Chapter 1
Role of Allelopathy During Invasion Process by Alien Invasive Plants in Terrestrial Ecosystems

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Abstract Biological invasion is causing serious current biodiversity loss in different parts of the world and involves different stages: introduction, establishment, naturalization, and fast dispersion outside the normal ranks. Invasion may cause a reduction in abundance of native species or the elimination of populations of a particular species. Exotic species have to surpass different biological filters to get to be invaded in a new habitat. Importance of allelopathy in the invasion process may include the release of secondary chemical metabolites into the surrounding environment to inhibit the seedling establishment and other ecophysiological attributes of native biota. Temperature, drought, cold, association, and feedback from soil microorganisms can also adversely affect the biological nutrient cycle, and other aspects that can favor the invading capacity of exotic species. Environmental problems generated by invading species can become serious in naturally protected and sensitive areas, where climatic circumstances may evolve in the shape of global warming. The purpose of this chapter is to highlight the role of allelopathy during the invasion process with special emphasis to ecophysiological relationships between exotic and native plants, and soil microorganisms.

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1.1 Introduction

In a simple way, the invading species are those, which came from other regions. This definition, merely biogeographically, implies exotic species in contrast to the native species (Rejmánek 1995). However, an exotic species would not have to be considered an invading if it does not settle successfully in the introduced area and it is not able to regenerate by itself or it is not, later, able to disperse without direct human support (Binggeli 1994). Theoretically, an alien species can be considered invading when it enters an exponential phase of dispersion (Pyšek 1995). On the other hand, biological invasion is not a localized phenomenon, but it is a dynamic process that occurs through years as the invading population crosses different stages: introduction, establishment, naturalization, and fast dispersal outside the normal ranks (Fig. 1.1).

The invasion of new territories by alien plant species threatens the biodiversity and the stability of the ecosystems (Davis 2003). This process is responsible for eliminating the presence of native and extinction of certain species (Richardson et al. 1989; Gaertner et al. 2009), changes in the relation between soil microorganisms population (Jacinthe et al. 2009), modifications in the availability of soil nitrogen (Chen et al. 2009) and other nutrients (Rodgers et al. 2008) and changes in the soil properties (Zhang et al. 2009). These results maintain the open debate on the paradox of invasion, depending on the space scale of the study of the existence of positive and negative relations between the biodiversity of exotic and native species (Fridley et al. 2007; Rout and Callaway 2009). On the other hand, Meisner et al. (2009) indicated that the paradox of invasion does not exist. They concluded that there are underlying mechanisms to explain species in the new habitats. Rout and Callaway (2009) pointed out that a general pattern of improvement of the cycle of nitrogen does not exist for the invading plants. Despite this controversy, the invasion would cause a reduction in the abundance of native species or the elimination of some populations that could reduce the genetic diversity (Davis 2009).

The characteristics which favor the capacity of a plant to become invaded are directly related to their ability to reproduce, grow quickly from germination to reproductive stage, and, particularly, of its phenotypic plasticity that will allow them to adapt to the environmental stress of the new habitat (Baker 1974; Shi and Ma 2006). Nevertheless, most of alien invasive species do not share all these characteristics (Roy 1990; Pyšek and Richardson 2007; Lorenzo et al. 2010a, b). There is sufficient scientific work to support the hypothesis that the success of invasion could be triggered by functional characteristics, which differ quantitatively from presence in the native flora (Lloret et al. 2005). A study conducted in Ireland (Milbau and Stout 2008), analyzing the importance of different historical factors (environment and species), taxonomic and ecophysiological, classified their importance in the preponderance of species' ability to transform itself into naturalized or invaded. The factors that differentiate the invading exotic species from non-invading ones were the introducing ornamental species, hermaphrodite

