TESIS DOCTORAL

CONGENERIC APPROACH FOR UNDERSTANDING INVASIVE ABILITY OF THE EXOTIC *PROSOPIS JULIFLORA* UNDER THE HYPER-ARID DESERT OF THE UNITED ARAB EMIRATES (UAE)

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Estudiante del programa de doctorado DIVERSIDAD BIOLOGICA Y MEDIO AMBIENTE de la Universidad de Málaga, autor/a de la tesis, presentada para la obtención del título de doctor por la Universidad de Málaga, titulada: CONGENERIC APPROACH FOR UNDERSTANDING INVASIVE ABILITY OF THE EXOTIC PROSOPIS JULIFLORA UNDER THE HYPER-ARID DESERT OF THE UNITED ARAB EMIRATES (UAE)

Realizada bajo la tutorización de MARIA TERESA NAVARRO DEL AGUILA y dirección de MARIA TERESA NAVARRO DEL AGUILA Y ALI EL-KEBLAWY

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Prefacio

Las investigaciones que han conducido a la redacción de la presente Tesis Doctoral se han realizado en el Departamento de Botánica y Fisiología Vegetal de la Universidad de Málaga, en el ámbito de las actividades del Grupo de Investigación RNM 115 “BIODIVERSIDAD, CONSERVACION Y RECURSOS VEGETALES” -del Plan Andaluz de Investigación, Desarrollo e Innovación de la Junta de Andalucía-.

Los trabajos de investigación han sido realizados en el Departamento de Biología Aplicada de la Universidad de Sharjah. Sharjah, Emiratos Arabes Unidos (UAE).

MEMORIA PRESENTADA PARA OPTAR AL GRADO DE DOCTOR EN BIOLOGIA

Visado en Málaga a 15 de octubre de 2022

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ACREDITA

Que D. François Mitterand Tsombou, Licenciado en Biología, ha realizado, en el Departamento de Botánica y Fisiología Vegetal Fisiología Vegetal de la Facultad de Ciencias de la Universidad de Málaga y en el Departamento de Biología Aplicada de la Universidad de Sharjah, las investigaciones que le han conducido a la redacción de la presente Memoria de Tesis Doctoral, titulada: CONGENERIC APPROACH FOR UNDERSTANDING INVASIVE ABILITY OF THE EXOTIC *PROSOPIS JULIFLORA* UNDER THE HYPER-ARID DESERT OF THE UNITED ARAB EMIRATES (UAE).

La presente Memoria, que recoge los resultados obtenidos, las publicaciones científicas de los mismos, así como su interpretación y reúne los requisitos necesarios para ser sometida al juicio de la Comisión correspondiente. Por tanto, como Directora y Tutora de la tesis, autorizo su exposición y defensa para optar al Grado de Doctor en Biología.

Y para que conste en cumplimiento de las disposiciones vigentes, firmo la presente acreditación en,

Málaga, 15 de octubre de 2022

Prof. Dra. Teresa Navarro

Directora y Tutora de la Tesis

This Thesis is dedicated to those who have exceptionally supported me through their appreciable motivations in accomplishing my PhD program and they are as follows:

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ABSTRACT

Anthropological activity is the major factor enhancing species movements throughout the globe. The magnitude of the movements of species around the globe associated with human activities is greatly impacted by the increase of commercialization, transportation, travelling and touristy. Consequently, the establishment of species into non-original regions intentionally or accidentally seems to be importantly affected, and inevitable. Either intentionally or accidentally, the introduction of a species into its non-original regions presents a significant risk for the local biodiversity. The introduced species presents a potential to disrupt the relationships existing between species-to-species and the different observable associations in the native ecosystem. Many of the exotics species have escaped experimental areas and invaded several pastoral lands. In this respect, many ecosystems in both terrestrial and aquatic ecosystems have been affected by invasive species, and the negative effects associated with their invasiveness are significantly high regionally and globally. Invasive species are identified and recognized in many plant species and the scientific studies on invasive plants addressed their noticeable negative ecological, social, and economic impacts in the introduced ecosystems. Globally, the findings of most studies showed that exotics invaders constitute the major cause of native habitats degradation. Invasive species present significant threats to ecosystem services and human health. In general, invasive plants cause biological pollution by reducing plant species diversity in addition to strongly impact on the underground water. Furthermore, invasive plants strongly affect the physiochemical properties of the native soils and therefore, interfere negatively on the local microbial activities. On the other hand, the global evaluation of the effect of invasive species is associated with the recent ecological impact of climate change.

Exotic invasive plants affect global biodiversity and ecosystem functioning in the invaded range, and their management is a complex and challenging task. One of the most widespread and high-impact invasive plant is the genus *Prosopis*. *Prosopis* comprises 44 species, out of which *P. cineraria* (L.) Druce is native to India, Pakistan, Afghanistan, and Iran. It is rarely reported as exotic outside its native range. However, the *P. juliflora* (Sw.) DC. and *P. pallida* (Humb. & Bonpl. ex Wild.) Kunth are the most documented species in the literature due to their greater capacity to colonize different ecosystems outside their native range. Both exotic species *P. juliflora* and *P. pallida* are thorny shrubs at approximately 15 m to 20 m high, respectively. In most cases, the invasive *Prosopis* form dense and impenetrable populations of much branched individuals. In particular, the invasive *P. juliflora* causes a considerable negative impact in many regions of the world, reducing biodiversity, water, and ecosystem services, and negatively affecting people livelihoods.

P. juliflora was introduced to the arid habitats of the United Arab Emirates (UAE) in the seventies to combat desertification and improve soil fertility as it tolerates drought, salinity, high temperature and fixes atmospheric nitrogen. However, seeds of *P. juliflora* can be disseminated by domestic live stocks such as goats, cattle, mules, camels, and wild fauna such as gazelles. Thus, the plant invaded large areas in the northern and western Emirates, such as Ras Al-Khaimah, Fujairah, Sharjah, Dubai, and Umm Al Quwain. Several years after its introduction, local farmers and environmentalists viewed it as an unwelcome, rapidly spreading, invasive species. The two exotic *Prosopis* species and *P. cineraria* grow in different habitats of the United Arab Emirates. Compared to invasive *Prosopis* species, which grows faster and has the potential to tolerate a wide range of environmental conditions, the native *P. cineraria* is slow growing and has limited distribution in its global range. Like the exotic invaders, *P. cineraria* could also fix atmospheric nitrogen, but the tolerable environmental conditions associated with its adaption are relatively less.

Prosopis species have naturalized and become problematic weeds in their introduced range. Importantly, they are reported to be unmanageable, and the costs allocated to their control are significantly higher globally. Accordingly, exotics *Prosopis* have been declared as a major noxious species in numerous world regions, including Ethiopia, Kenya, UAE, South Africa, India, Australia, Pakistan, and Sudan. Nevertheless, the rate of invasiveness and adverse effects strongly depend on the *Prosopis* species. It has been reported that *P. juliflora* is the main invader species that harmfully affect the indigenous ecosystem more than the other species of the same genus. In this respect, *P. juliflora* was considered the worst invasive species out of 36 plant species in the list of the world 100 worst species published by the Invasive Species Specialist Group. This species is expanding its range at an alarming rate and damaging native diversity and the ecosystem health of the arid and hyper-arid regions of Arabia. *P. juliflora* is often observed to form pure stands and does not allow other species to grow beneath or around its canopies.

The ecological impacts of invasive plants include displacement of indigenous species and declines in species richness and diversity. However, *P. juliflora* exerts a positive impact on species richness in its native range but a strong negative impact on species richness in its invaded range. In the introduced range of the arid climate of the United Arab Emirates, *P. juliflora* showed a depressive effect on the number, richness, evenness, density, and frequency of the associated native species. Especially important is that this depressive effect extended beyond the canopy-covered ground for dense sites. Old and dense sites of *P. juliflora* resulted in significantly lower density, frequency, and diversity for most associated annual species. Similarly, the growth of *P. juliflora* shrubs and exotic Eucalyptus in the forests of the UAE have also resulted in significant reductions in species diversity and abundance of understory species compared to the native *P. cineraria* and *Acacia arabica*.

Prosopis pallida is a highly adapted species to extremely dry and wet conditions. It is a tropical legume species native to arid and semi-arid areas of South America, mainly along the coast of Peru, Ecuador and Colombia. *P. pallida* is characterized by high intraspecific variability that helped the expansion of its geographic distribution. This species is invaded several places outside its native range, including Australia and the Caribbean islands. The global review of the distribution of *P. pallida* indicated that it had been introduced to Bolivia, Puerto Rico, the Virgin Islands (USA), Papua New Guinea, Colombia, Kenya, French Polynesia, Senegal, Mauritania, Djibouti, and Botswana. In addition, few countries in the Middle and far East have few occurrences of *P. pallida*, including Jordan, Israel and India. *P. pallida* has detrimental effects on the local habitats, such as depleting the groundwater and deterioration of associated native plant diversity. Recently, careful morphological investigations of *P. juliflora* plants in the UAE indicated the presence of another *Prosopis* species. According to the morphological and molecular features, we found it fits more with *P. pallida*. It forms monoculture in some places, especially around Sharjah City.

Unlike the exotic *P. juliflora* and *P. pallida*, the native *P. cineraria* can enhance the abundance and growth of the associated native flora. As reported in several comparative and congeneric studies, *P. cineraria* has important stimulatory compounds that interact with the surrounding environment and positively affect plants growing in its vicinity. Furthermore, documentation on the effects of *P. cineraria* addressed that this plant species had much higher plant species diversity than the exotic *P. juliflora*. For example, no significant difference in the density of the associated species beneath and away from the canopies of *P. cineraria* was found. However, the density of associated native plants was significantly lower beneath than away from the canopies of *P. juliflora*. Similarly, evenness and richness of associated species did not differ significantly beneath and at the margin of the canopy, but both were significantly lower compared with beyond the canopies of *P. cineraria*. However, evenness, richness and density of associated species were significantly lower beneath the canopies than with outside and at the margin of the canopies of *P. juliflora*.

Regarding the edaphic factors, exotic *Prosopis* invaders dramatically influence the soil quality in their introduced range. According to some recent findings, invader *P. juliflora* greatly improved the soil pH (1.5%), reduced the cation exchangeable (24.2%), percentage of sodium exchangeable (21.6%), and the percentage of water-soluble calcium and other constituents (39.9%) compared to the non-infested site. Interestingly, the soil properties improvements were greater under the canopies of *P. juliflora* than *P. cineraria*. The soil under *P. juliflora* was lower in pH and higher in % clay, % silt, total nitrogen, magnesium and sodium than the non-infested site and those occupied with the native *P. cineraria*. With the view on water consumption associated with the invasiveness of *P. juliflora*, the findings of some works carried out in Ethiopia revealed that this plant consumes huge amounts of water with around 3.1-3.3 billion m^3/year. Similar results were obtained in South Africa with approximately 1.5-2.5 billion m^3 of water consumption per year. Regarding UAE, the groundwater requirement of *P. juliflora* in three heavily invaded sites (near Sharjah Airport, Umm Fannan, and Al Talla) showed about a 7372% increase in groundwater consumption from the year 1990 to 2019.

Several mechanisms have been proposed to help understand the higher invasiveness of the exotics *Prosopis*. Specifically, allelopathy was proposed to be a strategy used by the invaders *Prosopis* to exclude the associated native species. Allelopathy is seen as a natural phenomenon by which the invasive plant releases chemical compounds known as allelochemicals into the environment through decomposition, leaching, vitalization, and root exudates. The effects of allelochemicals on the recipient plant might depend strongly on the type of compounds released by the donor plant. Therefore, allelopathic effects could be considered as beneficial or detrimental depending on the recipient organism. Exotics *Prosopis* are declared to present detrimental allelopathy with greater inhibitory bioactive compounds. Oppositely, the native *P. cineraria* is documented to have beneficial allelopathy effects on the associated native species.

As a cause of invasion, allelopathy has been studied in the context of three approaches: traditional, biogeographic and congenital. The traditional approach focuses on the fate, dose, replenishment, and effect of chemicals produced by invaders in the soil environment. However, the congeneric approach involves comparative studies of exotic species with natives in the same genus; more allelopathic effects are expected in the introduced than the native congener; both congeners do not share a co-evolutionary history. The biogeographic approach studies species ecological traits and processes in native and non-native ranges. In that approach, introduced species bring chemicals novel for invaded communities that has the potential to exhibit allelopathic effects due to naïve soil communities and sensitive neighbors.

The adverse effects of the allelochemicals on the recipient plants are physiologically, morphologically, anatomically and molecularly disastrous. With regards to *Prosopis* species, several published papers dealing with invasive plants addressed their noticeable impacts in the introduced range. The allelopathic effects of exotic and native congeners are studied in the congeneric approach. Assessable impact of allelopathy produced by *P. juliflora* and *P. cineraria* and soil properties on understory native plants in the arid deserts of the UAE, revealed that the aqueous extracts of fresh and old leaves of *P. juliflora* on the associated flora were inhibitory, but *P. cineraria* leaves and litter positively affected other native species. The inhibitory effect of *P. juliflora* was stronger on annual species than perennials. The biogeographic approach studies ecological traits of species and ecological processes in native and non-native ranges. Exotic species bring chemicals novel for invaded communities that has the potential to exhibit allelopathic effects due, as already mentioned, to naïve soil communities and sensitive neighbors.

Introduced species face environmental conditions that vary from those in the native range. Phenotypic plasticity is considered one of the primary ways plants can cope with environmental factor variability. Therefore, exotic invasive species seem to have distinguished adaptive evolutionary plasticity that allows them to colonize unreachable places and dominate in the introduced range. Such plasticity makes introduced plants more invasive and has more competitive ability than native plants. The phenotypic plasticity makes the invasive plants attain a higher growth rate and put greater reproductive efforts than the native species. For example, it has been reported that invasive plants had significantly higher plasticity in water use efficiency overall than native plants. The high plasticity in water use efficiency provided invasive species with a fitness advantage when the available water is either higher, or lower than the average conditions. Such plasticity in using the available water enhances the invasiveness ability of the exotic plants. The comparison of the water use efficiency of the exotic and native *Prosopis* could help understand the causes of the higher invasive ability of *P. juliflora* and *P. pallida* compared to the native *P. cineraria*.

