

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

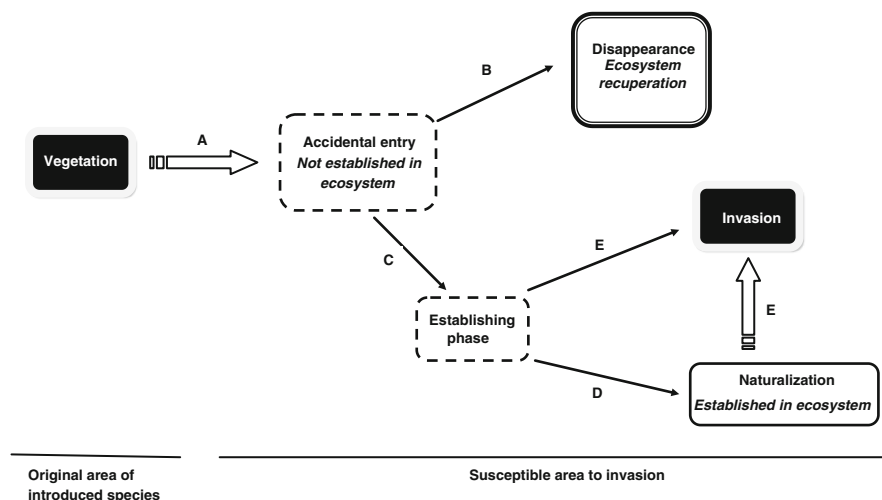


Fig. 1.1 Dynamic scheme of the invasion process. **A** introduction of propagules, **B** disappearance, **C** factors that influence in the establishment, **D** factors that influence the naturalization, **E** factors that influence the invasion

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 *propaguel pressure* hypothesis (PPH, di Castri 1989), *enemy release* hypothesis (ERH, Keane

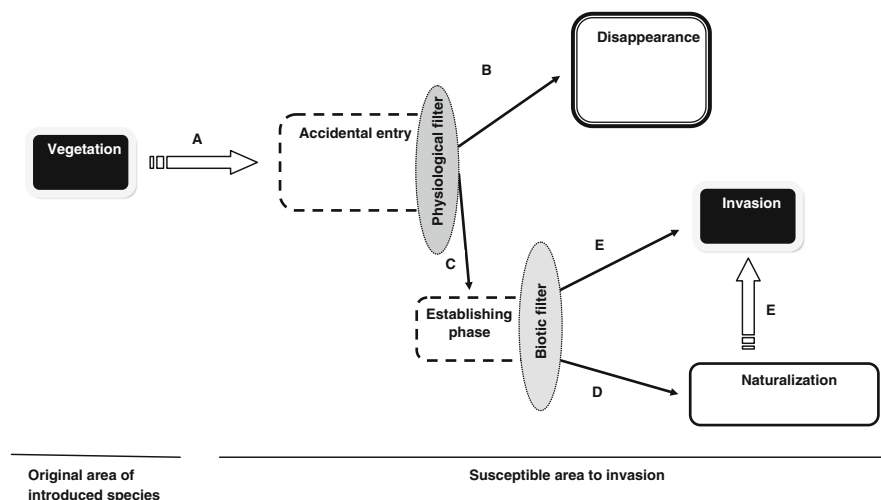


Fig. 1.2 Dynamic scheme of the invasion process including evolutionary filters like barriers. **A** introduction of propagules, **B** disappearance, **C** factors that influence the establishment, **D** factors that influence the naturalization, **E** factors that influence the invasion

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; Holzmüller 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

Allelopathy

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