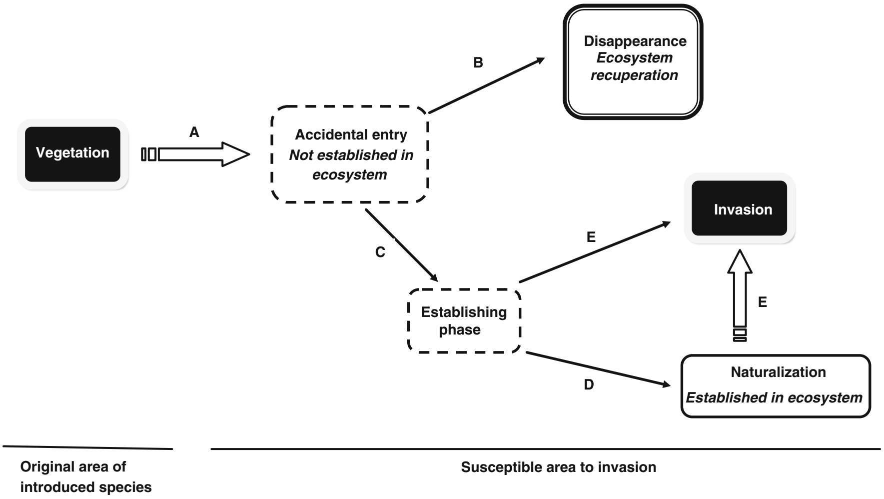

Fig. 1.1 Dynamic scheme of the invasion process. **A** introduction of propagules, **B** disappearance, **C** factors that influence in the establishment, **D** factors that influence the naturalization, **E** factors that influence the invasion

flowers, pollination types, time of flower initiation, indicating value of relative humidity, and the date of the first registry. The incorporation of phylogenetic information had little influence on the results, which suggested the capacity of exotic species to become naturalized and to become invading to evolve independently in different phylogenetic lineages. Jiang et al. (2007) suggested that different species that constitute the plant communities differ in their vital history, the biological and physiological characteristics, responsible for the existing relation between diversity, production of biomass, and capacity of invasion, are probably different. The invasive herb *Solidago canadensis* was introduced into Europe in the seventeenth century (Weber 2001). It is a perennial herb forming large clonal colonies that tend to reduce the abundance of native vegetation (Weber 1998). The taxon is highly variable and includes diploid, tetraploid, and hexaploid plants in the native range (Halverson et al. 2008), but only diploid cytotypes are found in Europe (van Kleunen and Schmid 2003).

It is well understood that the characteristics of the susceptible habitat to be invaded directly influence the invading capacity of the exotic species (Gaertner et al. 2009; Lorenzo and González 2010) and also that the abundance of the exotic species in the native range predicts the abundance in the colonized area (Firn et al. 2011). Without any doubt, a better knowledge of why some plants may act as invading could help us to identify species potentially detrimental and to control the present invading species, being a potentially useful criterion for the biosafety programs. This chapter covers the importance of allelopathy in the invasive process into the current context of exotic plant invasion, updating definitions and relationships with invasion, discussing the characteristics of exotics that make them invasive plants, reviewing allelopathic compounds that are involved in the invasion process, and revising ecophysiological aspects that could be affected by invasion process as physiological activity of native target species, soil microorganisms, and nutrient cycles.

1.2 Allelopathic Perspective

There are hundreds of thousands of plant species, but relatively few have the capacity to invade new habitats. We can understand the reason of this geographic specificity based on the different evolutionary filters (Lambers et al. 2008). The exotic plants would have to surpass these filters to get invaded (Lortie et al. 2004; Lorenzo and González 2010; Lorenzo et al. 2010a). The plant species are present in a determined area for historical reasons (plant evolution or derives continental) in spite of having appropriate environmental conditions in other regions, this one is the historical filter. Some species are absent from a certain area because they do not have the appropriate physiological characteristics to survive in that area (for example, they cannot tolerate conditions of extreme water deficit); this one would be the physiological filter. The interactions produced between exotic and native species in new atmosphere will determine the plant composition of the invaded area, being the biotic filter (Fig. 1.2). One of the components of this last filter is the allelopathic relations that can be produced between the plant species in the naturalized environment (Lorenzo et al. 2008), including alteration in soil microorganisms population (Zhang et al. 2009).