Moreover, the higher growth rate of the invasive species compared to the native could be attributed to their greater water use and photosynthesis efficiencies. Water use efficiency is considered as the fraction of water utilized in plant metabolism to water lost across evapotranspiration. Therefore, any changes associated with this plant attribute could be an important ecological indicator when this latter is exposed to drought stress. In this regard, invasive plants might increase their water use efficiency more than native to dominate the introduced range. In most cases, exotics *Prosopis* species grow faster than the local species and are evergreen throughout the year compared to the native *P. cineraria*. Furthermore, they are more drought tolerant than the native *P. cineraria*. So, intrinsic water use efficiency might be another strategy the exotics *Prosopis* invader uses to cope with the drought stress in the non-native range. However, there are not sufficient data, or there are not scientific documents dealing with this topic. This noticeable case was reported in the invasive plant *Berberis darwinii*. In this respect, congeneric comparison between species-to-species can give the opportunity to identify the evolutional traits that may help the exotics invaders to be stronger than the indigenous species. Yet, regrettably, the literature review seems to be very less documented with such important data. Many of the earlier works have aimed to explore the negative effects associated with plants invasiveness emphasizing invasive versus native, but with no concept about the congeneric approach.

Differences in photosynthetic efficiency traits are fundamental for invasion success. The invasive *P. juliflora* and *P. cineraria* species have higher growth rates than their native congener *P. cineraria.* In addition, the invasive plants have denser canopies, i.e., more branches and leaf density, than the native species. Such differences in the growth rate and canopy density might explain the greater invasive ability of the invasive than the native *Prosopis* species. The growing of the introduced and native populations of the invasive *Ageratina* in a common garden experimentally, showed that higher nitrogen was allocated to photosynthetic organs in introduced *A. adenophora*, which led to a higher photosynthetic rate than the native conspecifics, contributing to its successful invasion. The comparison of the photosynthetic efficiency of native and exotic species would help understand the invasive ability of the invasive species.

Globally, exotic *P. juliflora* is among the more redoubtable invasive plants worldwide. Therefore, its greater adaptability to a wide range of climates and its invasiveness ability compared to the indigenous congeners would have other evolutionary strategies. Therefore, deeper congeneric comparative studies within *Prosopis* species can bring out more understanding of their exceptional adaptive traits under the hot hyper arid environments of the UAE. However, only a few attempts have been made in this regard. Consequently, assessing more evolutionary traits considered as keys to invasiveness within the *Prosopis* species can clarify the mechanisms behind the higher invasiveness potential of the invaders *Prosopis* species.

Therefore, the objectives of this PhD thesis are to (1) Make congeneric comparisons of the impacts of *P. juliflora* and its congener *P. cineraria* on aboveground diversity of weedy and non-weedy plants in the UAE (2) Elucidate allelopathy as a mechanism of invasion success of *P. juliflora* in its introduced ranges. This will be through assessing the impact of allelochemicals from the litters on germination of associated plants in conventional controlled conditions (i.e., in Petri-dishes in growth chambers) and challenging conditions (i.e., potted soils), (3) Assess the intrinsic water use efficiency of invasive and native *Prosopis* congeners, and (4) Assess the thermal energy dissipation, photosynthetic efficiency, carbon gain and nitrogen partitioning in invasive and native *Prosopis* congeners.

Congeneric comparisons of the impacts of *Prosopis juliflora* and its congener *P. cineraria* on aboveground diversity of weedy and non-weedy plants in the UAE

The first chapter of this thesis explores the canopy-understory relationships between the two *Prosopis* congeners and the understory species that are considered agricultural weeds (ag-weeds) and non-agricultural weeds (non-weeds) in the United Arab Emirates. Exotic invasive plant species alter ecosystems and locally extirpate native plant species; therefore, altering community structure. Changes in plant community structure may be particularly important if invaders promote species with certain traits. For example, the positive effects of most invaders on soil fertility may promote species with weedy traits, whether native or not. The effects of the canopies of the *Prosopis* species have been extensively studied. However, few attempts have been focused on the relationships between the canopies of the *Prosopis* congeners and the understory species considered as agricultural weeds and non-weeds. So, here, we examined the effects of two co-occurring *Prosopis* congeners, the native *P. cineraria* and the exotic invader *P. juliflora*, on species identified as ‘‘agricultural weeds’’ and species that were not agricultural weeds in the UAE. We focused on the following questions: (1) Is non-weed diversity higher under canopies of the native *P. cineraria* and lower under canopies of the exotic *P. juliflora*? (2) Does the exotic *P. juliflora* increases ag-weeds more than the native *P. cineraria*, thus potentially creating reservoirs of these species? and (3) Does soil under canopies of the exotic *P. juliflora* have higher soil fertility than

the native *P. cineraria*? To answer these questions, we compared the richness and density of non-weeds and ag-weeds beneath *P. cineraria* and *P. juliflora* canopies. We also measured soil properties, litter depth, and fine tree root mass beneath the canopies of both species.

A total of 29 understory species (23 non-weeds 6 weeds or *P. juliflora* seedlings) were recorded. Compared to plots in the open, *P. cineraria* canopies were associated with lower richness and density of non-weeds while having no impact on agricultural weed species. In contrast, there was lower richness and densities of non-weeds under canopies of *P. juliflora* but higher densities of agricultural weeds than in the open surrounding the canopies. These patterns associated with *Prosopis* congeners and understory plant community composition might be due to the much higher litter deposition, if the litter is inhibitory, and shallow root biomass under *P. juliflora*, or the different soil properties that corresponded with the two *Prosopis* canopies. In general, soils contained more nitrogen under *P. juliflora* than *P. cineraria*, and both understories were more fertile than soil in the open. Our results suggest that evolutionary history may play a role in how exotic invasive species may select for some traits over others in plant communities, with an exotic invader potentially creating reservoirs of agricultural weeds.

Allelopathy as a mechanism of invasion success of *Prosopis juliflora* in its introduced ranges: Test of the congeneric approach

The second chapter of this thesis assesses the congeneric approach by comparing relative role of the allelopathic effect of the exotic invasive *Prosopis* compared to native congeners on seed germination and seedling growth of the associated species. The congeneric or phylogenetic approach assesses the relative role of exotic invasive compared to native plants on associated species. This approach was used to assess exotic species allelopathic impact on the associated flora compared to native congeners. Greater allelopathic effects of the alien invasive on native flora are expected compared with the native congeners. This is true as native plants typically do not share a co-evolutionary history with the exotic invasive species in the introduced range. Invasive plants produce allelochemicals that are new to the native plant communities (i.e., novel weapons). *Prosopis* species produce several chemicals such as phenolics, syringin, and (-)-lariciresinol, and tryptophan and Juliflorine. Besides, allelochemicals production explained the reduction in the abundance of several native species associated with *P. juliflora*. Some studies showed that litter leachates and aaqueous extracts of *P. juliflora* inhibited or significantly reduced seed germination of many associated natives, cultivated species and weeds. However, *P. cineraria* leachates of both

fresh and old leaves did not inhibit seed germination of four native species, especially in the lower concentrations.

The studies on seed germination were conducted in the laboratory in the Petri-dishes that do not reflect natural soil conditions. Here, we compared the effects of different litters extracts of the exotic invasive *P. juliflora* and *P. pallida*, and the native *P. cineraria* on seed germination and seedling dry weight of two weedy (*Amaranthus graecizans* and *Sisymbrium irio*) and the native *Senecio flavus* in Petri-dishes and potted soil experiments. The three species grew around and underneath the three *Prosopis* species. We hypothesize that the allelopathic effect of the exotic species is greater than that of the native species. Besides, we expect potting soil's environmental conditions to reduce the exotic plants allelopathic effect compared to Petri-dishes.

The results indicate that the three species non-treated seeds (control) attained more than 95% germination in the Petri-dishes (*in vitro*). The increase in the litter concentrations of both invasive *Prosopis* species inhibited the native *S. flavus* germination and significantly reduced the germination and seedling weight of the weedy *A. graecizans* and *S. irio*. The significant reduction in their germination when they were exposed to different *Prosopis* species extracts indicates their seeds ability to enter a dormancy stage under unfavorable conditions. The results also showed significantly greater germination of the three test species in Petri-dishes than in potted soil; the final germination reached over 90% in Petri dishes but below 50% in soils. This indicates that germination results in sterile Petri-dishes cannot predict what would happen in the field. In allelochemicals studies, the lack of drainage in Petri-dishes, for example, can help accumulate allelochemicals, but drained soil helps them wash away from the seedbed. Besides, both soil microflora and substrate conditions can determine the fate of allelochemicals. Despite the higher inhibition effect of the litter extracts of the invasive *Prosopis* species on germination and seedling growth of the three studied species, the native *P cineraria* extracts had significant depressive effects on seed germination and seedling growth of the native *S. flavus* but limited effects on the weedy *A. graecizans* and *S. irio*.

We can conclude that it is hard to understand germination results in general and allelopathy under sterile Petri-dishes conditions. The results support the congeneric approach of the greater impact of exotic *Prosopis* species allelochemicals than the native *P. cineraria* on germination and seedling growth of the associated plants.

Abstract

Intrinsic water use efficiency of invasive and native *Prosopis* congeners

The third chapter of this study assesses the intrinsic water use efficiency (iWUE) of invasive and native *Prosopis* congeners. Water use efficiency is defined as the fraction of water utilized in plant metabolism to water lost by plants through evapotranspiration processes. So, any changes associated with water used efficiency could be considered as the response of plant adaption to drought stress. Besides, carbon isotope ratios were considered effective for detecting environmental stresses in various crops, weeds, vegetables and herbaceous plants. Taken into consideration that the exotics *Prosopis* species. grow faster and tolerate more drought than the native *P. cineraria*, it is expected that the iWUE could be a strategy used by the exotics *Prosopis* invader to cope with the drought stress in the non-native range. This study involved the measurements of stable carbon isotope composition ($\delta^{13}C$) and intrinsic water use efficiency (iWUE) of three C_3 leguminous *Prosopis* species (two exotic invasive, *P. juliflora*, and *P. pallida*, and the native *P. cineraria*). The aim was to investigate the $\delta^{13}C$ and iWUE in the foliage of the three *Prosopis* species from different canopy positions (East, West) from saline and non-saline habitats. We also compared the occurrence and extent of carbon isotope discrimination ($\Delta^{13}C$) between young and mature leaves carbon pools on an organic matter basis and evaluated the magnitude of changes for predictions of iWUE. We hypothesize that invasive exotic plants might increase their water use efficiency than the native to dominate in the introduced range.

The results showed that the native shrub *P. cineraria*, the invasive shrubs *P. juliflora*, and *P. pallida* showed contrasted physiological and isotopic responses due to their leaf age, canopy position, and their interaction. The foliar $\delta^{13}C$ values from the three *Prosopis* species fell within the range of $\delta^{13}C$ of C_3 leguminous species (0+2‰). The results also revealed that the patterns of $\delta^{13}C$ are similar for the three *Prosopis* species. Besides, the difference in carbon isotope discrimination ($\Delta^{13}C$) between the canopy position (west and east) is relatively consistent among species and sites, ranging between 17.8 ± 4.43% for the young foliage in the west and 18.05 ± 4.35% for the east canopy position. We observed higher $\delta^{13}C$ (less negative) from the west than the east canopy position in the exoctic invasive *P. pallida* from saline habitat. This indicates that plants of the saline habitat might suffer from water limitation, less photosynthesis due to stomatal closure, and hence more carbon isotope discrimination.

The results also indicate that mature leaves possessed a higher iWUE than the young leaves. The iWUE of the exotic invasive *P. juliflora* was higher in the non-saline than saline habitats. Besides, the intercellular CO_2 concentration from inside to ambient air (Ci/Ca) values was higher on the west than east side in *P. juliflora* and *P. pallida* plants young leaves. However, an opposite trend was observed in Ci/Ca in young leaves of *P. cineraria*. This result indicates that young leaves in the west canopy position of the invasive *P. juliflora* and *P. pallida* might not suffer from excess light and heat stress compared with the native *P. cineraria*. A lower Ci/Ca ratio in young leaves of *P. cineraria* could result either from stomatal closure induced by water stress or higher photosynthetic capacity rates.

We concluded that exotic invasive *P. juliflora* and *P. pallida* have higher iWUE values than the native *P. cineraria*, which might be due to the rapid below ground development of plant roots in the Arabian deserts of the United Arab Emirates. This could enable the alien species to access deeper humid soil or water resources.

<u>Thermal energy dissipation, photosynthetic efficiency, carbon gain and nitrogen partitioning in invasive and native *Prosopis* congeners</u>

In this study of the thesis, we will discuss the photosynthesis efficiency of the *Prosopis* species. In the photosynthesis process, some of the sunlight is fixed and converted into chemical energy during photosynthesis. However, some sunlight can still not be fully utilized and might cause potential damage. In the hot hyper-arid deserts, higher solar radiation and heat are major limiting ecological factors challenging desert plants. Under the high solar intensity of hot hyper-arid deserts, some captured light is not used and might cause excess excitation energy that could result in a drop in photosynthetic capacity and restrict plant growth and development. The excess sunlight can combine with oxygen and convert into harmful reactive oxygen species (ROS), which might lead to photo-oxidative stress that can cause damage to the plant metabolic process. To escape and avoid the potential damage from excess sunlight, and accumulation of reactive oxygen species (ROS), plants exhibit a series of self-protection mechanisms that include efficient utilization of sunlight and dissipation of excess and through biochemical defense mechanisms such as antioxidant systems. Therefore, the present work was done to elucidate the survival mechanisms of *Prosopis* species congeners under different light intensities of shaded and exposed sun leaves at different directions of the canopies.

We evaluated the impact of surface canopy positions on the photosynthetic adjustments and chlorophyll fluorescence attributes (photosystem II photochemistry, quantum yield, fluorescence quenching, and photon energy dissipation), leaf biomass, and nutrient content of sun-exposed leaves at the southwest canopy position and shaded-leaves at the northwest canopy position in the invasive *P. juliflora* and native *P. cineraria* in the extreme environment (hyper-arid desert area, United Arab Emirates). The main aim of this research was to study the photo-protection mechanism in invasive and native *Prosopis* congeners via the safe removal -as thermal energy- of excess solar energy absorbed by the light collecting system, which counteracts the formation of reactive oxygen species (ROS).

Maximum photosynthetic efficiency (F_v/F_m) from dark-adapted leaves in *P. juliflora* and *P. cineraria* was higher in northwest than southwest canopy position. Such a result indicates that leaves at southwest canopy position were exposed to stronger light intensities and high temperatures that might reduce the photosynthetic efficiency. The results also demonstrated that the invasive *P. juliflora* maintain a slightly lower but stable photosynthetic efficiency (Fv/Fm) than the native *P. cineraria* under the hyper-arid environment of UAE. This result indicates that photosynthesis, as an individual trait, could not be held responsible for driving the invasive success of *P. juliflora,* and other factors might contribute to its range expansion and stand establishment in non native habitats.

