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ADAPTABILITY OF INVASIVE PLANTS TO CLIMATE CHANGE

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Abstract

Climate change represents one of the greatest environmental challenges of the 21st century, accentuated by deforestation and the degradation of habitats. Changes in vital aspects such as temperature, the amount and distribution of rainfall or the frequency of extreme meteorological phenomena will probably negatively affect ecosystems. The possibilities of invasion will predictably increase, being endemic species especially vulnerable to the effects of climate change. Invasive species are extremely adaptable to climate variability, as evidenced by their current large latitudinal ranges. Generally, invasive plants also have rapid dispersal characteristics, allowing them to vary their ranges in response to changing climatic conditions rapidly. As a result, these species could become more dominant in many areas under changing climatic conditions. In many situations, the environmental stress generated by climate change and invasive plants are synergistic: invasive species can exacerbate the impacts of climate change on ecosystems, and in the same way, climate change can allow new invasions.

***Key words**: climate change, invasive plants, adaptation, abiotic stress.*

INTRODUCTION

Predictions estimate that environmental conditions will become more stressful due to global warming, especially in semi-arid and arid areas (IPCC, 2014). These conditions may affect the presence of many wild species, especially those that are already threatened, rare or endemic. Thus, climate change represents one of the most significant environmental challenges of the 21st century.

Following the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC), the average increase in global surface temperature is predicted to range from 1.7 to 4.8 °C until the end of the 21st century (IPCC, 2014). However, climate change does not only imply an increase in temperatures. Drought and salinity are the most critical environmental stress factors that reduce plant yields worldwide (Boyer, 1982; Mahajan & Tuteja, 2005). Approximately 35 per cent of the total land area, including more than 120 countries and regions, are threatened by drought disasters (Wang et al., 2021), whilst salt-affected soils occur in more than 100 countries, with various extents, nature, and properties. No climatic zone in the world is free from salinisation, although the general perception focuses on arid and semi-arid regions (Rengasamy, 2006).

Further, additional effects of climate change include extreme weather events and natural disasters, such as floods, hurricanes, or tsunamis, increased frequency of heavy precipitation events, extended dry periods, and potentially rising sea levels (IPCC, 2014).

Climate variables are known to influence the presence, absence, distribution, reproductive success, and survival of both native and non-native species (Finch et al., 2021). These changes will affect plant species in several ways, especially invasive, opportunistic plants, predictably changing their geographic ranges into new habitats. Consequently, native species will also be affected.

CLIMATE CHANGE: INVASION OPPORTUNITIES

Invasive species are those taxa that have been introduced recently and exert a substantial negative impact on native biota, economic values, or human health (Lodge et al., 2006). Biological invasion occurs when a species is introduced into a habitat or ecosystem to which it is not native, and then becomes established, spreads, and causes damage (Mainka & Howard, 2010).

Climate change and biological invasions are two essential drivers affecting biodiversity and ecosystem services (Schröter et al., 2005). Therefore, their study should be considered in an integrated manner. At the broadest level, climate change creates conditions that favour introducing new invasive species or expanding the range of nearby exotic species into habitats that show enhanced suitability. In this way, the distribution of local species is altered (Hellmann et al., 2008; Walther et al., 2009). Moreover, as the climate warms, the ranges of many invasive species will also shift, creating new risks in some regions (Bradley et al., 2010).

Many regions will be confronted by climate change with species, mainly ornamental, that have not yet naturalised and will become a threat, as the expected changes will reduce the naturalisation barriers of some alien species (Haeuser et al., 2018). With a typical temperate flora, the northern Iberian Peninsula could be invaded by species with a precise Mediterranean distribution. These species constitute a challenge for monitoring and proactive management by researchers and administration. We are aware of the invasive plants in the Mediterranean area, many of them coming from other Mediterranean climate regions such as South Africa, Chile or California. It is expected that some of those species will increase its new distribution area northwards (Brundu & Richardson, 2016). For example, in Europe, the number of invasive alien species increased by 76% in the last 30 years (Butchart et al., 2010), a trend that will accelerate rapidly, due to climate change (Haeuser et al., 2018) and the enormous number of exotic plants stored in domestic back yards, botanical gardens and plant nurseries (Pergl et al., 2016; van Kleunen et al., 2018).