Within the framework of this text, the more accepted definition of allelopathy (Rice 1984) is "the effects (stimulatory and inhibitory) of a plant on other plants through the release of chemical compounds into the environment". This definition also includes microorganisms. The allelopathic process, from the perspective of the competition between species, constitutes a passive element of interaction (Reigosa et al. 1999); neither the excess nor the less important ones. The hypothesis of Rabotnov (1974) indicates that the allelopathy is, probably, less significant in plant communities in which they have coevolved than in native versus invasive species, which have evolved in different biogeographical areas (Reigosa et al. 1999, 2002; Callaway and Hierro 2006). The allelochemicals of exotic species have manifold functions within the biotic framework in area of original distribution (allelopathic defense as opposed to herbivorous transporting metal agents or agents of symbiosis between soil microorganisms and the plant). In addition, in the new area, the allelopathic potential of the invasive species would be increased to escape from natural enemies and allelochemicals lose some of their original function (Sinkkonen 2006).

In the ecological frame generated by the filters of Lambers et al. (2008), different hypothesis are included to explain the invading success of some alien invasive species (Lorenzo and González 2010; Lorenzo et al. 2010a): the *propaguels pressure* hypothesis (PPH, di Castri 1989), *enemy release* hypothesis (ERH, Keane

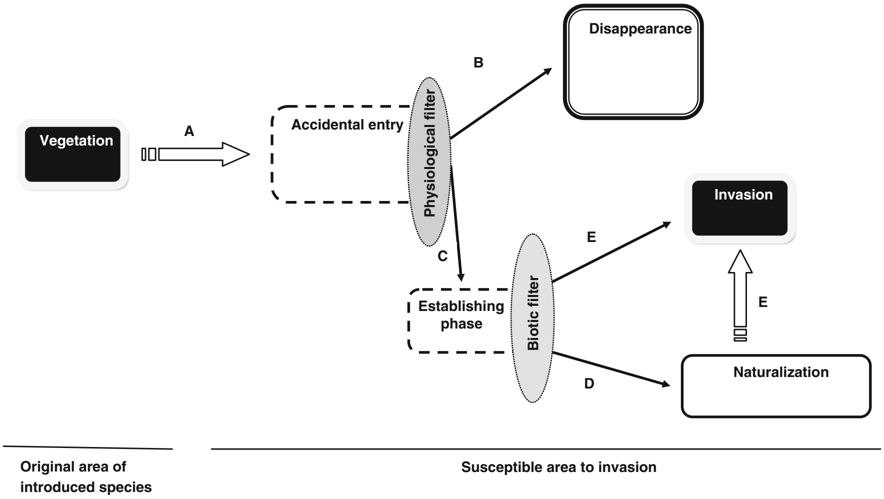

Fig. 1.2 Dynamic scheme of the invasion process including evolutionary filters like barriers. **A** introduction of propagules, **B** disappearance, **C** factors that influence the establishment, **D** factors that influence the naturalization, **E** factors that influence the invasion

and Crawley 2002), *superior competitor* hypothesis (SCH, Bakker and Wilson 2001), *Novel weapons' hypothesis* (NW, Callaway and Aschehoug 2000), *hypothesis of the evolution of the increased competitive capacity* (EICA, Blossey and Nötzold 1995), and *the hypothesis of resources fluctuation and disturb habitat* (FR & DHH, Davis et al. 2000). During the dynamic process of invasion, the exotic species use some of the mechanisms included in these hypotheses like expansion ways, being very probable, the participation of several of them throughout the invasive process (Jiang et al. 2007; Lorenzo et al. 2010a). From all these hypotheses, three of them, ERH, EICA, and NW, are most often suggested to explain the invasive ability of different plant species (Bais et al. 2003; Mitchell and Power 2003; Torchin et al. 2003; Callaway and Ridenour 2004; Callaway et al. 2005a, 2008; Gómez-Aparicio and Canham 2008; Handley et al. 2008; He et al. 2009; Hill and Kotanen 2009; Te Beest et al. 2009; Lind and Parker 2010; Lankau 2011).