Quantum yield (ΦPSII) was lower in both *P. juliflora* and *P. cineraria* on the southwest than in the northwest canopy position. Such reduction in ΦPSII could coincide with a decrease in the efficiency of excitation energy trapping of PSII reaction centers on the SE side. It has been well documented that ΦPSII is reduced under water-limited conditions. The high temperature increased transpiration due to excess sunlight, which might cause stress that reduced ΦPSII values on the southwest canopy position. Furthermore, the non-photochemical fluorescence quenching (NPQ) value was also higher in *P. juliflora* than *P. cineraria*, indicating that the former is more adapted to local climatic conditions and can dissipate excess energy as heat, which otherwise might disturb the photosynthetic machinery. The protective ability of non-photochemical fluorescence quenching (NPQ) decreased in the native *P. cineraria*, which led to the accumulation of excess excitation energy and the aggravation of photo-inhibition. *Prosopis* leaves dissipated excess light energy in the southwest canopy position by increasing the NPQ.

The results also explain the role of different physiological attributes contributing to the invasiveness of exotic invasive *P. juliflora* and evaluate the relationships between the plasticity of these characters and invasiveness potencial.

RESUMEN

La actividad antropológica es el principal factor que favorece los movimientos de especies en todo el mundo. La magnitud de estos movimientos asociados a las actividades humanas se ve afectado por el aumento del comercio, transporte, viajes y turismo. En consecuencia, el establecimiento de especies en otras regiones, intencional o accidentalmente es un hecho importante e inevitable. La introducción de una especie en regiones no nativas presenta un riesgo significativo para la biodiversidad local ya que la especie introducida puede potencialmente interrumpir las relaciones existentes entre especies en el ecosistema nativo. Muchas de las especies exóticas que han escapado de áreas experimentales han invadido diferentes ecosistemas, entre ellos las zonas pastoreadas. Muchos ecosistemas, tanto terrestres como acuáticos, se han visto altamente afectados por especies invasoras, y los efectos negativos asociados con su invasividad. Estudios sobre plantas invasoras abordan sus multiples impactos negativos en el ambito ecológico, social y económico ya que constituyen la principal causa de degradación de los habitats presentando amenazas significativas para los servicios ecosistémicos y la salud humana. Las plantas invasoras causan contaminación biológica al reducir la diversidad de especies de plantas, además de tener un fuerte impacto en las aguas subterráneas y en las propiedades fisicoquímicas de los suelos y, por lo tanto, interfieren negativamente en las actividades microbianas locales. Por otro lado, la evaluación global sobre el efecto de las especies invasoras se asocia al impacto del cambio climático.

Las plantas exóticas invasoras afectan la biodiversidad global y el funcionamiento de los ecosistemas en el área de distribución invadida, y su manejo es un desafio y una tarea compleja. Uno de los taxones de especies invasoras más difundido y de mayor impacto es el género *Prosopis*. *Prosopis* comprende 44 especies, de las cuales *P. cineraria* (L.) Druce es nativa de India, Pakistán, Afganistán e Irán y ha sido raramente documentada su capacidad invasora fuera de su área de distribución natural. Sin embargo, *P. juliflora* (Sw.) DC. y *P. pallida* (Humb. & Bonpl. ex Wild.) Kunth son especies con elevada capacidad para colonizar diferentes ecosistemas fuera de su área de distribución natural. Tanto la exótica *P. juliflora* como la *P. pallida* son arbustos espinosos de aproximadamente 15 m a 20 m de altura, respectivamente. En la mayoría de los casos, las especies de *Prosopis* invasoras forman poblaciones densas e impenetrables. En particular, la especie *P. juliflora* causa un impacto negativo considerable en muchas regiones del mundo, reduce la biodiversidad, el agua y los servicios ecosistémicos, y tiene un impacto negativo en los medios de subsistencia de las personas.

P. juliflora se introdujo en los hábitats áridos de los Emiratos Árabes Unidos (EAU) en los años setenta para combatir la desertificación y mejorar la fertilidad del suelo, ya que tolera la sequía, la salinidad, las altas temperaturas y es fijadora de nitrógeno. Sin embargo, las semillas de *P. juliflora* pueden ser diseminadas por ganado doméstico y la fauna silvestre. Así, la planta invadió grandes áreas del norte y oeste de los Emiratos, como Ras Al-Khaimah, Fujairah, Sharjah, Dubai y Umm Al Quwain. Varios años después de su introducción, los agricultores locales y los ambientalistas la vieron como una especie invasora no deseada, que se propagaba rápidamente. Las dos especies exóticas de *Prosopis* y *P. cineraria* crecen en diferentes hábitats de los EAU. En comparación con las especies invasoras de *Prosopis*, que crecen más rápido y toleran una amplia gama de condiciones ambientales, *P. cineraria* nativa es de crecimiento lento y tiene un rango de distribución limitado. *P. cineraria* también puede fijar nitrógeno atmosférico, pero tiene menos tolerancia a las condiciones ambientales.

Las especies de *Prosopis* se han naturalizado y se han convertido en 'malas hierbas' problemáticas. Es importante destacar que que son inmanejables y que los costos asignados a su control son muy altos. En consecuencia, las especies exóticas de *Prosopis* han sido declaradas como una de las principales especies nocivas en numerosas regiones del mundo, incluidas Etiopía, Kenia, Emiratos Árabes Unidos, Sudáfrica, India, Australia, Pakistán y Sudán. Sin embargo, la tasa de invasividad y los efectos adversos dependen en gran medida de la especie de *Prosopis*. *P. juliflora* es la principal especie invasora que afecta negativamente al ecosistema autóctono más que las otras especies del mismo género. *P. juliflora* fue considerada la peor especie invasora entre 36 especies de plantas en la lista de las 100 peores especies del mundo publicada por el Grupo de Especialistas en Especies Invasoras. Esta especie está expandiendo su rango de distribución a un ritmo alarmante y dañando la diversidad nativa del ecosistema de las regiones áridas e hiperáridas de Arabia.

Los impactos ecológicos de las plantas invasoras incluyen el desplazamiento de especies autóctonas y la disminución de la riqueza y diversidad vegetal. *P. juliflora* ejerce un impacto positivo en la riqueza de especies en su área de distribución natural, pero un fuerte impacto negativo en el área de distribución invadida. En su rango de distribucion dentro de los hábitats áridos de los Emiratos Árabes Unidos, *P. juliflora* mostró un efecto depresivo en el número, riqueza, uniformidad, densidad y frecuencia de las especies nativas asociadas. Especialmente importante es que este efecto depresivo se extendió más allá del suelo cubierto por el dosel de la especie. Los habitats densamente cubiertos por *P. juliflora* dieron como resultado una densidad, frecuencia y diversidad significativamente más bajas para la mayoría de las especies anuales asociadas. De manera similar, el crecimiento de arbustos de *P. juliflora* y eucaliptos exóticos en los bosques de los EAU también ha originado reducciones significativas en la diversidad y la abundancia de especies del sotobosque en comparación con las formaciones nativas de *P. cineraria* y *Acacia arabica.*

Prosopis pallida es una especie adaptada a condiciones extremadamente secas y húmedas. Es una leguminosa tropical nativa de las zonas áridas y semiáridas de América del Sur (Perú, Ecuador y Colombia) con una alta variabilidad intraespecífica que favorece su expansión geográfica. Esta especie es invasora en Australia y las Islas del Caribe. La revisión global de la distribución de *P. pallida* indica que se ha introducido en Bolivia, Puerto Rico, las Islas Vírgenes, Papua Nueva Guinea, Colombia, Kenia, Polinesia Francesa, Senegal, Mauritania, Djibouti y Botswana. Pocos países del Medio y Lejano Oriente tienen ocurrencias de *P. pallida*, incluidos Jordania, Israel e India. *P. pallida* tiene efectos perjudiciales en los hábitats locales, como el agotamiento de las aguas subterráneas y el deterioro de la biodiversidad. Recientemente, investigaciones basadas en estudios morfológicas de plantas de *P. juliflora* en los EAU indicaron la presencia de otra nueva especie de *Prosopis*. Según las características morfológicas y moleculares, estas plantas son más afines a *P. pallida* que a *P. juliflora*, formando monocultivos alrededor de la ciudad de Sharjah.

A diferencia de las especies exóticas *P. juliflora* y *P. pallida*, la nativa *P. cineraria* puede mejorar la abundancia y el crecimiento de la flora nativa asociada, tal y como consta en el resultados de diferentes estudios comparativos. *P. cineraria* tiene importantes compuestos estimulantes que interactúan con el entorno circundante y afectan positivamente a las plantas que crecen en su vecindad. *P. cineraria* favorece la diversidad de especies bajo su dosel más que la exótica *P. juliflora*. Por ejemplo, no se encontraron diferencias significativas en la densidad de las especies asociadas debajo y fuera del dosel de *P. cineraria*. Sin embargo, la densidad de plantas nativas asociadas fue menor debajo que fuera del dosel de *P. juliflora.* La riqueza de las especies asociadas no difirieron significativamente debajo y en el margen del dosel, pero fueron significativamente más bajas en comparación con *P. cineraria*.

Abstract

Con respecto a los factores edáficos, las invasoras *Prosopis* influyen dramáticamente en la calidad del suelo. Según investigaciones recientes *P. juliflora* mejora en gran medida el pH del suelo (1,5 %), reduce los cationes intercambiables (24,2 %), el porcentaje de sodio intercambiable (21,6 %) y el porcentaje de calcio soluble y otros constituyentes (39,9%) en los suelos invadidos. Curiosamente, las mejoras en las propiedades del suelo son mayores bajo los doseles de *P. juliflora* que de *P. cineraria*. El suelo bajo *P. juliflora* tiene un pH más bajo y más alto en % de arcilla, de limo, nitrogeno, magnesio y sódio que el suelo no invadiso y los que estaban ocupados con *P. cineraria*. En relación al consumo de agua asociado a la invasividad de *P. juliflora*, estudios en Etiopía revelan que esta planta consume grandes cantidades de agua, alrededor de 3,1-3,3 mil millones de m^3/año. Resultados similares se obtuvieron en Sudáfrica con aproximadamente 1,5-2,5 mil millones de m^3 de consumo por año. Con respecto a los EAU, el requerimiento de agua subterránea de *P. juliflora* en tres sitios fuertemente invadidos (aeropuerto de Sharjah, Umm Fannan y Al Talla) mostró un aumento de aproximadamente 7372 % en el consumo de agua subterránea desde 1990 hasta el 2019.

Se han propuesto varios mecanismos para comprender la mayor invasividad de las especies exóticas de *Prosopis*. Específicamente, se propuso la alelopatía como estrategia utilizada por las *Prosopis* invasoras para excluir a las especies nativas. La alelopatía se considera un fenómeno natural por el cual la planta invasora libera compuestos químicos conocidos como aleloquímicos a través de la descomposición, la lixiviación, la vitalización y los exudados de las raíces. Los efectos de los aleloquímicos en la planta receptora pueden depender en gran medida del tipo de compuestos liberados por la planta donante. Por lo tanto, los efectos alelopáticos podrían considerarse beneficiosos o perjudiciales según el organismo receptor. Se conoce que las *Prosopis* exóticas presentan alelopatía perjudicial con mayor cantidad de compuestos bioactivos inhibitorios. Por el contrario, se documenta que *P. cineraria* nativa tiene efectos alelopáticos beneficiosos en las especies nativas asociadas.

Como causa de invasión, la alelopatía ha sido estudiada en el contexto de tres enfoques: tradicional, biogeográfico y congénito. El enfoque tradicional se centra en el destino, la dosis, la reposición y el efecto de las sustancias químicas producidas por las invasoras. Sin embargo, el enfoque congenérico implica estudios comparativos de especies exóticas con nativas del mismo género; se esperan más efectos alelopáticos en el congénere introducido que en el nativo; ambos congéneres no comparten una historia coevolutiva. El enfoque biogeográfico estudia los caracteres

y procesos ecológicos de las especies en su rango de distribución nativo y no nativo. En ese enfoque, las especies introducidas aportan sustancias químicas novedosas para las comunidades invadidas que tienen el potencial de exhibir efectos alelopáticos.

Los efectos adversos de los aleloquímicos en las plantas receptoras son fisiológica, morfológica, anatómica y molecularmente negativos. El impacto de la alelopatía producida por *P. juliflora* y *P. cineraria* y las propiedades del suelo en las plantas nativas en los desiertos áridos de los EAU reveló que los extractos acuosos de hojas frescas y maduras de *P. juliflora* en la flora asociada eran inhibidores, pero el de las hojas de *P. cineraria* eran positivos para las especies nativas. El efecto inhibitorio de *P. juliflora* fue más fuerte en las especies anuales que en las perennes. El enfoque biogeográfico estudia las características ecológicas de las especies y los procesos ecológicos en rangos de distribución nativo y no nativo. Las especies exóticas aportan productos químicos novedosos para las comunidades invadidas que tienen el potencial de exhibir efectos alelopáticos debido como a la sensibilidad de las especies vecinas.

Las especies introducidas se enfrentan a condiciones ambientales diferentes del área de distribución nativa. La plasticidad fenotípica se considera una de las principales formas para hacer frente a la variabilidad de los factores ambientales. Las especies invasoras exóticas parecen tener una especial plasticidad evolutiva adaptativa que les permite colonizar lugares inalcanzables y dominar en el área de distribución introducida con unacapacidad más competitiva que las plantas nativas. La plasticidad fenotípica favorece una mayor tasa de crecimiento y un mayor esfuerzo reproductivo que las especies nativas. Las especies invasoras tienen una plasticidad significativamente mayor en la eficiencia del uso del agua que nativas. La plasticidad en la eficiencia del uso del agua proporciona a las especies invasoras una ventaja cuando el agua disponible es más alta o más baja que en condiciones promedio. Tal plasticidad mejora la capacidad de invasividad. La comparación de la eficiencia en el uso del agua de *Prosopis* exótica y nativa podría ayudar a comprender las causas de la mayor capacidad invasiva de *P. juliflora* y *P. pallida* en comparación con *P. cineraria.*

La mayor tasa de crecimiento de las especies invasoras en comparación con las nativas puede atribuirse a su mayor eficiencia en el uso del agua y la fotosíntesis. Cualquier cambio asociado con el uso del agua podría ser un indicador ecológico importante cuando la planta está expuesta al estrés por sequía. Las plantas invasoras podrían aumentar su eficiencia en el uso del agua más que las nativas para dominar en los habitats invadidos. Las especies exóticas de *Prosopis*

crecen más rápido que la nativa *P. cineraria* y son más tolerantes a la sequía. La eficiencia intrínseca del uso del agua podría ser otra estrategia que utiliza *Prosopis* para hacer frente al estrés por sequía en la invasion de habitats no nativos. Sin embargo, no hay suficientes estudios científicos que traten este tema en el género *Prosopis*, aunque si los hay para otras especies como la invasora *Berberis darwinii*. La comparación congenérica entre especies puede ofrecer la oportunidad de identificar los caracteres evolutivos que ayudan a las invasoras exóticas a ser más fuertes que las especies autóctonas. Generalmente se han estudiado los efectos negativos asociados con la invasividad de las plantas, enfatizando lo invasivo *versus* lo nativo, pero no en el enfoque congenérico.

