Herbivory induced non-local responses of the clonal invader *Carpobrotus edulis* are not mediated by clonal integration

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**HIGHLIGHTS**

- Clonal growth enhances the invasiveness of *Carpobrotus edulis* to colonize new habitats.
- Physiological integration to induce systemic resistance in clonal plants is little studied.
- Labor division favoured photosynthesis potential in un-attacked integrated ramets.
- Herbivory induced a non-local compensatory response in un-attacked apical ramets.
- Non-local responses of apical ramets may be mediated by belowground communication.

**GRAPHICAL ABSTRACT**

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The anthropogenic displacement of species around the world results in new environmental situations where native and exotic species coexist. Exotic plants have to face native herbivores, and interactions between introduced plants and native herbivores seem to play an important role in the invasiveness of some exotic plant species. We studied the role of clonal integration in induce morphological, physiological, and biochemical responses in the clonal invader *Carpobrotus edulis* against the attack of the native snail *Theba pisana*. Our results demonstrated the presence of labour division mediated by physiological integration, with a significant increase of photosynthesis potential (both at morphological and physiological) in un-attacked integrated ramets. This response could be especially important under herbivory, as the negative impact of *T. pisana* on the photosynthetic structures of attacked *C. edulis* ramets could be buffered by transferring the dependence of photosynthetic activity to the un-attacked ramets. Our results also showed a constitutive resistance in un-attacked apical ramets, showing a similar amount of defence compounds to those exhibited in the basal branches attacked by snails. Results reported a non-local compensatory response, which there was an increase of total biomass in apical ramets when their basal ramets were attacked by the herbivore. We interpret this result as a compensatory response, with these apical ramets increasing shoot biomass to compensate for the biomass loss due to a potential attack from herbivores. However, this non-local response was not mediated by physiological integration but probably due to belowground communication, with the presence of alarm signals released by root exudates. We conclude that the attack of this snail is not enough to be a possible biological control due to the compensatory response to this snail by...
1. Introduction

The introduction of exotic species is often considered one of the most severe threats to biodiversity at a global scale (Sala et al., 2000; Vitousek et al., 1997). These organisms may get to convert into invasive species, increasing dramatically their distribution in newly colonized areas and influencing seriously indigenous communities, causing diversity loss and alterations in ecosystems (Degra et al., 2010). One of current challenges of invasion ecology is to explain why some species have more potential to spread rapidly and become dominant in the invaded community than others (Richardson and Pyšek, 2006). The anthropogenic displacement of species around the world results in new environmental situations where native and exotic species coexist (van Kleunen et al., 2015). In an invaded area, exotic plants have to face native herbivore pressure (Keane and Crawley, 2002; Parker et al., 2006). These new interactions that take place between invasive and native species may be antagonistic or mutualistic, and the degree of naturalization of introduced species depends directly on the attributes and intensity of these new reciprocal actions (Levine et al., 2004; Richardson et al., 2000). In this sense, the interactions between introduced plants and native herbivores seem important to understand the invasiveness of some exotic plant species (Harvey et al., 2010; Maron and Vilà, 2001). Thus, one of the most extended hypotheses to explain the success of exotic plants in a new range is the Enemy Release Hypothesis (ERH), which is based on that species introduced into an exotic region would experience a decrease in herbivore and other natural enemies’ pressure, resulting in a benefit in survival, growth, and reproduction (Keane and Crawley, 2002). However, it is reasonable to assume that even when the pressure from specialist herbivores decrease, as stated by ERH, generalist herbivores present in the new range can still depredate over the introduced plants, with the derived costs (Inderjit, 2012). In fact, generalist herbivores at the native range can acclimate quickly to the presence of exotic plants, being capable of exerting a certain pressure on them, as stated by the biotic resistance hypothesis (Parker and Hay, 2005). As reported by Maron and Vilà (2001) native herbivores could lower exotic plants performance during early life cycle stages, cutting seeds and seedling production up to a third, and halve adult plant population. So far, the effect of native herbivore species on the fitness of invasive plants has not been completely clarified.