According to ERH hypothesis the alien invasive species have the ability to increase its population density in the new geographical area because they are free of the predators that attack in their native range (Dostál 2010; Andonian and Hierro 2011; Vasquez and Meyer 2011). The EICA is based on the idea that when the invasive plants are released from their specific enemies, they can invest more resources in growing and less on defending (Herrera et al. 2011; Holzmueller and Jose 2011), which confers a competitive advantage forehead to the native species. Hypothesis NW asserts that the exotic species release allelochemicals that are relatively ineffective against their neighboring plants in the native range but highly inhibiting against the native plants in the new habitat. Factually, this phenomenon can be given mainly to the native species that are not adapted to the allelochemicals of the exotic species, being the evolutionary relations among the plant species to a key part of the hypothesis of the novel weapons (Inderjit et al. 2006). This theory is supported by biogeographical studies (He et al. 2009; Callaway et al. 2008; Thorpe et al. 2009) in which it was demonstrated that the invasive species produce more effects on the native communities of the invaded area than on the same types of native species in the original area. It seems, therefore, that the allelopathy plays an important role in the invasive success of these exotic plants that are able to dominate in the ecosystems where they are introduced. In fact, the allelopathy has been widely studied in the last decades within the context of the hypothesis of new weapons, because of the invasions of numerous plants originated by different reasons (Carballeira and Reigosa 1999; Callaway and Ridenour 2004; Callaway et al. 2005a; Lorenzo et al. 2008, 2010b; Ens et al. 2009a; Jarchow and Cook 2009; Lind and Parker 2010; Lankau 2011; Barto et al. 2010).

A large number of allelopathy experiments with exotic species evaluated the phytotoxic activity of the invasive species by means of bioassays in which the germination, seedling growth, and plant biomass are determined under laboratory or greenhouse condition (González et al. 1995; Carballeira and Reigosa 1999, Hoagland and Williams 2003; Lorenzo et al. 2008, 2010b; Hussain et al. 2011b). However, the study of the allelopathy in nature has been accompanied by great skepticism as a result of the inherent methodological difficulties to demonstrate this phenomenon under natural field conditions (Gómez-Aparicio and Canham 2008). To end this debate, it is necessary to design or carry out allelopathic experiments in natural conditions, which differentiate the resource competition from the allelopathic phenomenon. Although during the last years progress was made in the use of more realistic and sophisticated techniques, the studies of allelopathy in real conditions continued to be very small (Gómez-Aparicio and Canham 2008). One of the tools used in the allelopathic research, that separate allelopathy from resource competition, is the use of the activated charcoal. This element has the capacity to adsorb organic compounds released by the invading species (Inderjit and Callaway 2003). Nevertheless, recent investigations have found that the activated charcoal interferes with the availability of nutrients and growth of plants (Weißhuhn and Patri 2009; Lau et al. 2008) that represent an insecure methodology. Lorenzo et al. (2010a, b; 2012) has designed a new method maintaining the interaction of the donating and receiving species in an inclined plane that would allow detecting the allelopathic effect without the need to add external elements, which based on the capacity of the allelochemicals move in the soil solution. Although the preliminary results obtained with this method are promising, and we can suggest introducing improvements in the technique that will be effective tools for differentiating the allelopathy from other competitive mechanisms in the invasion processes.