Las diferencias en la eficiencia fotosintética es fundamental para el éxito en la invasión. Las invasoras *P. juliflora* y *P. cineraria* tienen tasas de crecimiento más altas que su congénere nativo *P. cineraria*. Además, las plantas invasoras tienen doseles más densos, más ramas y densidad de hojas. Tales diferencias podrían explicar la mayor capacidad invasiva. El crecimiento experimental de las poblaciones introducidas y nativas de la invasora *Ageratina adenophora* en un jardín mostró una mayor cantidad de nitrógeno en los órganos fotosintéticos en la *A. adenophora* introducida, lo que condujo a una tasa fotosintética más alta que la de los congéneres nativos, contribuyendo a su invasion. La comparación de la eficiencia fotosintética de especies nativas y exóticas ayudaría a comprender la capacidad invasiva de las especies.

Prosopis juliflora se encuentra entre las plantas invasoras más temibles del mundo por su adaptabilidad a una diferentes climas y a su capacidad invasora en comparación con sus congéneres indígenas. Estudios comparativos congénericos dentro de las especies de *Prosopis* pueden ofrecer una mayor comprensión de sus excepcionales caracteres adaptativos en los ambientes hiperáridos cálidos de los Emiratos Árabes Unidos. En consecuencia, la evaluación de los caracteres evolutivos considerados como claves para la invasividad dentro de las especies de *Prosopis* podría aclarar los mecanismos responsables del potencial invasor.

Por lo tanto, los objetivos de esta tesis doctoral son (1) Realizar comparaciones congenéricas de los impactos de *P. juliflora* y su congénere *P. cineraria* en la diversidad de plantas consideradas como malezas agricolas y no malezas agricolas en los EAU (2) Esclarecer la alelopatía como mecanismo del éxito de la invasión de *P. juliflora* en su rango de distribucion como especie introducida ; evaluando el impacto de los aleloquímicose en la germinación de las plantas asociadas en condiciones controladas convencionales (es decir, en placas de Petri en

cámaras de crecimiento) y condiciones no controladas (es decir, tierra en macetas), (3) Evaluar el uso intrínseco de la eficiencia del agua de los congéneres invasivos y nativos de *Prosopis*, y (4) Evaluar la disipación de energía térmica, la eficiencia fotosintética, la captura de carbono y la partición de nitrógeno en los congéneres invasivos y nativos de *Prosopis*.

Comparaciones congenéricas de los impactos de *Prosopis juliflora* y su congénere *P. cineraria* en la diversidad de especies consideradas como malezas y no malezas agricolas en los EAU

El primer capítulo de esta tesis explora las relaciones entre las especies asociadas al dosel de los dos congéneres de *Prosopis* y las especies del sotobosque que se consideran malezas y no malezas agrícolas en los EAU. Las especies de plantas invasoras alteran los ecosistemas alterando la estructura de las comunidades vegetates nativas. Los efectos positivos de la mayoría de las invasoras sobre la fertilidad del suelo pueden promover las malezas. Pocos estudios se han centrado en comparar el efecto de los doseles de los congéneres de *Prosopis* sobre las especies asociadas a ellas. Se examinan los efectos de dos congéneres concurrentes, la nativa *P. cineraria* y la invasora *P. juliflora*, en especies identificadas como "malezas agrícolas" y en especies que no son malezas agrícolas en los EAU. Se plantean las siguientes preguntas: (1) ¿La diversidad de no-malezas es más alta bajo el dosel de la *P. cineraria* nativa y más baja bajo el dosel de la exótica *P. juliflora*? (2) ¿La exótica *P. juliflora* aumenta la presencia de las malezas agrícolas más que la nativa *P. cineraria*, creando así potencialmente reservorios de estas especies? y (3) ¿El suelo bajo el dosel de la exótica *P. juliflora* tiene mayor fertilidad que la nativa *P. cineraria*? Se compara la riqueza y la densidad de las malezas agrícolas debajo de los doseles de *P. cineraria* y *P. juliflora*. Se miden las propiedades del suelo, la profundidad de la hojarasca y la masa de raíces finas debajo del dosel de ambas especies.

Se registraron un total de 29 especies (23 no malezas, 6 malezas y las plántulas de *P. juliflora*). Comparación de parcelas fuera del dosel y bajo el dosel de *P. juliflora* mostraron mayor densidad de malezas agrícolas que fuera del dosel. Estos patrones asociados con los congéneres de *Prosopis* y la composición de la comunidad de plantas podrían deberse a la deposición mucho más alta de hojarasca, si la hojarasca es inhibidora, y a la biomasa de raíces poco profundas bajo *P. juliflora*, o las diferentes propiedades del suelo bajo los dos doseles de *Prosopis*. En general, los suelos contenían más nitrógeno bajo *P. juliflora* que bajo *P. cineraria*, y bajo ambos doseles el suelon más fértiles que el suelo al aire libre. Nuestros resultados sugieren que la historia evolutiva puede desempeñar un papel en cómo las especies invasoras exóticas pueden seleccionar algunos caracteres sobre otros en las comunidades de plantas, con una invasora exótica que podría favorecer los reservorios de malezas agrícolas.

Alelopatía como mecanismo de éxito en la invasión de *Prosopis juliflora* en el área de distribucion introducida: Prueba del enfoque congenérico

El segundo capítulo de esta tesis evalúa el enfoque congenérico comparando el efecto alelopático de la exótica *Prosopis* invasora con los congéneres nativos en la germinación de semillas y en el crecimiento de plántulas de las especies asociadas a elllas. El enfoque congenérico o filogenético evalúa el papel relativo de las plantas invasoras exóticas en comparación con las plantas nativas en las especies asociadas. Este enfoque se utilizó para evaluar el impacto alelopático de las especies exóticas y su comparación con los congéneres nativos. Se esperan mayores efectos alelopáticos de la exótica invasora sobre la flora nativa que de su congenere. Las plantas nativas normalmente no comparten una historia coevolutiva con las especies exóticas invasoras en el área de distribución introducida. Las plantas invasoras producen aleloquímicos que son nuevos para las comunidades de plantas nativas. Las especies de *Prosopis* producen varias sustancias químicas, como fenoles, siringina y (-)-lariciresinol, y triptófano y juliflorina. Además, la producción de aleloquímicos explica la reducción en la abundancia de especies asociadas a *P. juliflora.* Los lixiviados de la hojarasca y de los extractos acuosos de *P. juliflora* inhibieron o redujeron significativamente la germinación de semillas de muchas especies nativas, cultivadas y malas hierbas asociadas. Sin embargo, los lixiviados de *P. cineraria* no inhibieron la germinación de semillas de cuatro especies nativas, especialmente en concentraciones bajas.

La mayoría de los estudios sobre la germinación de semillas se realizaron en placas de Petri que no reflejan las condiciones naturales. Se comparan los efectos de diferentes extractos de *P. juliflora* y *P. pallida*, y la nativa *P. cineraria* sobre la germinación de semillas y el peso seco de las plántulas de dos malezas (*Amaranthus graecizans* y *Sisymbrium irio*) y *Senecio flavus* en placas de Petri y en tierra en macetas. Las tres especies crecieron alrededor y debajo de las tres especies de *Prosopis.* Nuestra hipótesis es que el efecto alelopático de las especies exóticas es mayor que el de las nativas y que la tierra en macetas reduzca el efecto alelopático de las plantas exóticas en comparación con las placas de Petri.

Los resultados indican que las semillas no tratadas de las tres especies alcanzaron más del 95% de germinación en las placas de Petri. El aumento en las concentraciones de hojarasca de ambas especies invasoras de *Prosopis* inhibió la germinación de *S. flavus* y redujo significativamente la germinación y el peso de las plántulas de *A. graecizans* y *S. irio*. La reducción significativa en su germinación indica la capacidad de sus semillas para entrar en una etapa de latencia en condiciones desfavorables. Los resultados también mostraron una germinación significativamente mayor de las tres especies en placas de Petri que en tierra en maceta; la germinación final alcanzó más del 90% en cajas Petri y debajo del 50% en tierra en maceta. Esto indica que los resultados de la germinación en placas de Petri estériles no pueden predecir lo que sucedería en el campo. La falta de drenaje en las placas de Petri puede ayudar a acumular aleloquímicos, pero el suelo drenado ayuda a eliminarlos. Además, la microflora del suelo como las condiciones del sustrato pueden influir en el efecto de los aleloquímicos. A pesar del mayor efecto de inhibición de los extractos de hojarasca de las especies invasoras sobre la germinación y el crecimiento de las plántulas de las tres especies estudiadas, los extractos nativos de *P. cineraria* tuvieron efectos depresores significativos sobre la germinación de semillas y crecimiento de las plántulas de *S. flavus* y efectos limitados sobre *A. graecizans* y *S. irio*.

Se concluye que es difícil comprender los resultados de germinación y el efecto de la alelopatía en placas de Petri. Los resultados apoyan el mayor impacto de los aleloquímicos de las especies exóticas de *Prosopis* que los de la nativa *P. cineraria* en la germinación y el crecimiento de las plántulas de las plantas asociadas.

Eficiencia intrínseca en el uso del agua de los congéneres invasivos y nativos de *Prosopis*

El tercer capítulo evalúa la eficiencia intrínseca del uso del agua (iWUE) de los congéneres invasivos y nativos de *Prosopis*. La eficiencia en el uso del agua se define como la fracción de agua utilizada en el metabolismo de las plantas hasta el agua perdida por la evapotranspiración. Cualquier cambio asociado con la eficiencia del uso del agua puede considerarse una respuesta de adaptación de la planta al estrés por sequía. Además, las proporciones de isótopos de carbono se consideraron efectivas para detectar el estrés ambiental en plantas. Tomado en consideración que las especies exóticas de *Prosopis* crecen más rápido y toleran más la sequía que la nativa *P. cineraria*, se espera que el iWUE pueda ser una estrategia utilizada por la invasora exótica *Prosopis* para hacer frente al estrés por sequía en el área de distribución no nativa. Este estudio involucró las mediciones de la composición de isótopos de carbono estables (δ13C) y la eficiencia intrínseca del uso del agua (iWUE) de tres especies de *Prosopis* C3 (dos exóticas invasoras, *P. juliflora* y *P. pallida,* y la nativa *P. cineraria*). El objetivo fue investigar el δ13C y el iWUE en las hojas de las tres especies de *Prosopis* en diferentes posiciones del dosel (Este, Oeste) en hábitats

salinos y no salinos. También se comparó el alcance de la discriminación de isótopos de carbono (Δ13C) entre los reservorios de carbono de hojas jóvenes y maduras sobre la base de materia orgánica y se evaluó la magnitud de los cambios para las predicciones de iWUE. Nuestra hipótesis es que las plantas invasoras podrían aumentar su eficiencia en el uso del agua en comparación con las nativas para dominar en el área de distribucion introducida.

Los resultados mostraron que la especie nativa *P. cineraria* y las invasoras *P. juliflora* y *P. pallida* tiene respuestas fisiológicas e isotópicas contrastadas segun madurez de las hojas, posición del dosel y su interacción. Los valores foliares de δ13C de las tres especies de *Prosopis* están dentro del rango de δ13C de las especies de leguminosas C3 (0+2‰). Los resultados también revelaron que los patrones de δ13C son similares para las tres especies de *Prosopis.* Además, la diferencia en la discriminación de isótopos de carbono (Δ13C) entre la posición del dosel (oeste y este) es relativamente consistente entre especies y sitios, oscilando entre 17,8 ± 4,43 % para las hojas jovenes en el oeste y 18,05 ± 4,35 % para el este del dosel. Observamos un δ13C más alto (menos negativo) desde el oeste que desde el este en *P. pallida* del hábitat salino. Esto indica que las plantas del hábitat salino pueden sufrir limitación de agua y menos fotosíntesis debido al cierre de estomas y, por lo tanto, más discriminación de isótopos de carbono.

Los resultados indican que las hojas maduras poseen una mayor iWUE que las jóvenes. El iWUE de *P. juliflora* fue mayor en los hábitats no salinos que en los salinos. Además, la concentración de CO_2 intercelular del interior al aire ambiente (Ci/Ca) fue mayor en el lado oeste que en el este en las hojas jóvenes de *P. juliflora* y *P. pallida.* Pero se observó una tendencia opuesta en Ci/Ca en hojas jóvenes de *P. cineraria*. Este resultado indica que las hojas jóvenes en la posición oeste del dosel de *P. juliflora* y *P. pallida* podrían no sufrir exceso de estrés por luz y calor en comparación con *P. cineraria*. Una relación Ci/Ca más baja en las hojas jóvenes de *P. cineraria* podría deberse al cierre de estomas inducido por el estrés hídrico o a tasas más altas de capacidad fotosintética.

Concluimos que *P. juliflora* y *P. pallida* tienen valores de iWUE más altos que *P. cineraria*, lo que podría deberse al rápido desarrollo de las raíces en los desiertos de los EAU. Esto podría permitir que las especies exóticas accedan a suelos húmedos más profundos o a recursos hídricos.

<u>Disipación de energía térmica, eficiencia fotosintética, obtención de carbono y partición de nitrógeno en congéneres invasivos y nativos de *Prosopis*</u>

Abstract

Se analiza la eficiencia de la fotosíntesis de las especies de *Prosopis*. En la fotosíntesis, parte de la luz se fija y se convierte en energía química. Sin embargo, parte de la luz solar no utilizada por completo podría causar daños a la planta. En los desiertos, la mayor radiación solar y el calor son los principales factores ecológicos limitantes para estas plantas. Bajo la alta intensidad solar, parte de la luz capturada no se utiliza y puede causar un exceso de energía de excitación que provoca una caída en la fotosintesis restringiendo el crecimiento de las plantas. El exceso de luz solar puede combinarse con el oxígeno y convertirse en especies reactivas de oxígeno (ROS), lo que conduce a un estrés fotooxidativo que daña el metabólismo de la planta. Para evitar este daño y la acumulación de ROS, las plantas exhiben una serie de mecanismos de autoprotección que incluyen la utilización eficiente de la luz solar y la disipación del exceso mediante mecanismos bioquímicos de defensa como los sistemas antioxidantes. En este studio se analizan los mecanismos de supervivencia de las especies de *Prosopis* congénericas bajo diferentes intensidades de luz en hojas expuestas y no expuestas a la luz y en diferentes direcciones del dosel.