Plants, as sessile organisms, need to develop strategies to avoid or buffer herbivore attacks. Constitutive defences are developed permanently, with the consequent energy cost (Wittstock and Gershenzon, 2002). On the other hand, the induced defence (i.e. changes in plants following damage) allows plants to activate defences only when attacked (Karban and Myers, 1989). This strategy will allow reducing defence costs, and therefore to optimize resource allocation to other key activities, such as growth and reproduction (Herms and Mattson, 1992; Karban and Baldwin, 1997). This induced defence can be developed at a non-local scale, that is, the activation of the defences occurs in an un-attacked part of the plant, being denominated induced systemic resistance (Agrawal et al., 1999; Tollrian and Harvell, 1999).

Clonal growth has been suggested an attribute that could enhance the invasiveness of plants (Pysek, 1997). In particular, physiological integration (i.e. resource sharing between connected members of the clonal system) has been found as a key trait to facilitate the colonization of new habitats by clonal invaders (Roiloa et al., 2013; Song et al., 2013; Wang et al., 2017; Yu et al., 2009). This benefit of physiological integration for the expansion of clonal invaders is based on the support from established units to developing ramets occupying a new area (Lechuga-Lago et al., 2016; Portela and Roiloa, 2017; Roiloa et al., 2016). Little is known about the production of chemical defences in C. edulis, and also about its interactions with native herbivore species in non-native range (Rodríguez et al., 2017, 2015). However, the importance of physiological integration to induce systemic resistance to herbivores in clonal plants has been only recently tested (Gómez et al., 2010, 2008, 2007; Gómez and Stuefer, 2006), and no previous work has been conducted specifically to link this response with plant invasiveness.

In this study, we examined the role of physiological integration in inducing systemic resistance and its contribution to promoting the expansion of a clonal invader. In particular, we aim to determine the role of connections in inducing defence responses in the problematic clonal invader Carpobrotus edulis, when interacting with a native generalist herbivore, Theba pisana. We test the following specific hypotheses: (i) herbivore will trigger an induced defence in the attacked ramets; (ii) physiological integration will allow the transport of defences’ signals from attacked to un-attacked ramets, inducing an increase of protective compounds on the latter, and (iii) due to costs of the production of protective compounds when defence is not needed, systemically induced un-attacked ramets will perform worse than un-induced ramets.

2. Material and methods

2.1. Study species

\textit{Carpobrotus edulis} (L.) N.E. Br. (Aizoaceae) is a succulent native to South Africa, perennial plant showing mixed sexual and asexual breeding system (Suets et al., 2004). It inhabits in suitable habitats in many coastal Mediterranean regions around the world, where it has become a problematic invader (D’Antonio and Mahall, 1991; Novoa and González, 2014; Traveset et al., 2008; Vilà et al., 2008). Clonal propagation allows \textit{C. edulis} to spread horizontally by the production of apical ramets that can remain physiologically integrated, and that allows a successful colonization of the surrounding area (Fenollosa et al., 2016; Roiloa et al., 2010). Previous studies have been conducted with this species to determine the effect on plant-pollinator networks (Bartomeus et al., 2008), plant-soil feedbacks (de la Peña et al., 2010), or hybridization studies (Suets et al., 2004; Vilà and D’Antonio, 1998). In addition, the importance of clonal traits in the expansion of this problematic invader has recently been studied (Lechuga-Lago et al., 2016; Portela and Roiloa, 2017; Roiloa et al., 2014, 2013, 2010; Roiloa and Retuerto, 2016; Souza-Alonso and González, 2017).

White garden snail \textit{Theba pisana} (Müller, 1774) (Gasteropoda, Helicidae) is a generalist coastal snail with a broad diet (Baker and Vogelzang, 1988). This species is native to Mediterranean and Western Europe. It has also been introduced to the USA, South Africa, Australia, and Argentina, where it has gained its reputation as a pest species (Däumer et al., 2012). Recently, we observed some interactions with the invasive plant \textit{C. edulis} in the field. Thus, we detected the presence of seedless fruits of \textit{C. edulis} in the dunes of Punta de Rons (NW Spain). This condition could have been caused by the presence of individuals of the native \textit{T. pisana} feeding on the interior of flowers, consuming the stigma, style and stamens, thus preventing the fertilization of the plants (Rodríguez et al., 2017).
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