INVASIVE SPECIES ADAPTATION MECHANISMS

The mechanisms by which species spread and adapt to new habitats have become a growing focus of research, particularly in the context of climate change and species invasions. Invasive species are rarely competitively dominant or major components in their native systems; however, in novel communities they often have larger populations, grow more densely, show higher fitness, and outcompete natives (Vilà et al., 2011).

Invasive species utilise a wide array of trait strategies to establish in novel ecosystems. Rapid adaptation to local climates can facilitate the expansion of their ranges (Colautti and Barrett, 2013), even beyond the climatic distributions in their native habitats (Petitpierre et al., 2012). They are usually successful and abundant, also showing in many cases characteristics that differ from endemic species. Thus, invasive plants generally grow faster and larger than native species, allocating more resources to leaf area and shoot growth, and possessing advantageous physiological traits (van Kleunen et al., 2010; Dawson et al., 2011). Furthermore, many invasive plants have broad climatic tolerances and large geographic ranges (RejmáZhangnek, 1995; Goodwin et al., 1999; Qian & Ricklefs, 2006), characteristics that will affect their response to climate change. They may also present other features facilitating their rapid dispersals, such as low seed mass and a short time to maturity (Rejmánek & Richardson, 1996). In addition, plant architecture and resource allocation patterns contribute as well to tolerance; for example, individuals that store more resources below ground may be more tolerant to aboveground damage (Hochwender et al., 2000).

Focusing on specific cases, Colautti and Barrett (2013) showed that, in *Lhitrum salicaria,* the evolution of earlier flowering is adaptive at the northern invasion front. It increases fitness as much as, or even more than the effects of specialist herbivores and the evolution of enhanced competitive ability. Some invasive plant species can also modify the soil they occupy to improve their fitness relative to native species. Positive feedback occurs if a heightened invader species increases the degree or extent of soil modification, in turn further favouring these invaders over natives (Jordan et al., 2008; Zhang et al., 2019; Tian et al., 2021). Another strategy of invasive plants to establish themselves in novel ecosystems is the ability to produce allelopathic compounds that can inhibit neighbouring native plants, either directly or suppressing native plants through disruption of beneficial subterranean microbial communities, or by alteration of ecosystem soil resources (Kalisz et al., 2021; Kato-Noguchi and Kurniadie, 2021; Qu et al., 2021).

ECONOMIC AND ENVIRONMENTAL COSTS

Currently, invasive alien species are considered one of the most relevant causes of biodiversity loss and one of the primary drivers of global change (Sala et al., 2000), entailing significant adverse environmental and socioeconomic impacts (Blackburn et al., 2019). Control of these invasive plants is a management priority, as they reduce native communities, ecological processes and ecosystem services (Zhang et al., 2019; Milanović et al., 2020), and can disturb socioeconomic systems (Rockwell-Postel et al., 2020), especially if their impact is high (Coville et al., 2021). Overall, invasive plants' negative ecological and socioeconomic consequences justify the advantages of proactively identifying and preventing high-impact species from gaining a foothold in a favourable new habitat. Furthermore, once invasive alien species are established, eradication is time-consuming and costly (Angulo et al., 2021; Diagne et al., 2021; Haubrock et al., 2021; Kourantidou et al., 2021; Novoa et al., 2021), so the prevention of future invasions is considered the most cost-effective management approach (Genovesi, 2005).

The Spanish government estimates that up to 190 exotic species have already established invasive populations in the country (Spanish Catalogue of Invasive Alien Species, Royal Decree 630/2013). According to Angulo et al. (2021), invasive species management cost Spain at least 231.1 million € between 1997 and 2019. Compared to other countries in the Mediterranean basin, Spain is the fifth most impacted country by the costs associated with invasive alien species (Kourantidou et al., 2021), after France (690.9 million €), Italy (504 million €), Libya (300.8 million €) and Turkey (288.4 million €). From a continental perspective, Haubrock et al. (2021) ranked Spain as similar to The Netherlands and Ireland, both countries being much smaller than Spain. Using a robust dataset, we showed that from all exotic invading species, the highest costs were reported for invasive plants (66%), especially from the orders Myrtales and Commelinales (Angulo et al., 2021). Figure 1 shows a few examples of some of the most problematic plant species invading different habitats in Spain.