Evaluamos el impacto de la posición del dosel en los ajustes fotosintéticos y los atributos de fluorescencia de la clorofila (fotoquímica del fotosistema II, rendimiento cuántico, extinción de la fluorescencia y disipación de energía de fotones), biomasa y contenido de nutrientes de las hojas expuestas al sol en la posicion dosel sureste, y hojas no expuestas en la posición noroeste en la invasora *P. juliflora* y la nativa *P. cineraria*, en un ambiente extremo (desierto de EAU). El objetivo fue estudiar el mecanismo de fotoprotección en congéneres de *Prosopis* que contrarresta la formación de especies reactivas de oxígeno.

La eficiencia fotosintética máxima (Fv/Fm) de las hojas adaptadas a la oscuridad en *P. juliflora* y *P. cineraria* fue mayor en la posición del dosel noreste que en el sureste. Tal resultado indica que las hojas en la posición sureste estuvieron expuestas a intensidades de luz más fuertes y altas temperaturas que podrían reducir la eficiencia fotosintética. Los resultados también demostraron que *P. juliflora* mantiene una eficiencia fotosintética ligeramente más baja pero estable (Fv/Fm) que *P. cineraria*. Este resultado indica que la fotosíntesis no podría ser responsable del éxito invasor de *P. juliflora*.

El rendimiento cuántico (ΦPSII) fue menor tanto en *P. juliflora* como en *P. cineraria* en el sureste que en la posición del noreste del dosel. Tal reducción en ΦPSII podría coincidir con una disminución en la eficiencia de captura de energía de excitación de los centros de reacción de PSII en el lado SE. El ΦPSII se reduce en condiciones de agua limitada. La alta temperatura aumentó la transpiración debido al exceso de luz, lo que podría causar el estrés que redujo los valores de ΦPSII en la posición sureste del dosel. Además, el valor de extinción de la fluorescencia no fotoquímica (NPQ) también fue más alto en *P. juliflora* que en *P. cineraria*, lo que indica que la primera está más adaptada a las condiciones climáticas locales y puede disipar el exceso de energía en forma de calor. La capacidad protectora de NPQ disminuyó en *P. cineraria*, lo que condujo a la acumulación de un exceso de energía de excitación y al agravamiento de la fotoinhibición. Las hojas de *Prosopis* disiparon el exceso de energía luminosa en la posición sureste del dosel aumentando el NPQ.

Los resultados también explican el papel de diferentes atributos fisiológicos que contribuyen a la invasividad de *P. juliflora* y evalúan la relación entre la plasticidad de estos caracteres y la invasividad.

INTRODUCTION

INTRODUCTION

1. Biological invasion

Biological invasion can be defined as the movement of livings organisms from their native ecosystem to new geographical areas where they expand their population spectacularly and exert significant depressive impacts on the local diversity. The processes of moving species from place to another around the globe can be done intentionally or accidentally. The distribution of species on the earth is controlled by some natural barriers such as mountains, seas, and oceans. However, removing these barriers, both species connection and exchange could be observable (Censky et al., 1998; Vermeiji, 1991; Velde et al., 2006). In general, species dispersion throughout the globe constitutes an important process that ensures the distribution and perpetuation of each species. To date, anthropological activities significantly impact the movements of species around the globe. Accordingly, the magnitude of moving organisms from point-to-point worldwide has increased. For example, the European market, which is the largest market in the world, remarkably noticed that there was a significant increase in trade associated with the large Dutch rose from 1990 to 2002 (World Bank Working Paper, 2005).

It is well-known that introducing alien species to new regions where they did not have any previous existence can constitute a potential risk of invasiveness (Garcia-Espinosa and Villasenor, 2017; Pearson et al., 2017). Species invasiveness constitutes its potential capacity to overcome natural barriers and conquer new geographical regions (Mcneely et al., 2001). The successful establishment of alien species into new areas is completed in five sequential phases: transport, arrival, establishment, spread, and impact (Mack et al., 2000; Hulme et al., 2008; Ricciardi, 2013). Briefly, transport is the action of an organism to move from one location to another using propagules, and the process is carried out by some vectors such as water, air, land, and human. Arrival can be seen as the act of individual to being reaching the recipient region. Establishment is the stable growth stage for the introdcuced species in the non-native range. Spread means extending or increasing the existing area. Generally, the spread can be defined as a biological process during which the introduced organisms expand over a large area within the native ecosystem. The impact is considered as the last phase of the biological invasion. Traditionally, impact means coming into forceful contact with another or having stronger effects on another. So, biologically, the impact can be seen as a precise stage where the signs of disturbances appear in the ecosystem due to the introduction of new organisms (Mack et al., 2000)

Introduction

Biological invasions cause many native habitat degradations. The ecological costs associated with their invasiveness are importantly high regionally and globally. The problem posed by biological invasions has been considered as a sort of nuclear threat, war, or biological explosion. Species invasiveness is, at the moment, considered as an important component associated with climate change and is argued to significantly alter the functioning of the ecosystem services (Murphy and Romanuk, 2014; Chabrerie et al., 2019). Most species introductions depend on human movements and activities, and this trend is even more emphasized when focusing on invasive species (Bellard et al., 2016; Bonnaud, 2020).

To ensure their success in the new habitats and regions, the non-native invaders have developed spectacular morphological, physiological, anatomical, and molecular adaptations to resist and tolerate any environmental conditions (Ozaslan et al., 2016). In general, their present exceptional metabolism compared to the non-invasive that has a higher capacity to change depending on the adjustments occurring in the milieu (Riess et al., 2010).

2. The invasive species *Prosopis juliflora*

The genus *Prosopis* comprises 44 species out of which *P. cineraria* (L.) Druce is native to India, Pakistan, Afghanistan and Iran (Burkart, 1976). In the arid and semiarid regions of India, *P. juliflora* (Sw.) DC. (the common name Mesquite) is an exotic invasive species that is expanding its range at an alarming rate and damaging native diversity and ecosystem health (Figure 1). *P. juliflora* (native to Central America, the Caribbean and northern South America) was introduced to southern India in 1877 due to its valuable benefits like drought tolerance, source of firewood, timber, fencing, livestock feed (pods), gum for textile industries. It has now expanded its range very fast throughout tropical India through the formation of impenetrable thickets. Cattle is the main vector for seeds dispersal of *P. juliflora* and *P. cineraria*, and the two species are among few large shrubs species growing in the arid deserts of the United Arab Emirates (UAE), and currently they are co-occurring in some habitats. They constitute a major ecological feature in the Northern Emirates of the UAE.

P. juliflora is a drought-resistant and evergreen species (Tewari et al., 2013). *P. juliflora* is considered as a multipurpose shrub because of the high benefits associated with its utilization. For example, many bioactive metabolites have been identified and isolated from *P. juliflora*, and those are argued to have significant socio-economic importance (Le Maitre et al., 2002; Shackleton et al., 2011; Ravhuhali et al., 2021). Therefore, due to the higher benefits associated to *P. juliflora*, it has been largely introduced in many countries worldwide (Pasiecznik et al., 2001; Shackleton et al., 2014). However, regrettably, the species is considered today as one of the most problematic invasive plants globally (Prasad and Tewari, 2016). According to this, *P. juliflora* was highlighted in the world top 100 weed species as the worst (Lowe et al., 2000).

Prosopis was introduced intentionally in the semi-arid and arid regions, including UAE, to stabilize the soil against natural erosion (Hussain et al., 2019). However, many of those exotics *Prosopis* have escaped plantations and invaded several pastoral lands (El-Keblawy and Al-Rawai, 2007; Maundu et al., 2009; Borokini and Babalola, 2012; Tewari et al., 2013; Al-Assaf et al., 2020). Many comparative studies dealing with the congeneric approach demonstrated that *P. juliflora* is far the recalcitrant one with huge adverse impacts in the introduced range (Kaur et al., 2012; El-Keblawy and Mahmoud, 2014; Slate et al., 2020; Tsombou et al., 2021). *P. juliflora* is a fast-growing shrub, nitrogen-fixing and extremely adapted to harsh environmental conditions such as very poor soils, drought, and saline soils. Therefore, *P. juliflora* is considered as one of the most invasive plants globally (Brown and Sax, 2004; Luque et al., 2014; Dakhil et al., 2021).

Prosopis species have many features which enable them to exploit, invade, and alter ecosystems services. These include high growth rate, deep taproots and long lateral roots, long-lived seeds, high germination rates over a wide range of temperature and moisture conditions, ability to withstand high negative water potentials, high water use efficiency, and the ability to regenerate from dormant underground buds following injury (Hennessy et al., 1983). *P. juliflora* has similar characters that enable it to invade large areas around the world, especially tropical and arid subtropical regions (Pasiecznik et al., 2001)

Prosopis juliflora can be considered as a species with unspecific environmental adaptation. In fact, it grows well and expands in the regions with extreme conditions, such as poor soils, and dry lands with very low scant of precipitation (Pasiecznik et al., 2001). Morphologically, *P. juliflora* can reach 12 m in height with persistent and evergreen leaves and, thorny branches. Its tap root can go up to 50 m underground, the lateral roots grow up to 10 m. The seeds are oval and brown (Mwangi and swallow, 2005). In addition, seeds produced by mesquite plant could reach about 980,000 per year, and they have greater germinability capacity to emerge, where seeds of many other species could not (Pasiecznik et al., 2001). Besides, in most cases, mesquite seeds do not require any pre-treatment to germinate (El-Keblawy and Al-Rawai, 2005, 2007).

In general, mesquite plants seem to have distinguishable adaptive traits compared to the local flora, which might explain their higher superiority over the indigenous species. Similar invasiveness characters were addressed in many other exotic invaders. For example, comparable characters were observed in *Lantana camara* (Day and Zaluki, 2009), *Chromolaena odorata* (Zachariades et al., 2009), *Eichhornia crassipes* (Albano et al., 2011), *Ageratum conyzoides* (Kanissery et al., 2019), *P. pallida* (Pasiecznik et al., 2001). Furthermore, earlier studies have shown that polyploidy, which is considered as a whole genome duplication, positively affects plant invasiveness (Beest et al., 2012). Genetically, genome duplication has been seen as a key for plant evolutional traits that can potentially facilitate plant invasiveness processes. The polyploidy of *P. juliflora* was highly differentiated from the rest of the (diploid) species within the genus. Polyploidy explains the successful invasion of *P. juliflora* in Eastern Africa (Castillo et al., 2021).

Prosopis juliflora has adapted to both sexual and vegetative propagation to ensure its success in colonizing new geographical areas (Patnaik et al., 2017). Plant reproduction by vegetative ways contributes to the fast establishment of plant population that is homogeneous in terms of resistance against pests and disease (Christopher, 2015). Similar statements were addressed in *Imperata cylindrica*, which is considered by the Global Invasive Species Database (GISD) (2021) as a very aggressive perennial grass. *I. cylindrica* is native to Southeast Asia, Australia, China, Philippines and East Africa (McDonald and Chandler, 1994). However, to date, it is highlighted as the most noxious weed in 73 countries and constitutes a significant threat to global biodiversity and sustainable agriculture (Burrell et al., 2015). An estimated 500 million hectares have been invaded worldwide by *I. cylindrica* with 100 000 ha of lands allocated to Florida (Dozier et al., 1998; Estradas and Flory, 2015), about 35 million ha in Asia (Garrity et al., 1996; Rusdy, 2020).

The depressive impacts associated with the invasiveness of *P. juliflora* can be noticeable on the ecosystem functioning in addition to human activities. Today, semi-arid and arid regions, including other parts of the world, have been infested (Pasiecznik et al., 2001; Ravhuhali et al., 2021). For example, GIS (Geographical Information System) revealed that *P. juliflora* is a redoubtable plant weed in UAE (Issa and Dohai, 2008; Dakhil et al., 2021), which has a higher potential to alter the local ecosystem. Issa and Dohai (2008) showed that *P. juliflora* stands interestingly increased between 1986 to 2005 from 1.19 to 39.43 percent in the study site in UAE. Consistent data obtained by Tadros et al. (2020) showed that water surface areas, urban and bare soil decreased by 3, 6 and 11 percent respectively in Jordan valley from 1999-2017. Similar findings were reported by AlMaazmi and Al-Ruzouq (2021) in the UAE. In fact, their results revealed that the area covered by the infestation of *P. juliflora* has not stopped or slowed down. Furthermore, Howari et al. (2022) showed that the *P. juliflora* invasion in a certain area around Sharjah and Ajman cities, UAE, expanded to 16 Km in 2019 compared to 0.2 km in 1990. Moreover, Dakhil et al. (2021). Indicated that the potential invasion risk of *P. juliflora* increases globally with increases in mean temperature of the driest quarter, soil alkalinity and clay fractions. Arid and semi-arid lands are at the highest risk of invasion than other moist biomes (Dakhil et al., 2021).

Several comparative and congener studies carried out on *Prosopis* species have shown the greatest depressive impacts associated with the invasiveness of the species under *Prosopis* genus on the related native species. In this respect, species richness in India is expected to reduce by 63% under the canopies of mesquite compared to the open places (Kaur et al., 2012; Sivakumar et al., 2018). Additionally, Aditi et al. (2017) showed through spatial comparison of species dominancy that mesquite stands greatly increased between 1985 to 2015, displacing the most dominant local plants such as *Ziziphus mauritiana*, *Salvadora persica*, *S. oleides*, *Mitragyna parvifolia*, *Acacia nilotica* and *Prosopis cineraria*. Analogical statements were addressed by El-Keblawy and Al-Rawai (2007) in UAE. In South Africa, 1.8 million hectares of the land are covered by *P. juliflora* (Zachariades at al., 2011; Ravhuhali et al., 2021). In Somalia, *P. juliflora* invasion covered about 550, 000 hectares of land. In Ethiopia, 1.18 million lands were covered by *P. juliflora* plants (Shiferaw et al., 2021).

In general, mesquite trees not only affect the different services of ecosystem, but the negative impacts associated with their spread have important adverse effects on human health. The findings of the earlier studies in this regard reported by Muller (2017) showed that, mesquite trees negatively alter human health. In fact, the results of their work demonstrated that *P. juliflora* significantly increases the risk of malaria transmission in the study site. Furthermore, the leaves of mesquite tree were reported by Almeida et al. (2017) to contain important secondary metabolites which are highly toxic to the ruminants. Several studies have reported allergenic effects for pollen grains of *Prosopis* species that cause respiratory problems. In some parts of Kingdom of Saudi Arabia, *P. juliflora* has been introduced by millions as roadside ornamentation (Al-Frayh et al., 1999). There, it has four flowering seasons during which pollen grains float in all directions and large amounts of pollen debris are deposited underneath the trees. *Prosopis* pollens were detected in the air of Gizan, KSA, and exceeded 90 grains m^3 of air. A total of 473 allergic patients suffering from bronchial asthma in four different geographical regions of Saudi Arabia (Abha, Qassim, Hofuf and Gizan), and attending allergy clinics and chest disease centers of university and Ministry of Health hospitals in the region were tested for immediate hypersensitivity reaction to *P. juliflora* allergens. Their results showed that 76.1% of patients in Qassim, 37.5% in Gizan, 29% in Abha and 11% in Hofuf reacted positively to *Prosopis* antigen (Al-Frayh et al., 1999). Extracts from *Prosopis* pollen grains had 16 allergenic components; nine were recognized as major allergens (Hussain et al., 2020).