Majority of compounds released by the plants are produced as off shoots of primary metabolic pathways (Hadacek 2002). Following the phytotoxic action, the bioactive concentration and its persistence and fate in the surrounding area in which they are released can act like allelopathic compounds (Inderjit and Duke 2003). In addition, in nature, the allelopathic activity is probably originated by the joint operation of several allelochemicals, as compared to action of single

Table 1.1 Effect of allelopathic compounds, which take part in the invasion process, on different receiving species

Allelopathic compounds	Invasive species	Inhibitory effects	Native species	Reference
Sesquiterpenes	*Chrysanthemoides monilifera* (L.) Norl. spp. *rotundata*	Inhibition in seedling growth	*Isolepis nodosa* (Rott.) R. Br *Acacia longifolia* var. *sophorae* (Labill.) F. (Muell.) *Banksia integrifolia* (L)	Ens et al. (2009b)
Soluble phenolics	*Typha angustifolia* L.	Reduction in germination	*Bolboschoenus fluviatilis* (Torr.) Soják	Jarchow and Cook (2009)
Glucosinolates and their hydrolysis products	Species from family *Brassicaceae*	Plant–plant, plant–microorganism and plant–insect interaction	Native species of invaded areas	Müller (2009)
7,8-benzoflavane	*Acroptilon repens* (L.) DC.	Effect on four plant species and their associate rhizosphere	*Astragalus cicer* L. *Hedysarum boreale* Nutt *Lupinus sericeus* Pursh *Medicago sativa* L.	Alford et al. (2009)
(±)-catechin	*Centaurea maculosa* Lam.	Effect on four plant species and their associate rhizosphere	*Astragalus cicer* L. *Hedysarum boreale* Nutt. *Lupinus sericeus* Pursh *Medicago sativa* L.	Alford et al. (2009)
(±)-catechin	*Centaurea maculosa* Lam.	Effect on seedling growth	Species that coexist with the invader in their native and invaded area	Thorpe et al. (2009)
Isopropilo and sec-butilo glucosinolatos and their degraded product Secondary butyl glucosinolates and their degraded products	*Sisymbrium loeselii* L.	Inhibition of germination and seedling growth	*Centaurea maculosa* Lam. *Pseudoroegneria spicata* (Pursh.) Love *Festuca idahoensis* Elmer. *Glomus intraradices* Schenck & Smith.	Bainard et al. (2009)

(continued)

Table 1.1 (continued)

Allelopathic compounds	Invasive species	Inhibitory effects	Native species	Reference
Cariofilone oxide, linoleic acid, germacrene B	*Centaurea diffusa* Lam.	Released into soil		Quintana et al. (2009)
(±)-catechin	*Centaurea maculosa* Lam.	Reduction of the biomass, reduction of the germination and increase of the mortality of the germinates	Native species of invaded area	He et al. (2009)
Monoterpenes	*Artemisia vulgaris* L.	Reduction of the above ground biomass	*Solidago canadensis* L.	Barney et al. (2009)
Poliacetilenes and diterpenes	*Solidago canadensis* L.	Effect on seedling growth	*Species nativas*	Abhilasha et al. (2008)
Cnicine	*Centaurea diffusa* Lam.	Reduction of germination, weight and inhibition of the growth of some gram (−) phytopathogenic bacteria	*Lycopersicum esculetum* L. *Lactuca sativa* L. *Triticum aestivum* L. *Leonorus sibiricus* L. *Pseudomonas syringae* Van Hall *Xanthomonas campestris (Pammel) Dowson* *Erwinia caratovora* Smith	Cabral et al. (2008)
Onopordopicrine	*Centaurea tweediei* Hook. & Arn.	Reduction of germination, weight and length of radical	*Lycopersicum esculetum* L. *Lactuca sativa* L. Disappearance *Ecosystem recuperation* *Triticum aestivum* L. *Leonorus sibiricus* L.	Cabral et al. (2008)

chemical (Inderjit et al. 2002; Inderjit and Duke 2003). Nowadays, there is a great debate in relation to the role of secondary metabolites such as allelochemicals in the natural ecosystems in general and invasion process in particular. The main problem is that low concentration of secondary metabolites under field conditions is insufficient to bring out a phytotoxic solution (Tharayil 2009).

