Hierro and Callaway, 2003).

Despite a much larger body of evidence for allelopathy as an important plant interaction in agroecosystems (Narwal and Tauro, 1994), still some skepticism remains. For a critical evaluation of ecological significance of allelopathy in forest see Wardle et al. 1998; Hierro and Callaway, 2003; Zedler and Kercher, 2004. Disruption of native communities by odd allelochemicals or the release of chemicals at higher concentrations or in different period of the year by an exotic plant would suggest that invasions disrupt co-evolved interactions among long-associated native species. If allelopathy is more important in exotic invasion than in natural communities it is possible that interactions among plant species may drive natural selection in communities. This positive statement implies that natural communities may gradually change (evolutionary time) and, in some way, act as functionally organized units (Wilson, 1997).

Allelopathy seems to be more intense in poor soils (Inderjit and Callaway, 2003, Beltz and Hurle, 2004 and Suding et al. 2004). The hypothesis that allelopathy increases the invasive potential of exotic plants in environments with low resource availability awaits evaluation but its more likely (Hierro and Callaway, 2003). This supposition gives to us a reason to predict that some plants become invasive monotypes through the release of allelochemicals that inhibit the growth and germination of species in the area of introduction. The overall effect of one plant on another is the result of several interacting mechanisms (Ridenour and Callaway, 2001 and Zedler and Kercher, 2004) but the balance of competition in the broader context of interference shifted when allelopathy was ameliorated indicating the important role of allelopathy in exotic plant invasion.

TREE REGENERATION

One of the greatest challenges for plant ecophysiologicalists today is restoring natural and crop forests. This restoration will require understanding complex processes that shape successional pathways, including biochemical interactions between trees and other plants.

Shrub species often quickly invade disturbed woody lands (Duncan and Chapman 2003) and form a dense understory that can alter natural regeneration of trees after removal of canopy trees by forest harvesting (Mallik and Prescott, 2001). This remark has been attributed to allelopathy, competition, and soil nutrient imbalance (Smith et al. 2002 and Mallik, 2003) but its role in forest succession is unclear (Duncan and Chapman 2003).

Usually some understory plants as ericaceous or compositae perpetuate in the community after the disturbance related to forest harvesting, thanks to their stress-tolerating strategies. Different mechanisms have been proposed to explain failure of natural regeneration of trees at the ecosystem level (Mallik, 2003) but habitat degradation by allelochemicals from understory species has earned great significance in the last years. Sometimes this inhibition includes planted tree seedlings that exhibit stunted growth in these forest areas (Mallik, 1992 and Pellissier, 1993) with serious ecological, economic, and social consequences. Unfortunately, to date, the study of disturbance in woodlands by forest management has been primarily anecdotal and resistant to generalization.

Coevolution plays a role in the manifestation of allelopathy (Rabotnov, 1982, Reigosa et al. 1999a). Additionally, there may be genetic and evolutionary dynamics that alter the competitive ability of plant species (Ellstrand and Schierenbeck, 2000; Siemann and Rogers, 2001). Delayed germination in treatments with shrub leachates and humus supports Rabotnov's hypothesis if we accept the tendency of the understory system after release of trees to safeguard internal stability (Mallik and Pellissier, 2000). They found that germination and primary root growth of an exotic spruce was more affected by humus and its allelochemicals than a native spruce thus strengthening the idea of a coevolutionary process in allelopathy.

It is not clear if allelopathy exerts a primary role in forest succession after disturbance. The negative influence of some shrubs on tree growth was through root competition for nutrients rather than allelopathic effects of litter leachates (Mallik and Prescott, 2001). Tree harvesting and non adequate management of the forest can cause a long term occupancy of a site by understory species with irreversible habitat degradation, converting conifer forests into ericaceous heath. Different experiments suggest that tree inhibition phenomenon in this area is more than just a case of nutrient deficiency (Mallik, 2001). In other way, the presence of plants has been shown to influence small-scale patterns of nutrient availability in various ecosystems by changing the quantity and quality of organic matter in the nearby soil (Chen and Stark, 2000). These effects are species specific since plants differ in litter production quantity and litter chemical composition. Ericaceous litter has a high content of phenolic compounds (Gallet et al. 1999) and phenolic compounds may play a dominant role in controlling many aspects of plant-plant interactions through soil, especially those related to organic matter dynamics and nutrient cycling (Northup et al. 1998). One of