Masters and Norgrove (2010) argued that the negative impacts of plant invasiveness could constitute an important result of climate change. Even climate change can further facilitate the allergenic effects of *Prosopis* species (Hussain et al., 2020). For example, in arid and semiarid lands, the demand for water currently exceeds the renewable freshwater supply (Oki and Kanae, 2006). Ground water levels in arid environments are dropping worldwide due to human extraction, and precipitation events are predicted to become rarer and more intense in many arid areas with global climate change (Dudley et al., 2014). In arid-land countries, groundwater resources are heavily used for agriculture and domestic use. Additionally, water consumption in excess of recharge rates has resulted in region-wide reductions in groundwater tables (Stromberg et al., 1992; Postel, 1993; Shah and Danishwar, 2003; Yang et al., 2003; Scanlon et al., 2006; Rodell et al., 2009). Howari et al. (2022) stated that the amount of groundwater consumed by *P. juliflora* through evapotranspiration was 22.22 million m^3 of groundwater in 2019, which is 7372% increase above that consumed in the same area in 2019.

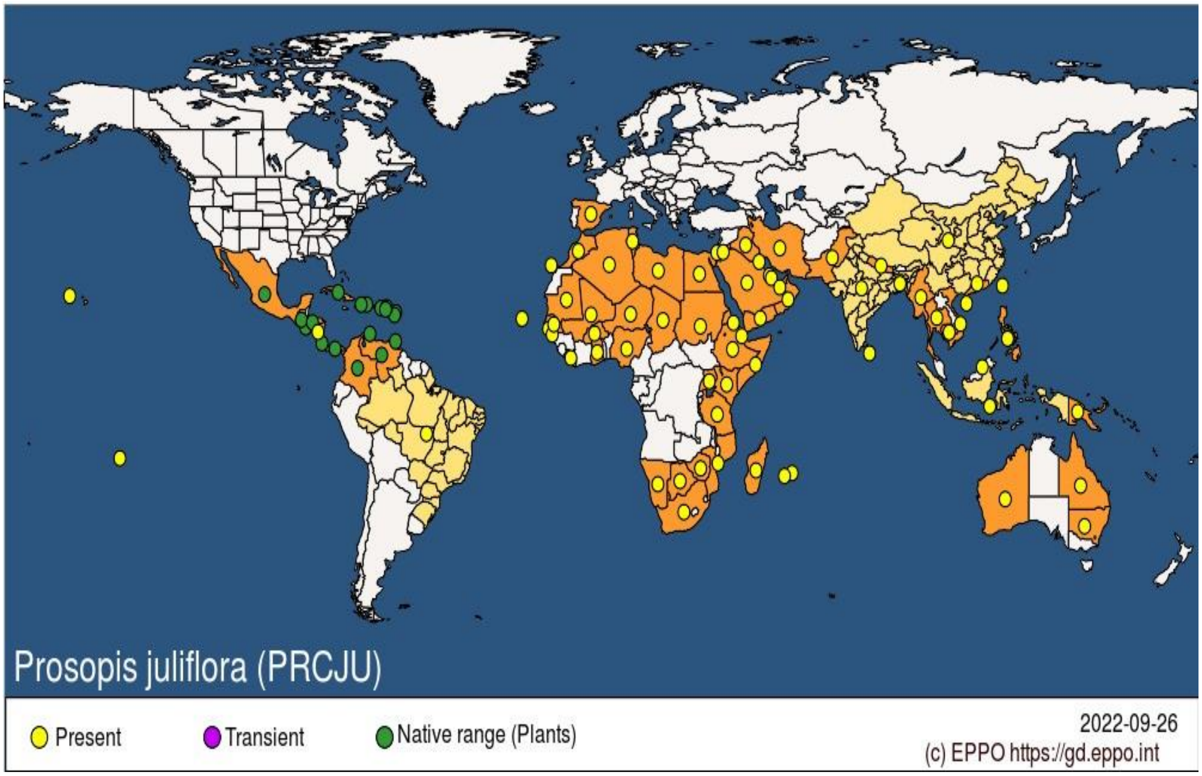

Figure 1. Global distribution of Prosopis juliflora (European and Mediterranean Plant Protection Organization, 2020)

3. Possible Mechanisms explaining the Invasive ability of *Prosopis juliflora*

Three approaches (traditional, congeneric, and bio-geographical) have examined the mechanisms the success of *P. juliflora* invasion (Inderjit et al., 2008). The traditional approach focuses on the fate, dose, replenishment, and effect of chemicals produced by invaders in the soil environment (El-Keblawy and Abdelfatah, 2015; Hierro and Callaway, 2003). In the congeneric approach (also called phylogenetic), the allelopathic effects of exotic and native congeners are studied. Native plants have not evolutionary evolved with the exotic invasive species. Therefore, greater allelopathic effects of the exotic invasive plant are expected than of the native congeners in the introduced range. The allelochemicals produced by the exotic invasive plants are new to the native plants; the allelochemicals produced by the exotic in their introduced range are called novel weapons (Callaway and Ridenour, 2004). For example, El-Keblawy and Abdelfatah (2015) assessed the impact of allelopathy produced by *P. juliflora* and its native congener *P. cineraria*, and soil properties on understory native plants in the arid deserts of the UAE. They found that the aqueous extracts of fresh and old leaves of *P. juliflora* on the associated flora were inhibitory, but

P. cineraria leaves and litter positively affected other native species. The inhibitory effect of *P. juliflora* was stronger on annual species than perennials. Similarly, Kaur et al. (2012, 2014) found that more allelochemicals, e.g., phenolics and tryptophan, are produced in *P. juliflora* leaves in India than in *P. cineraria*. The L-tryptophan was recorded in leaf leachates of both *P. juliflora* and *P. cineraria*, but the amounts were greater in the leaf leachate of *P. juliflora* (73%) than that in *P. cineraria* (Kaur et al., 2012)

The biogeographic approach studies species-ecological traits and processes in native and non-native ranges. Exotic species bring chemicals novel for invaded communities that has the potential to exhibit allelopathic effects due to naïve soil communities and sensitive neighbors (Callaway and Ridenour, 2004). The 'novel weapons hypothesis' was posed by Callaway and Aschehoug (2000) to study the role of allelochemicals in ecological processes and evolutionary context. Several chemicals, such as phenolics, tryptophan and juliflorine, that are produced in *P. juliflora* foliage (Nakano et al., 2003). Kaur et al. (2012, 2014) found that the amounts of phenolics and tryptophan produced by *P. juliflora* have no obvious effects on the naïve plants in the native range but have inhibitory effects in the introduced range. Besides, *P. juliflora* appears to coexist with large numbers of other native species in its native range (Kaur et al., 2012). The canopies of mesquite have much stronger facilitative effects on neighbors than other leguminous tree species (Larrea-Alcázar and Soriano, 2008). In its introduced range, however, *P. juliflora* strongly suppresses species native to those regions (Pasiecznik et al., 2001). *P. juliflora* usually grows in non-saline soils in most of its native and introduced range, but it has been recorded to occur in saline habitats in Hawaii USA (Kaur et al., 2012) and Nevada, Arizona, USA. In the UAE, *P. juliflora* grows in many habitats, including salt marshes, non-saline sand dunes, abandoned fields, and even inside the cities.

4. Successful traits of invasiveness of *Prosopis juliflora*

4.1. Allelopathy

It has been suggested that allelopathy is a mechanism driving invaders to become more abundant and competitively dominant in their introduced range than native range. In fact, some plant species might metabolite and then release toxic or harmful bioactive substances in their vicinity to enhance their competitive ability for water and nutrients uptake (Figure 2). However, other plants might liberate simulative compounds that beneficially improve the neighboring species growth. Allelopathy is considered as a natural phenomenon with higher ecological importance that involves the synthesizing and releasing of some secondary metabolites in the plant environment to enhance its chances of survival (Rice, 1984; Seigler, 1996; Mondal et al., 2015; El-Shabasy, 2017; Tsombou et al., 2021). There are two concepts about the effects of allelopathy on the surrounding environment. Allelopathy could be beneficial or detrimental depending on its resultant observable effects on the recipient species.

Regarding the *Prosopis* species, the allelopathy effects of the exotics invaders were declared to be detrimental in the exotic species, such as *P. juliflora* and *P. pallida*. However, the beneficial allelopathy effects were reported in *P. cineraria* (Kaur et al., 2012; Tsombou et al., 2021). Allelopathy should involve the production of the chemical compounds by the living plants or the chemical resulting from the plants' tissue decomposition, which affects the behaviors of the neighboring plants (Willis, 2007).

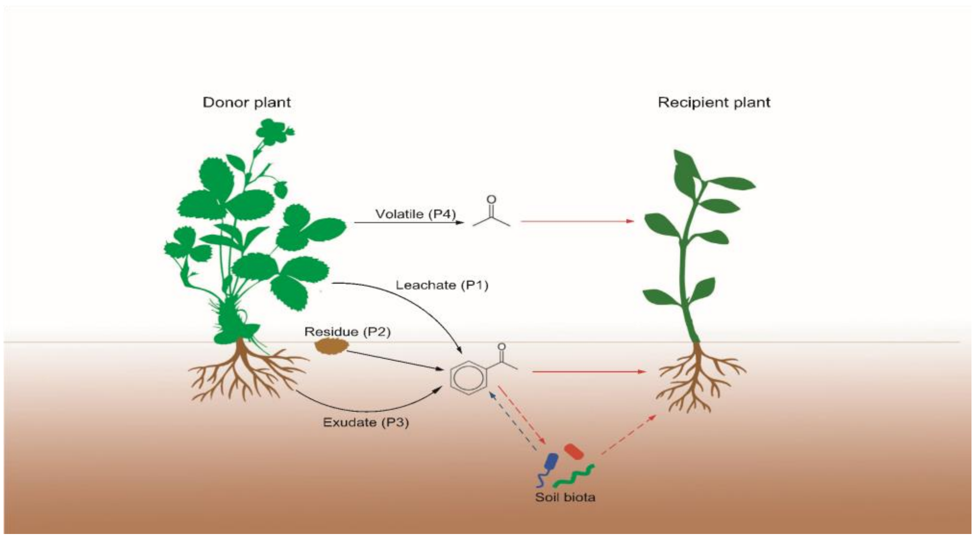

Figure 2. Different pathways and the effects of allelochemicals from the donor to the recipient plant (Zhang et al., 2020).

In the last decades, the effect of allelopathy has been greatly explored with most of the works done in the Petri dishes. However, assessing the impact of allelochemical extracts on seed germination in Petri-dishes does not mimic that in the natural soil conditions. However, fewer attempts have been made in potting soil that reflects the natural conditions. Several researchers have indicated difficulties in assessing the allelopathic effects on seed germination and seedling growth in sterile Petri dishes (Hershey, 1996: Hershey and Latto, 1996; Qasem, 2012; Baličević et al., 2015). Those researchers pointed out the difficulties of relying on assessing allelopathic effects on seed germination in sterile Petri dishes compared to potting soils and natural ecosystems.

In allelochemical studies, Petri dishes experiments cannot predict what would happen in the field (Qasem, 2010). For example, the lack of drainage in Petri-dishes can help accumulate allelochemicals, but drained soil helps them wash away from the seedbed (Puig et al., 2014). Besides, both soil microflora and substrate conditions can determine the fate of allelochemicals (Inderjit, 2005). Soil microflora decomposes allelochemical faster in the soils than in Petri-dishes, which reduces the toxicity of allelochemical molecules in soils (Inderjit. 2005). Moreover, Baličević et al. (2015) attributed the higher phytotoxic effect for extracts of aromatic and medicinal plants on germination of *Tripleurospermum inodorum* in Petri-dishes to the direct contact of seeds with extracts on filter paper. It has been concluded that the strong inhibitory extract effects of certain invasive plants on germination and seedling establishment of native plants could not be interpreted in light of controlled conditions in Petri-dishes and growth chambers (Qasem, 2010; Baličević et al., 2015). It was also concluded that this leads to overestimated false results of suppressive activity of allelochemicals in the dishes (Puig et al., 2014).

Allelopathic plants might affects the surrounding environments differently, and the amplitude and the frequency of their effects could associate with biotic and abiotic factors (Schafer and Wink, 2009; Madiha et al., 2018). The synthesized secondary metabolites released in the milieu may depend on the plant organ producing them at the allelopathic plant level. Besides, the amounts and the specificity of those metabolites released in the plant environment would depend on the types of interactions the plant would need to establish, or the effects that plant would need to generate. Therefore, those compounds might have stimulatory, regulating, or inhibitory effects. It is reported that secondary metabolites help plants as antifungal and antibacterial. (Prusakova et al., 2008; Babenko et al., 2019). Furthermore, they are documented to have indirect functions in the plants' reproduction (Cheng and Cheng, 2015).

Various products derived from the plant secondary metabolism classified according to their respective function for the plant. In general, higher plants produce many identifiable compounds to cope with unfavorable environmental factors, and various metabolites are still increasing (Lattanzio, 2013). The phenolic compounds are among the secondary metabolism products. They constitute the major group in the plant allelopathy interactions and were largely noticed in the natural and managed ecosystems associated with significant negative economic impacts (Li et al., 2010). Phenolic compounds are considered as the more predominant allelochemicals in plant allelopathic processes. Three major groups of phenolic compounds are well-known to play crucial functions in plant allelopathic interactions, and they are as follows: flavonoids, phenolic acids, and tannin. *Prosopis* species produce several phenolic chemicals such as, syringin, and (-)-lariciresino (Nakano et al., 2002), and tryptophan and juliflorine (Nakano et al., 2001, 2003).

Succinctly, the different groups forming the phenolic acids give them important roles in helping plants fight against oxidative alteration (Lisete-Torres et al., 2012; Kiokias et al., 2020). Furthermore, plants phenolic acids have been associated with many vital functions such as photosynthesis, structural components, enzyme activity, protein synthesis, allelopathy, and nutrient uptake (Luy et al., 2010; Goleniowski et al., 2013). Concerning flavonoids, they greatly impact the plant photosynthesis processes, preventing this latter from light stress and having an important role in plant reproduction (Khoddami et al., 2013; Cosme et al., 2020). Tannins, commonly considered tannic acids, constitute a major group of phenolic compounds that help plants interact with their environment. In general, tannic acids are involved in plant defense and act against herbivores and microbial attacks, and they have an important function in litter decomposition and metal complexation (Fraga-Corral et al., 2020).