In spite of controversial debates, considerable efforts have been used to demonstrate the mediation of compound released by invasive plants in the invasion processes (Carballeira and Reigosa 1999; Callaway and Ridenour 2004; Callaway et al. 2005b; Lorenzo et al. 2008, 2010b; Ens et al. 2009b; Jarchow and Cook 2009). Effects of different allelopathic compounds on native species and involved in invasion process are summarized in Table 1.1. Generally, allelopathic study of invasive species has been realized through bioassays in which extracts obtained of invasive species were applied on target species. The identification of chemical compounds of the extract and to determine which allelopathic compound is responsible for the invasion is a complicated and difficult task. Nevertheless, there are studies in which the allelopathic activity in the ecosystems is related to certain allelochemical groups, for example, simple phenols, flavonoids, terpenoids, alkaloids, fatty acids, poliacetilenos, sulfurated, oligopeptides, and glucosinolates (Müller 2009). There are few studies in which the allelopathic effect of an invasive species is associated to one or several identified molecules.

1.3 Ecophysiological Processes Affected by Allelochemicals During Invasion

In spite of its ecological relevance, as stated above the allelopathy is highly under debate these days (Fitter 2003; Fridley et al. 2007; Tharayil 2009). The ecological and physiological processes affected by the release of secondary metabolites from invasive species to soil solution are different. The plant invasions can not only disturb the diversity of plant species but also increase the plant productivity (Rout and Callaway 2009), and this phenomenon is the result of different interactions in the ecosystem that includes the soil microorganisms. The invasion processes often increase the deposits and flow of nitrogen through processes regulated by the soil microbial communities favoring the productivity (Rout and Callaway 2009) but, other times, inhibit the capacity of the native plants to take up nutrients through the suppression of associate mycorrhizae (Callaway et al. 2008). Under laboratory conditions, effects produced by the invasive species have been detected on physiological processes in the native species such as changes in the rate of germination or inhibition and stimulation in the growth of seedlings (Mei et al. 2005; Sun et al. 2006; Lorenzo et al. 2008, 2010b; Hussain et al. 2011a, b, c). In the last years, researchers have tried to know the mechanism of action of allelochemicals from invasive species and for this the strategy of investigators is to deepen the knowledge of primary effects in target plant (see Weir et al. 2004).

One of the better studied processes in allelopathy is the inhibition of the photosynthesis and the evolution of oxygen through interaction with components of the photosystem II (Martínez-Otero et al. 2005; Zhou and Yu 2006; Lorenzo et al. 2008, 2010b) and RuBisCO activity (Allen and Ort 2001). There are several reports regarding the effect of allelochemicals on respiration and ATP synthesis (Ishii-Iwamoto et al. 2006), carbon isotope discrimination (Hussain et al. 2008; Hussain et al. 2011a), photosynthetic efficiency, quantum yield, and heat energy dissipation (Hussain and Reigosa 2011), lipid and hydrogen peroxidation (Sánchez-Moreiras et al. 2011), on the respiration of native species (Lorenzo et al. 2008, 2010b). Gene expression studies have shown that Benzoxazolin-2(3H)-one (BOA) induces the transcription of a number of genes associated with cell detoxification and defense pathways (Baerson et al. 2005). Although the way of action of some allelochemicals has also been studied on redox system (reactive oxygen species), lignifications, stomatal conductance, foliar transpiration, metabolism of the amino acids, regulation of the concentration of hormones ,and cell cycle, these studies are not realized with extracts or allelochemicals derived from invasive species.