the most characteristic properties of phenolic compounds is their capacity to constitute recalcitrant complexes with proteins and thus to modify nutrients availability (Hättenschwiler and Vitousek, 2000). Significant amounts of phenolic compounds can be released by rainfall from green foliage and decomposing litter (Gallet and Pellissier, 1997), thus affecting nutrient cycling. The ecological relevance of phenolic compounds in degraded forest can be of especial interest, especially in N-limited systems with slow decomposition, such as boreal ecosystems, where slow growing species with high concentrations of carbon-based secondary compounds predominate (Castells et al. 2003). Then, the poor tree seedling growth that is observed in some tree crops or natural forest may have resulted from the adverse effects of understory litter, causing allelopathy and nutrient imbalance. However, it is still not clear whether changes in N cycling related to plant phenolic compounds (Souto et al. 2001) can be found in natural conditions since these effects have been mainly tested in laboratory experiments with individual compounds or soil samples. Castells et al. (2003) support the hypothesis that potentially negative interactions among plants could be caused by changes in nutrient dynamics although allelopathic effects cannot be excluded.

In a forest ecosystem, allelochemicals can be released to the soil by several ways. Decaying of residues is usually predominant, but in forest crop systems the biomass of stump-roots left in the cutting area is really important (Huang et al. 2000) and the content of allelopathic compounds in roots was thought to be the highest among all parts of the tree (Bertin et al. 2003). Phenols from stump-roots exert an allelopathic influence on tree seed germination and seedling growth (Huang et al. 2000).

CHEMICAL INFORMATION BETWEEN PLANTS

Plant-plant signaling is the flow of information between individuals. An interaction is considered to be informational when it involves the exchange of an insignificant amount of matter or energy (Aphalo et al. 1999). To exploit the common environmental conditions to maximize reproductive success, organisms can take advantage of information (Dicke and Bruin, 2001) and an important form of information consists of chemical signals (Bais et al. 2004). We consider the mechanisms by which a plant could signal to a neighboring plant, and thus elicit a physiological response.

There is detailed information on how plants respond to environmental stimuli and regulate their internal physiology in response to several stressing conditions, including damage by insects or infection by pathogens (Hunter, 2000). Plants are subjected to multiples interactions in their natural environments and often respond inducing defensive pathways that usually increase the production of secondary metabolites, and in evolutionary sense, can enhance plant fitness (O'Reilly-Wapstra et al. 2004) but many secondary metabolites do not enhance the fitness of the producer plant (Firn and

Jones, 2000). Recent assays provide ample evidence that, for any biological target, most chemicals are inactive unless tested at high concentrations (Firn and Jones, 1999) but it could be due to the result of using inappropriate screening methodologies. If the proper target species or physiological parameter were used, a very high frequency of biological activity would be found (Berenbaum and Zangerl, 1996). The main problem deals with the definition of 'biological activity' (Firn and Jones, 2000). When studied at a molecular level, biological activity can have a different meaning than if it is studied at a whole organism or ecosystem level. Evolution of secondary metabolism is better understood if studied at ecosystem level.

It has been well established that plants obtain ecological profit from their relation with soil microorganisms. Permanent organization of many forest ecosystems depend on the ability of roots to communicate with microbes. Associations between plants and many bacteria and fungi are often regulated by root exudates (Bais et al. 2004). The mechanism by which proteins are secreted is not completely understood, but it has been proposed that proteins are actively secreted from the root epidermal cells (Flores et al. 1999).

Communication between plants is related to plasticity that is essential for plant survival (Aphalo et al. 1999). We can recognize plasticity in the vast range of secondary metabolites present in plants. However, apart from mechanistic questions, evolutionary questions should be addressed asking why plants exploit their neighbor's information and whether their strategy (modulating their developmental programme) is affected by physical, biological or previous experience.

INHIBITION OF SEEDLING UNDERSTORY

Trees modify their environment for more effective and efficient interference. Competition for resources in trees and subcanopy species is a constant in woodland. In order to compete for these resources, many plants have adopted strategies of chemical usage to attain benefit over others. The interaction between exploitative and interference competition remains largely unexplored for species that exploit dynamic resources (Amarasekare, 2002). In this sense the role of allelopathy in the interaction between forest trees and their understory is very interesting.

Allelochemicals are released into the environment by trees and ecologically modify growing sites (Sánchez-Moreiras et al. 2003) affecting the development of the understory. The way these organic chemicals escape the tree are through aboveground parts, roots exudation, and the action of many soil microorganisms on litter (González et al. 1995).

The plant diversity and richness of species found beneath allelopathic trees is significantly lower than in adjacent plots without the cover plant (Souto et al. 1995).

Some tree crops have a sparse understory growth around the trees, with a denser and more varied growth in areas not strongly populated by the dominant tree species or compared with natural woodland (Souto et al. 1992 and Souto et al. 1994). The allelopathic activity of trees is thought to play an important role as leaf decomposition of these plants inhibit the soil microorganisms development (Souto et al. 2001) and germination of target seeds (Souto et al. 1994).