FUTURE MANAGEMENT SOLUTIONS

The future of invasive species management will require new tools, developed from research integrating invasion and climate-change biology. To control these invaders under a changing climate scenario, it is essential to anticipate which species will spread to new habitats and how rapidly they will do it. Also, it is necessary to understand how the characteristics of specific invaders may disrupt or have the potential to disrupt invaded ecosystems (Finch et al., 2021).

Climate change poses a threat to native species, as it may reduce barriers to the naturalisation of some alien species. Identifying such species is very important to anticipate imminent invasions (Haeuser et al., 2018). Therefore, early detection is a key principle of invasive species management (Reaser et al., 2020). As monitoring for new species is costly, priority should be given to those invasive plants that will shift their range (Rockwell-Postel et al., 2020) from the Mediterranean area because of global climate change. Proactive responses could be further enhanced by anticipating future threats (Hulme et al., 2017). Eradication efforts must be accomplished within weeks, a few months or, at most, 1-2 years, for a rapid response to be successful (Lodge et al. 2006). Invasion scenarios are unique and, therefore, the period to achieve eradication depends on the context.

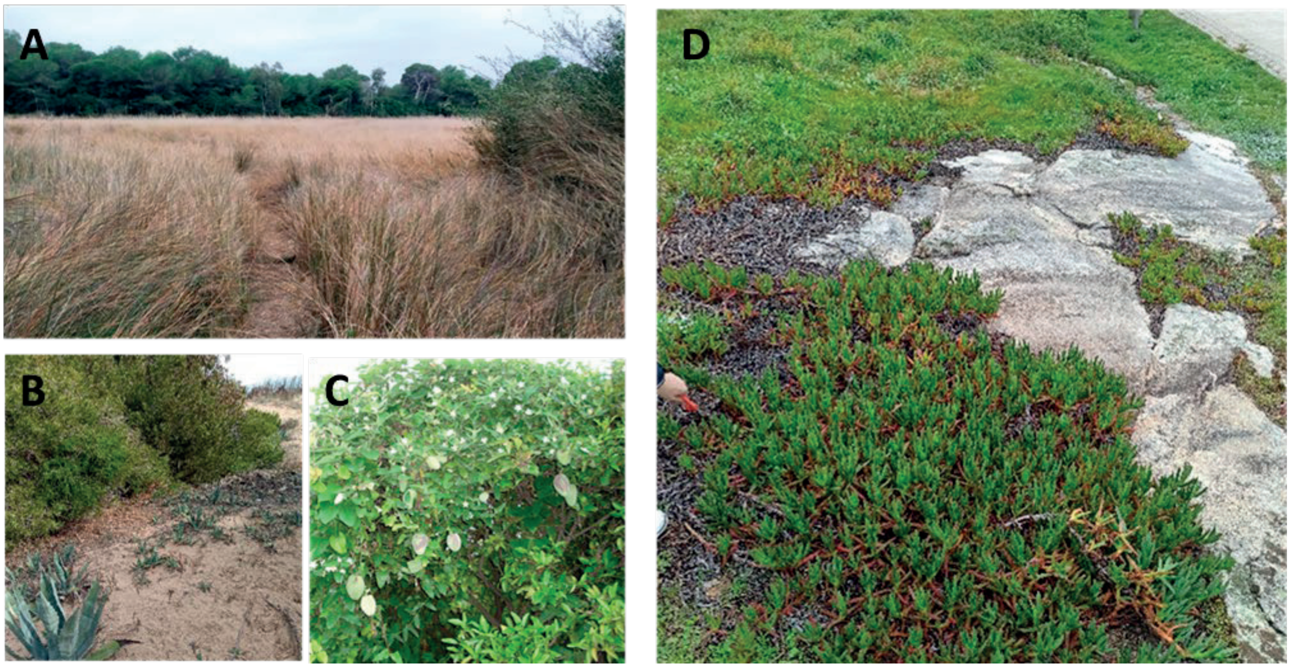

Figure 1. Presence of invasive species in Spain. *Spartina patens* in a coastal salt marsh in Valencia (A), *Agave americana* on a beach in Alicante (B), *Araujia sericifera* in a citrus grove in Valencia (C), and *Carpobrotus edulis* in Pontevedra (Galicia) (D).

In this sense, the resilience of the invaded space and the endangered species play a fundamental role, but the lack of a rapid and well-coordinated response will impede eradication.