Invasive species also pose a significant threat to biodiversity. Moreover, compelling evidence exists, based on global trade and movement patterns, that the magnitude of this threat is increasing globally (Hulme 2009). Invasive species alter ecosystem processes (Raizada et al. 2008), decrease native species abundance and richness via competition, predation, hybridization, and indirect effects (Blackburn et al. 2004; Gaertner et al. 2009) change community structure (Hejda et al. 2009) and alter genetic diversity (Ellstrand and Schierenbeck 2000). For example, in Europe, the large majority of the most invasive species reduces diversity and change community structure, whereas a smaller percentage directly harms threatened species (Vilâ et al. 2009). Increases in the number and spread of alien species appear to be strongly associated with substantial increases in the extent and volume of trade and transport, particularly over the last 25 years (Levine and D'Antonio 2003; Ruiz and Carlton 2003; Hulme et al. 2009). Since global trends in trade and movement are clear, related patterns of the extent of biological invasion, their impacts on biodiversity, and societal responses to these impacts remain poorly quantified at a global scale. The Convention on Biological Diversity's (CBD) 2010 Biodiversity Target (UNEP 2002) and the associated Invasive Alien Species Indicator under the focal area 'Threats to Biodiversity' (Walpole et al. 2009) present one of the first concerted and globally coordinated efforts to do so.

In the small-scale experiments, the relation between the plant diversity of the community and the invasion by non-native species is negative (Maron and Marler 2007; Lorenzo and González 2010a); therefore, the resistance of the system to the invasion should increase with the diversity of species (Elton 1958). The arguments in favor of this old idea seems to reside in rich communities in species and offer few vacant niches (niche complementarily effect) or present a great probability that an invading plant is competitively excluded by a superior competitor (sampling effect) (Tilman 1999; Wardle 2001; Fargione and Tilman 2005). Although the studies realized in short periods of time indicate that the impact of invasive plants on ecosystems is relatively small, the future incidence on the native flora could be very high (van Wilgen et al. 2008) and the indications obtained until now suggests that the effect on biodiversity would have to be a reason for preoccupation.

During the process of invasion and its effect on the autochthonous diversity, the possibility of interaction with other environmental stress factors such as drought, more pronounced in a global warming context (van der Wal et al. 2008) that affect the native species, should be take into account (Maron and Marler 2007). Although wide scope exists in the field of ecophysiological interactions within the frame of the invasive species, the present data indicate that the plant communities do not respond similarly, which leads to significant changes in the composition and dominance of the species (Richardson et al. 1989; Gaertner et al. 2009; Matesanz et al. 2009). Black wood (*Acacia melanoxylon* R. Br.) has its origin in the temperate forests of southeast Australia and Tasmania currently considered as invasive in Galicia (Xunta de Galicia 2007) and currently covers a considerable area in the coastal zone of north-western Iberian Peninsula, both in monocultures and in mixed stands with *Eucalyptus globulus*. Upon invasion, it quickly establishes in the alien environment, thereby resulting in changes in structure and dynamics of native ecosystems. Recently, Hussain et al. (2011b, c) reported the inhibitory effects on seedling establishment and ecophysiological characteristics (leaf water contents, growth, photosynthetic efficiency, quantum yield, carbon isotope discrimination, and protein contents) of native species. The cause of inhibition was concluded to be the presence of growth inhibitory phenolic and flavonoid compounds present in flowers and phyllodes of *A. melanoxylon* R. Br. The differences in the ecophysiological characteristics also confirmed in lab tests where a positive relation has been elaborated between plant diversity and production and a negative relationship between plant diversity and invasion has also been verified. Nevertheless, the mechanisms that underlie in the invasion process are different according to the type of invaded community (Jiang et al. 2007).