Most of the experiments and interaction processes in forest are related with different types of organic chemicals as terpenes (Paavolainen et al. 1998 and Abraham et al. 2000), phenolics (Souto et al. 1995, Souto et al. 2000 and Huang et al. 2000) and alkaloids (Wink and Latz-Brüning, 1995 and El-Khawas and Shehata, 2005) but the chemistry of interaction is too complex and it has been demonstrated that allelochemicals released by trees can affect plant growth (Durán-Serantes et al. 2002), absorption of water and mineral nutrients (Booker et al. 1992), ion uptake (Yu and Matsui, 1997), membrane permeability and cell cycle (Sánchez-Moreiras et al. 2003) plant water relationship (Barkosky and Einhellig, 2003), protein biosynthesis (Wink, 2003) leaf area expansion (Hane et al. 2003), respiration (Abraham et al. 2003), and photosynthesis (Kagan et al. 2003) and many other physiologica processes.

Most forest are managed for timber production. In such forests the fate of indigenous understory plant communities, and thus of plant diversity in general, is a function of silvicultural practices, that promote rapid decomposition of plant material Roth et al. 2000), designed with the primary intent of maximizing the value of the dominant tree crop (Thomas et al. 1999). Silvicultural practices can change the physico-chemical conditions of the soil or the biotic relations into the soil solution (Leckie et al. 2004) and therefore, change the allelopathic tree-understory relationships. This should be kept in mind if we are interested in diversifying farm income and reducing environmental impacts of agriculture (Jose and Gillespie, 1998).

IMPACT ON PHYSICO-CHEMICAL AND BIOLOGICAL CHARACTERISTICS OF SOIL.

Our understanding of the effects of tree species on soils remains very incomplete (Augusto et al. 2002). Composition of the overstory has an impact on soil structure and the effect on forest communities and soil environment having different tree species in the canopy is significant. Secondary metabolites released into the soil solution by plants can affect abiotic and biotic soil processes that affect other plants and it is difficult to distinguish of direct allelopathy (Inderjit and Weiner, 2001).

There is a massive interface between plant roots and soils where chemical exchanges are highly probable, mainly carbon-containing compounds (Uren, 2000).

Allelopathy influences the ecology of the tree-soil interface and modifies relationships between organisms in forest (Bertin et al. 2003).

The total amount of root exudates produced in a tree ecosystem varies with the plant species, cultivar, age, and stress factors (Uren, 2000). Tree roots exude high molecular weight organic compounds such as flavonoids, enzymes, fatty acids, growth regulators, nucleotides, tannins, carbohydrates, steroids, terpenoids, alkaloids, polyacetylenes and vitamins (Rovira, 1969) that provide a suitable environment for the growth and development of microorganisms through establishment of mucigel (Bertin et al. 2003). Soil microflora seems to be strongly influenced by the plants of the ecosystem, allelochemicals influence directly the development of microorganism colonies (Reigosa et al. 1998), microorganisms have a large impact on the total allelochemical load on a site (Reigosa et al. 2000) and fungi and bacteria can transform exudates into inactive molecules or process them into allelopathic agents modify and interfere with growth regulation signals surrounding fungal growth and infection in mycorrhizal associations affecting indirectly resource competition (Reigosa et al. 1999a). Interactions are too complex to generalize (Pellissier and Souto, 1999). Tree roots secrete many different low molecular weight substances, including sugars and simple polysaccharides, amino acids, organic acids and phenolic compounds (Bertin et al. 2003) with allelopathic activity (Reigosa et al. 1998 and Reigosa et al. 1999b). Then, root exudates play important roles in a number of plant-microbial relations (Inderjit and Weston, 2003) and they have also important function in the determination of microbial community structure in the tree rhizosphere (Grayston et al. 1994).

Allelochemicals that reach soil solution interact with organic and inorganic substances regulating not only their bioavailability in the soil environment, but also their transport (Bertin et al. 2003). The action of those allelochemicals alter soil microflora, which subsequently alter nutrient status through decomposition and mineralization of organic substances, and through the formation of soil organic matter influencing competition for nutrients (Hodge et al. 2000).

Tree composition significantly influences the physical, chemical and biological characteristics of top-soil. By modifying the fluxes of matter or energy, allelochemicals secreted by forest species have the potential to affect strongly soil characteristics (Augusto et al. 2002). More studies are needed to understand the effects of allelochemicals on organic matter, reactive mineral surfaces, ion exchange capacity, inorganic ions and specific microbes.

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