Environmental stresses can induce the production of allelopathic substances (Figure 3) allelochemicals could be released from plants into the environment as root exudation, leaching, and decomposition of plant residues in the soil. Allelochemicals could be used as herbicides for weed management. Selective pressure of environmental stress can induce the production and release of allelochemicals (Chuihua et al., 2000). Besides, indicated that natural and anthropogenic biotic and abiotic stresses are important external signals that induce the production of allelochemicals (Pedrol et al., 2006).

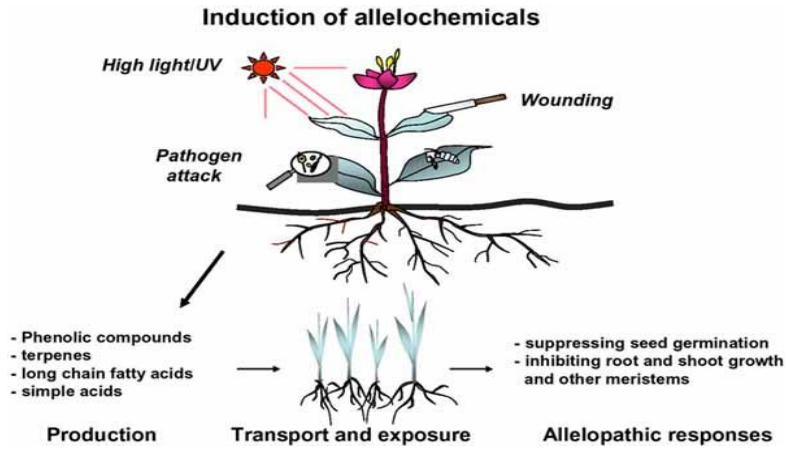

Figure 3. Induction of allelochemicals by environmental stresses (Kim and Shin, 2003).

In the context of *Prosopis* species, phenolic compounds have been identified and isolated, and the types of those compounds might strongly depend on the isolable plant part and the invasiveness ability. For example, the allelochemicals of *P. juliflora* were declared to be detrimental to the surrounding organisms, while that of *P. cineraria* was argued to positively affect the associated diversity (Kaur et al., 2012; Tsombou et al., 2021). *P. juliflora* is considered one of the species in the genus *Prosopis* with significant depressive effects on the biodiversity and other components of the ecosystem. Therefore, the findings of phytochemicals related to *P. juliflora* revealed different types of allelochemicals, and the more predominant were alkaloid, tannin, flavonoids and phenolic compounds (Almaraz-Abarcaa et al., 2007; Kaur et al., 2012; Prabha et al., 2014; Henciya et al., 2017; Prabha et al., 2018). Specifically, in the leaves, juliflorine and juliprosinene were reported by Ahmad et al. (1989) as the main alkaloids, and their negative effects were documented by Ahmad et al. (1992) in *Listeria homlysin*. Corroborating data were published by Choudhary et al. (2005) in acetylcholinesterase enzyme.

Seed germination of many species has been inhibited when treated with a water-soluble extract from different parts of *P. juliflora*, including litter and rhizosphere soil. For example, germination and early seedling growth of various cultivars of *Zea mays*, *Triticum aestivum* and *Albizia lebbeck* was inhibited by aqueous extracts from soil under the canopy and from different parts of *P. juliflora* (Noor et al., 1995). Similarly, water-soluble chemicals in *P. juliflora* leaves inhibited seed germination level and speed and reduced the rate of seedling growth of *Cynodon dactylon* (Al-Humaid and Warrag, 1998). In addition, the allelopathic effects of leaf litter of *P. juliflora*, was significantly decreased the germination of *Vigna mungo* and *Sorghum bicolor*

(Chellamuthu et al., 1997). In UAE, El-Keblawy and Abdelfatah (2015) showed that seed germination of five native plants associated with *Prosopis* species was significantly inhibited with the aqueous extracts of *P. juliflora*, compared with control (non-treated) seeds and seeds treated with different concentrations of *P. cineraria* extracts. Conversely, seeds of four native species germinated to significant proportions in the extract of both fresh and old leaves of *P. cineraria*, especially in the lower concentrations (El-Keblawy and Abdelfatah, 2015).

4.2. Shade effect

Prosopis juliflora exerts negative impacts on neighbors through shade and competition for water and nutrients. The growth of *P. juliflora* has shown to improve soil physical and chemical properties in the UAE, which might have a positive effect on the associated species (El-Keblawy and Abdelfatah, 2015). Litterfall from *P. juliflora* throughout the year increases organic matter, macro-nutrients, potassium, nitrogen and phosphorous in the soil below its canopies. Increasing organic content could improve water holding capacity, positively affect soil texture and increase soil moisture (El-Keblawy and Abdelfatah, 2015).

4.3. Competition

The theme competition has been intensively used in many disciplines with similitudes. In ecological sciences, competition is considered as the interactions between individuals sharing similar environmental requirement supply at limited levels, which could significantly affect the species survival capacity (Longstaff, 1998). Most interactions in plants occur below the soil surface compared to that observed in the above parts (Brenda et al., 1997). In general, below-ground competition importantly affects plant performance compared to that of aboveground interactions (Wilson, 1988; Brenda et al., 1997), and it is considered the main type of competition occurring in regions with harsh conditions such as arid systems and other inhospitable places of the world (Fowler, 1986; Brenda et al., 1997). Many environmental factors affect the structure of plants community (Martorell et Freckleton, 2014), but competition has been pointed out as the major key that shapes the structural organization of plant associations (Tilman, 1985; Golberg and Barton, 1992; Chesson, 2000; Baron et al., 2015).

In plant communities, water, light, and nutrients are considered the major elements that reduce plant performance and are those for which plants compete (Craine and Dybzinski, 2013). Water deficiency is the main factor limiting plant physiology in desert systems. Therefore, desert soils are extremely poor in biological activities responsible for the soil quality, and only selective plants could establish in these hostile milieus. Some plants are considered opportunistic because they have a greater ability to thrive in areas where soil moisture, nutrient availability, and other ecological factors constitute the major limiting environmental conditions for plant growth (Behzadi et al., 2010). Among those types of plants, exotic invaders present exceptional evolutionary adaptive features that allow them to colonize unreachable places and, therefore, could quickly expand in these fragile environments competing with the local species. The depressive impacts resulting from the competition between the exotic invaders and the local species might be disastrous in the desert systems due to the less diversification in plant species observable in these milieus. Their higher competitiveness capacity might quickly force some sensitive species of those environments to extinction.

Globally, invasive species have strategically evolved depending on the providing environmental factors. In most cases, they have exceptional traits that give them a chance to colonize a broad range of climates and out-compete with the native diversity. In most cases, studies dealing with comparisons between invaders species and native diversity demonstrated that invasive species have a greater capacity to compete and to exclude the non-invasive (Vila and Weiner, 2004; Dangremond et al., 2010; Brueno et al., 2019). The negative impacts associated with species invasiveness are considered the main factors affecting global change (Vitousek et al., 1996; Gioria and Osborne, 2014).

Competition is another mechanism that would enable *P. juliflora* to replace native flora. The morphological, physiological, and genetic traits and the reproductive rate related to *P. juliflora* significantly enhance its competitive behavior. For example, root density of *P. juliflora* was 3 cm of root/cm^3 of soil in the upper 15 cm of the soil profile, dropping to less than 0.5 cm root/cm^3 of soil at below 45 cm depth and less than 0.2 cm root/cm^3 of soil at 1.8 m depth (Jones et al., 1998). Hoshino et al. (2011) indicated that *P. juliflora* could detect very tiny soil moisture and grow under various conditions. Some of the many adaptive abilities that allow *P. juliflora* to thrive under such conditions include the ability of roots to adapt to a wide variety of soil conditions (Hoshino et al., 2011). Roots can grow upwards towards the soil surface to capitalize on little rainfall but can also grow to depths of 80 m and extend laterally more than 30 m (Hoshino et al., 2012). This root length allows the invader to regulate and tolerate extreme drought conditions (Desta et al., 2021). Besides, the high density of shallow roots could enhance the competitive ability of *P. juliflora* to extract the arid deserts limited nutrients and water resources (El-Keblawy and Abdelfatah, 2015). This could explain the high aggressive ability and how it could crowd out native vegetation in most invaded sites. It has been noticed that farmers in many places in the UAE just ruin their farms once they are invaded by this species.

In comparison with the root length of *P. juliflora*, the tap and the lateral of the native *P. cineraria* were estimated at 20 m and 1.5 m only, and its growth is relatively slow (Sandison et al., 1991; Kumar et al., 2011). Recently, Slates et al. (2020) estimated the lateral root length of *P. juliflora* at around 3.5 m from the tree trunk to the canopy edge in UAE, whereas the lateral length of the native *P. cineraria* could not be observed at the same distance. The lateral root of the *P. cineraria* could be less than 1 m. Furthermore, the fine root mass collected under the canopy of *P. juliflora* was 57 times greater under the canopy of the invader *P. juliflora* than that of the *P. cineraria* canopy. Moreover, litter depth was six to nine times more important under the canopies of the exotic *P. juliflora* compared to the native *P. cineraria.* On the other hand, Hussain et al. (2019) demonstrated that mesquite plants are both water use and photosynthetically efficient compared to *P. cineraria*. Therefore, such plant attributes associated with the *P. juliflora* tree can explain its higher dominance in the non-native range. Figures 4 and 5 show the greater competitive ability of the exotic *P. juliflora* that negatively affected the native *P. cineraria.*

Figure 4. The exotic *Prosopis juliflora* (dense green) is growing in great numbers under the canopy of the native *P. cineraria*

Figure 5. The dense thicket of the exotic *Prosopis juliflora* killed the native *P. cineraria* in many places of the UAE

Both intraspecific and interspecific competitions were reported in the *Prosopis* species. However, their ability to compete and to have adverse effects on the neighboring plants might depend on the type of interaction and the competing plants groups. The negative effects might be less when the competition occurs between the invader and the tree, and it may be more pronounced when the invader competes with the herbaceous species. Furthermore, the invader plant growth stage might strongly influence its veracity when competing with other species. Ansley et al. (1998) observed that *P. glandulosa* growth was limited while increasing the densities of associated plants under less environmental resources such as water. Contrary, Auken Van and Bush (1987) observed that the growth of *P. glandulosa* was greater than that of *Diospyros texana* when growing together in lower soil fertility. Besides, *P. glandulosa* was reported by Simmonsa et al. (2008) to have greater depressive impacts on the grass *Nassella leucotricha*. Corroborating findings were obtained by Chen et al. (1995) with *Heterodera glycines* and *Chenopodium album*. Similar statements were reported by Agami and Reddy (1990) in the *Eichhornia crassipes* and *Pistia stratiotes*.

Regrettably, the literature review seems to do not have sufficient experimental works on the competitiveness ability within the *Prosopis* species emphasizing the phylogenetic approach. Furthermore, very few publications assessed the intra- and inter-specific competition associated with the invader *P. juliflora* and other plants. Most of the observations were done in the field works where *P. juliflora* excludes the associated native species. The native *P. cineraria* is considered one of the highly valued trees in many arid and dry areas in the world (Kumar and Singh, 2009;

Gallacher and El-Keblawy, 2016; Al Ghais et al., 2020). Therefore, the competitive ability of *P. cineraria* and *Tecomella undulata* on *Vigna radiata* based on agroforestry systems in degraded lands of the Indian desert (Singh, 2009) showed that *P. cineraria* has significant positive effects on the growth and the yield of *Vigna radiata*.

4.4. Water use and photosynthesis efficiency of *Prosopis* species

Hydric stress is the predominant ecological condition that significantly impacts the desert plant physiology. Therefore, to overcome it, many desert plants, especially the true xerophytes, have adjusted their metabolism. Water stress has direct effects on the photosynthesis processes. Therefore, the combination of both water and heat stresses would significantly impact the plant performance. In fact, as the hottest places of the world receive more radiation than the other parts, therefore, heat stress can be considered another ecological issue that considerably influences the physiology of desert plants. Hence, many plants in these environments have strategically evolved to cope with heat and water stresses without damaging their photosynthetic apparatus. Accordingly, there are a variety of ways that plants survive in arid environments (Mulroy and Rundel, 1977). Among these, water use and photosynthesis efficiencies are considered major mechanisms involved in the adaptations of desert plants (Cui et al., 2017; Avila-Lovera et al., 2019; Hussain et al., 2019). Water use efficiency is referred to the fraction of carbon assimilation to water loss (Baldocchi, 1994; Malone et al., 2016; Zhu et al., 2020). Besides, photosynthesis efficiency refers to the amount of light energy plants convert into chemical energy through photosynthesis (Hussain et al., 2019). Light is considered one of the main factors affecting the photochemical reactions of photosynthesis in plants. In general, light intensities depend strongly on the periods of the days and the seasons. Therefore, in the natural environment, light intensity varies greatly and can exceed the tolerable range of plant physiology (Eppel et al., 2013). Accordingly, plants exposed to excessive light can be greatly damaged.

Alien invasive species have been presented to out-compete native plants (De Rouw, 1991; El-Keblawy and Al-Rawai, 2007; McAlpine et al., 2008; Aguilera et al., 2010; Kaur et al., 2012; Lucardi et al., 2014; VonBank et al., 2018; Ruwanza, 2020; Tsombou et al., 2021). Therefore, water use and photosynthesis efficiencies of invasive species could be significant than that of the native species. With this regard, the findings of comparative water use efficiency between invasive and native species at multiple scales reported by Molly et al. (2010), corroborated these observations. Additive findings of the work argued that water use of invasive plants is greater in the hottest places than the other regions of the world. Similar findings were highlighted by McAlpine et al. (2008) in the invasive species *Berberis darwinii* and the co-occurring native plants. In addition, it was pointed out by Stratton and Goldstein (2001) that both water use and photosynthesis efficiencies of the non-native *Schinus terebinthifolius* were greater than that of the native species.

Congeneric comparison between species can allow identifying the evolutionary traits that may help the non-native species to out-compete the native species. The earlier few studies done in this regard mostly concentrated on comparing the morphological attributes of the experimental plants with little focus on plant physiological attributes. Mesquite trees and the native *Prosopis cineraria* are present in UAE habitats. So, their occurrence in UAE regions could be a good opportunity to study their competitiveness capacity with the ascent of plant physiological attributes. In this respect, Hussain et al. (2019) assessed the water use efficiency in a native and two exotic *Prosopis* species. They showed that exotic *P. juliflora* and *P. pallida* plants water use efficiency was greater than that of the native *P. cineraria*. Hussain et al. (2020a) also pointed out that the photosynthesis efficiency of the exotic *Prosopis* invaders was better than that of the native *P. cineraria*. Furthermore, their findings revealed that the maximum photosynthetic efficiency and other physiological attributes were correlated with the canopy position. Similar trends were obtained by Chen et al. (2013) in the *Alternanthera* genus without taking into account the canopy position.