The allelochemicals coming from invasive species have a strong impact on the dynamics of nutrient cycling in the soil of invaded area. The great diversity of invasive plant species and susceptible places for invasion showed that proposed patterns of differentiation between invaded areas by exotic species and free areas are inconsistent. Generally, the concentration of C, N, and P is increased with the growth of the invading species (Li et al. 2007). Studies realized with nitrogen-fixing invasive plants indicate that invaded areas showed a high content in N and a low C:N ratio. These variations with an increase in the contents of organic C, N, and interchangeable cations result in changes in the soil microorganisms (Marchante et al. 2008). These changes can be produced by different forms, for example, varying the entrance of organic matter in the invaded ecosystem (litter) or changing the radical system (Yan and Tong 2008). Some non-fixing invaders have also found to increase the total C, N, and net rate of nitrification (Chen et al. 2009). Although some non-invasive and invasive species have the same effect on the soil nutrients, we cannot affirm that a generalized phenomenon exists. In fact, other authors have published different results in the invaded areas where total N, P, N (NO_3^-) available P, and the stability of aggregates were decreased, while organic C and N (NH_4^+) were increased (Zhang et al. 2009).

The interactions between plants and their associated soil communities can result in dynamic feedbacks, where plants influence soil organisms and soil organisms in return influence plants (Bever et al. 1997; Wardle et al. 2004). The outcome of these interactions can range from negative to neutral or positive. Interactions are considered negative when the net effects of all soil pathogens, root herbivores, symbiotic mutualists, and decomposers reduce plant performance, whereas interactions are considered positive when the benefits brought about by symbionts and decomposers overwhelm the negative effects of soil pathogens and root herbivores and enhance plant performance (Wardle et al. 2004). Negative interactions enhance plant community diversity by exerting density-dependent control (Klironomos 2002; Reinhart et al. 2003) and speed up successional replacement (Van der Putten et al. 1993). The rate at which plants promote soil-borne pathogens differs among species (Klironomos 2002), functional groups (Kardol et al. 2007), and successional position (Kardol et al. 2006). As seen above, most of the effort to assess the invasion effect by alien plant has been done on the biodiversity of plants and animals species. However, attention has been devoted recently to the effects of plant invasion on soil microorganisms that could play a fundamental role in the invasion processes (e.g. Callaway et al. 2005a, b; Marchante et al. 2008; Rodríguez-Echeverría 2009).

Soil enzyme activities have been used as effective indicators of the capacity of the microbiota to mineralize carbon and mineral nutrients, and thus they can be used as measures of the functionality of the microbiota (Kourtev et al. 2003). Invasive plants can alter the microbial community surrounding the roots through root exudates (Bais et al. 2004). The obtained results indicate an increase in microbial biomass, increase in the density of the invasive species in invaded areas (Li et al. 2007; Jacinthe et al. 2009), metabolic activity (basal respiration) (Zhang et al. 2009, Jacinthe et al. 2009) and the functional diversity (Zhang et al. 2009).

Recent research has shown that some invasive species establish positive feedback cycles with the soil in which they invade and rhizosphere of the invasive species becomes rich in mutualistic organisms to get benefit from them (Rodríguez-Echeverría 2009). It has also been found that invaded soils have a high fungi/bacteria ratio, as compared to microbial communities in invaded soils or where native flora are different (Jacintheet al. 2009). Nevertheless, own results (Lorenzo et al. 2010b) obtained in different invaded ecosystems indicate that the ratio fungi/bacteria cannot be generalized, and probably it depends upon degree of time of the invasion and the floral typology of the invaded zone.

1.4 Conclusions

The invasions by alien species are responsible to a great extent for the current biodiversity loss and modification of the ecosystems. The invasive species use different mechanisms to invade new areas; among them the allelopathy seems to have an important role. During the invasion process, the invasive species release allelochemicals that seem to affect different primary and secondary physiological processes in the native species and soil microorganisms that are close to their rhizosphere altering the biodiversity. One more efficient use of resources and the competitive interaction by these resources based on allelopathic processes makes the exotic plants more invaders. A deeper knowledge of the underlying eco-physiological mechanisms to the invasion process will give a base to raise new control mechanisms and to avoid the loss of indigenous biodiversity of the threatened areas. Otherwise, the associated ecophysiological effects to this type of disturbance can be serious, mainly under the environmental conditions derived from the global warming (UNEP-WMO, 2001) and to show a new scene for the invaded areas.

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