If monitoring fails, the new species will naturalise within the area and modify the biogeochemical processes of the ecosystem (Milanović et al., 2020). The chances of eradicating the species will decrease, and control will only be possible at a high cost and, probably, with little success (Westbrooks, 2004). The use of robust and transparent protocols (Blackburn et al., 2014; Hawkins et al., 2015; Haeuser et al., 2018) to prioritise invasive plants that are likely to shift their range with climate change, is the best method to prevent their access to pristine habitats (Rockwell-Postel, 2020). This approach will provide insight into those high-priority species for early detection and rapid response, increasing the likelihood of successfully preventing future invasions.

First, it is necessary to identify or predict which species are invasive, or possible invaders as candidates to respond positively to climate change. Once the invasive species is known, one of the critical scientific issues in invasion ecology is understanding the mechanisms underlying a successful invasion. The analysis of the physiological variability in functional traits is essential to aid the prediction of how invasive species will respond to climate change. For example, osmotic adjustment, antioxidant responses (Pintó-Marijuan & Munné-Bosch, 2013), hormonal responses (Fenollosa et al., 2018), phenols and tannins (Núñez-González et al., 2021), C and N isotopic composition, chlorophyll and xanthophyll cycle pigment contents (Campoy et al., 2021) and photosynthetic parameters (Souza-Alonso et al., 2019), amongst others, are important physiological traits that describe the adaptation state of species in worldwide habitats. This information will be helpful for predicting the potential distribution of invasive plants and for designing appropriate management strategies (Campoy et al., 2021).

Tolerance limits against abiotic and biotic stress of invasive plants are poorly understood (Nischal & Sharma, 2019). Additionally, the degree of invasion differs between different habitats within the same species (Medvecká et al., 2018). Therefore, the combined study of field parameters in the different habitats invaded by a species and its responses under controlled conditions is necessary to understand the degree or capacity of invasion of the species of interest and its potential to affect native endangered species. Analysing ecophysiological responses by characterising physiological and biochemical markers, such as osmotic adjustment or indicators of antioxidant protection under stress conditions, could help predict future invasiveness patterns and understand how widespread they will be.

Different stresses cause the activation of a series of physiological, biochemical and molecular responses in plants, including the control of ionic transport, the accumulation of compatible solutes or osmolytes for osmotic adjustment, the activation of antioxidant systems to counteract the stress-induced generation of reactive oxygen species (ROS), hormonal balance or pigment relations (Fahad et al., 2015; Pessarakli et al., 2015; Kumar, 2018; Zhao et al., 2021). When dealing with invasive plants, most studies have focused only on their invasiveness in a particular habitat and their relationship with other species. The stress tolerance mechanisms of plant species of specific habitats, for example, structural halophytes in salt marshes (e.g., Al Hassan et al., 2016b; Pardo-Domenech et al., 2016) have been investigated, as well as those of differential taxa, such as endemic or endangered species (Lampert et al., 2014; Duenas et al., 2018; González-Orenga et al., 2020a; 2020b). However, there are very few comparative studies on the physiological and biochemical responses to stress of native and invasive plants competing in the same habitat (e.g., Al Hassan et al., 2016a). Therefore, the mechanisms underlying the presence of these plant taxa in the different habitats are still poorly understood. Incorporating these biochemical stress markers into the existing models will provide powerful tools to be used by modelling experts to improve their databases and design accurate models to predict future invasions (Pintó-Marijuan & Munné-Bosch, 2013).

CONCLUSIONS

Invasive plants already pose a major threat to biodiversity and natural habitats, a problem that will worsen progressively because of the climate change, which creates conditions that favour the expansion of invasive species, causing significant negative environmental and socioeconomic impacts. Invasive species generally can adapt more efficiently and rapidly than the native flora to the new environmental conditions, as they have broad climatic tolerances, as shown by their large geographic ranges. They possess other traits contributing to their expansion, such as rapid growth, easy seed dispersal and high competitiveness. Native endangered taxa, such as rare and endemic species, are the most threatened by biological invasions.

Control of these invasive plants is a management priority, which will require new tools, developed from research on plant stress physiology, climate change and invasion biology. It will be necessary to identify potential invasive species and proactively prevent their expansion, as eradication once they are established in the new habitats will be difficult and costly. Particularly relevant will be the elucidation of the mechanisms of tolerance to abiotic stress (drought, salinity, high temperatures) of invasive species, which are at present poorly understood.

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