4.5. Root system of *Prosopis* species

The root system of each plant species has evolved depending on the environmental conditions. Therefore, the root system length and density can be key to understanding the changes associated with the plant environment. There is a proper correlation between root and shoot growth when the plant is exposed to normal conditions. In general, the ratio of roots to shoots is considered as the fraction of the weight of the roots to the weight of the above plant parts (Harris, 1992). Therefore, any significant changes occurring in the environment would strongly affect this ratio. With this scenario, the ratio of roots to shoots can constitute an important ecological indicator to understand and predict the changes that could occur in the environment. Plants found in the regions with extreme environmental conditions have considerably adjusted their ratio of the roots to shoots (Aphalo et al., 1999; Qi et al., 2019). It was reported by Qi et al. (2019) that plants usually allocate more biomass to the root than the shoot when exposed to environmental stresses such as soil poor in nutrients and dry soils.

The hottest places in the world are dry most of the year, and desert soil does not retain sufficient humidity even when the rains come. Consequently, desert plants have adapted to have deeper roots. Therefore, the length of the root and especially the tap root for the perennial desert plants should be correlated with the level of drought. Besides, competitive interactions in the desert ecosystem might positively affect this length. For example, the tap and the lateral roots of the exotic *P. juliflora* are estimated at 80 and 30 m, respectively (Canadell et al., 1996, Hoshino et al., 2012). However, the tap and the lateral roots of the native *P. cineraria* were reported to be around 20 m and 1.5 m only (Sandison et al., 1991; Kumar et al., 2011). Recent studies were done by Slate et al. (2020) in UAE reported that the lateral root of the invader *P. juliflora* was estimated at 3 m; these assessments were done from the trunk to the canopy edge. However, they did not find any lateral root at this length with *P. cineraria*, the native species. Furthermore, their studies also revealed that the fine root biomass under the canopies of *P. juliflora* was 57 times greater than the edge. However, the tap root length could not explain the competitive superiority of invasive plants over non-invasive ones. In this regard, *Acacia erioloba* and *Boscia albitrunca* are greater drought-resistant plants, and their tap root lengths were estimated at 60 and 68 m, respectively (Canadell et al., 1996). Nevertheless, they are not documented to be invasive plants, and according to Tshisikhawe and Malunga (2017), these two species are found in the protected areas of South Africa. Furthermore, Comparative studies done by Schachtschneider and February (2013) between the invasive *Prosopis glandulosa* and *P. velutina*, and native *Acacia erioloba* showed that native had shorter tap roots and are more water stressed than the exotic invasive *Prosopis* species.

4.6. Litter of *Prosopis* species

The different stages of plant growth are greatly impacted by the surrounding milieu. Among those factors, litter quality is considered as the main ecological element which directly and indirectly influences plant behavior and the neighboring environment. Since nutrients availability, soil moisture, soil temperature and light depend on the litter quality, therefore, this latter is considered as a vital component for the environment health (Facelli and Pickett, 1991; Muturi et al., 2017; Racheal and Olliff-Yang, 2019). Plant species can be characterized by its growth rate and therefore by its litter input. Plant growth rate depends strongly on its direct environment, so plant growing in the poorest milieus may have less production than those growing in the enriched habitats. Yet, plants growing in the poorest habitats may show less litter biomass than those growing in the favorable environment (Leon and Osorio, 2014; Bohara et al., 2019). Therefore, any expected or noticeable increasing in litter accumulation can significantly alter the dynamic of plants growing in those habitats.

Nowadays, alien invasive species are considered as the main cause of habitats degradation, and the costs associated to their management are importantly higher regionally and globally. Exotics invaders are mainly characterized by their faster growth, and such growth rate may be linked to the increase of resources acquisition from the environment (Montesinos, 2021). Therefore, alien invasive plants are documented to have very high water and nutrients use efficiencies than the non-invasive (Matzek, 2011; Hussain et al., 2020a) so, their growth rates are significantly higher (Chen et al., 2017) and may importantly impact on the produced biomass (Liu et al., 2019). Predictably, faster growth associated with species invasiveness would be led to important litter biomasses. It was reported by Slate et al. (2020) that litter accumulation under the canopies of mesquite tree was greater than that of the non-invasive *Prosopis cineraria*. This important amount of litter noticeable under the canopies of the invader *P. juliflora* can be considered as one of the key strategy used by mesquite trees to exclude the native species. Besides, litter deposition under the canopy of mesquite trees may contain important amount of secondary metabolites which could have depressive effects on the surrounding environment. In this context, Kaur et al. (2012) demonstrated that, litter of mesquite contained significantly amount of phenolic compounds than that of the non-invasive *Prosopis*. It was also pointed out by Tsombou et al. (2021) that, litters of mesquite trees had greater impacts on the both seeds germination and seedlings dry weight of *Amaranthus graecizans*, *Sisymbrium* and *Senecio flavus*. Analogical data were reported by Kim and Lee (2011) in the invasive species *Eupatorium rugosum*.

Congeneric studies within different genus of invasive plants have been done considering some important aspects and concepts associated with plants invasiveness (Kun et al., 2009). However, the literature review is relatively poor regarding the studies on invasive plants versus native plants addressing their litter biomasses and the different factors influencing the set-up process in the arid systems globally.

5. Mechanisms of allelochemicals

Allelochemicals are secondary metabolites produced by many living organisms, including algae, bacteria, coral, fungi, and certain plants (Bachheti et al., 2019). Regarding plants, allelochemicals mainly help plants interact with their surrounding environment. The secretion and of allelochemicals depend strongly on the types of interactions that plants would need to establish. Those chemicals may be secreted and released into the environment for cooperation, plant defense, or reproduction. Therefore, various groups of allelochemicals are synthesized within the plants and released in the plant environment depending on the plant-environment requirements.

In general, allelochemicals may have beneficial or detrimental effects on the surrounding environment. Globally, their effects range from stimulation to regulation and inhibition. Despite their high ecological importance, allelochemicals can cause significant damage to the surrounding organisms. At the plant level, many fundamental processes associated with plant growth and development may be importantly affected. Cheng and Cheng (2015) described different mechanisms underlying allelopathy (Table 1). At the cellular level, allelochemicals can negatively affect root cells, cell shape, and structure. They may induce nuclear abnormalities and significantly affect cell vacuolization processes. Besides, monoterpenoid allelochemicals significantly alter cell proliferation and DNA synthesis in plant meristem. Furthermore, allelochemicals can cause an imbalance in the antioxidant system, affect the permeability of cell membranes, negatively affect nucleic acid and protein metabolisms processes, and affect the balance of plant growth regulators. Moreover, allelochemicals can change soil properties, which in turn alter the soil microbial activities and quality (Table 1, Cheng and Cheng, 2015).

Table 1. Mechanisms underlying allelopathy (Cheng and Cheng, 2015)

Aspects affected by allelochemicals	Their effects at the plant level/surrounding environment
Cell structuralization	Some allelochemicals alter root cells and cell shape and structure. They may induce nuclear abnormalities and significantly affect cell vacuolization processes.
Negatively affect cell division processes	Monoterpenoid allelochemicals significantly alter cell proliferation and DNA synthesis in plant meristem.
Imbalance in the antioxidant system	Allelochemicals induce the production of reactive oxygen species in the plant.
Affect the permeability of cell membrane	The inhibition of antioxidant enzymes activities may alter the permeability of the cell membrane.
Negatively affect nucleic acid and protein metabolisms processes	Allelochemicals impact the DNA cleavage temperature. Some of them may alter the enzyme DNA polymerase, disrupting the different steps associated with DNA function.
Plant growth regulators	Allelochemicals may affect the balance of plant growth regulations, such as phytohormones.
Ecological environment	Changes in soil properties, which in turn alter the soil's microbial activities and quality.

6. Impacts of *Prosopis juliflora* invasion

6.1. On local floral or vegetation

Vegetation is considered as plant assemblage for a given area (Box and Kazue, 2013). Therefore, it integrates the different species and their population for the local flora, which differ genetically and historically (Maarel et al., 2014). Local climate plays a crucial role in the plant assembling and the types of vegetation. Locally, vegetation is strongly impacted by the topography, the seasons, and the edaphic properties. In addition to the local climate which shapes the vegetation, recently, invasive were reported as the key component of local habitats degradation. Today, many local habitats have been invaded and infested by invasive species.

In this regard, the introduction of *P. juliflora* in UAE and other arid parts of the world has led to the degradation of native diversity (Mwangi and Swallow, 2005; El-Keblawy and Al-Rawai, 2005; Kaur et al., 2012; Slate et al., 2020). According to the European and Mediterranean Plant Protection Organization (2018), *P. juliflora* was introduced into the Middle East in the 1950s and was probably introduced in UAE around the 1970s. Today, *P. juliflora* has been declared as an invasive species in UAE including many other regions of the world (Mwangi and Swallow, 2005; El-Keblawy and Al-Rawai, 2005). Its higher invasiveness capability is derived from its growth rate, reproduction rate, and lack of natural enemies (Van den Berg et al., 2013). At present, serval millions of land have been covered by the infestation of mesquite. For instance, one million hectares have been covered in Ethiopia (Zeray et al., 2017); 1.8 million in South Africa (Shackleton et al., 2015). Similarly, Kenya noticed an increment of land covered from 882 to 18.792 hectares between 1988-2016 (Mbaabu et al., 2019). Statically, there is no clear documentation about the total land cover by *P. juliflora* in UAE. However, the data on the invasion of *P. juliflora* using GIS (Geographic information System Mapping) addressed by (Isaa and Dohai, 2008) in two different sites in UAE (Filayah and Khut) confirmed the infestation of this species. Their findings showed that *P. juliflora* land coverage increased from 1.19 to 32.48 % for the Khut site during 19 years and 10.48 to 16.17 % for the Filayah site during 19 years (Figure 6).

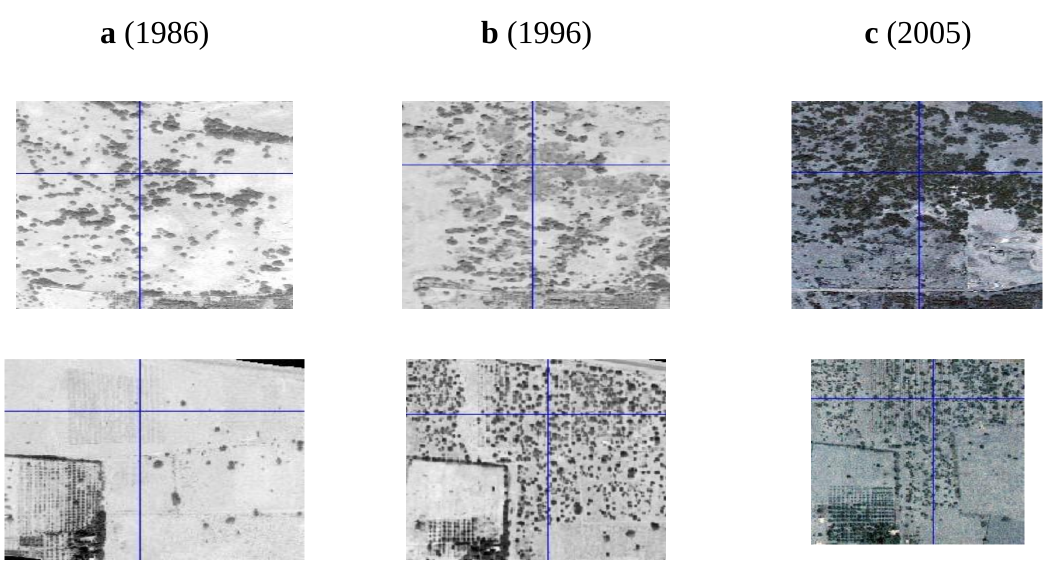

Figure 6. Time series of multi-temporal aerial photographs: **a** (1986), **b** (1996), **c** (2005); for Filayah (top) and Khut (bottom) (Isaa and Doahi, 2008).

Furthermore, El-Keblawy and Al-Rawai (2007) reported the depressive impacts of *P. juliflora* trees on the local species. Their findings showed that the depressive effects depended of the plant life forms. Additionally, the findings of congeneric studies obtained by El-Keblawy and Abdelfatah (2015) showed that *P. juliflora* plants have significant depressive effects on the native plant compared to the native *P. cineraria,* which positively affects the surrounding environment. According to the same authors, the depressive effect of *P. juliflora* was more prominent on the seed germination and annual species compared to the perennial. Moreover, recent work done by Slates et al. (2020) in UAE, showed a positive correlation between mesquite plants and agricultural weeds compared to non-agricultural weeds. Besides, low plant richness and densities for the non-weed were noticeably lower under the canopies of *P. cineraria* compared to the open places, but with no effect on the agricultural weed.

6.2. On the water table

Water table refers to underground water stored between soil spaces, or between soil fissures (Adams, 2016). Ecologically, underground water can be as considered a major factor influencing plant distribution on the terrestrial globe. The depth and the amount of such water may vary from point-to-point throughout the globe. Many local and external factors can significantly affect the quality and the amount of water table. Among those, droughts, seasonal rainfall, salts accumulation, fertilizers, and pesticides are the main factors affecting underground water (Moorhead, 2003). The effects of both drought and salts on the water table were reported by El-Mageed et al. (2018). Today, the depressive effects associated with plant invasiveness not only alter the different services of the ecosystem, but those effects can also be fully integrated into global warming processes. Phenotypic plasticity can be cited as one of the major key that enhances plants invasiveness potentialities. In fact, invasive plants have a high potential to adjust their metabolism as fast as possible, depending on the changes occurring in their habitats.

In general, plant morphology can be correlated with the plant capacity to use underground water and cope with stressful environmental conditions. Therefore, the volume of soil exploited by the roots of a tree will depend on the species, the size and age of the tree, and the soil type (Knight, 1999). In this regard, alien invasive plants have an important ratio of root to shoot compared to non-invasive plants; therefore, those plants attributes can allow them to alter the water table significantly. To illustrate this, the tap and the lateral roots of *P. juliflora* are estimated at 80 m (Canadell et al., 1996, Hoshino et al., 2012). Therefore, this greatly allows the invasive *P.*

juliflora plants to access underground (Desta et al., 2021). However, compared to the exotic *Prosopis*, the tap roots of the native *P. cineraria* are reported at around 20 m (Sandison et al., 1991; Kumar et al., 2011). Consequently, such root length associated with the native *Prosopis* may not allow it to have any negative impact on the water table. In Ethiopia Shiferaw et al. (2021) calculated water consumption associated with the invasiveness of *P. juliflora* using the Eddy covariance method, and estimated it at around 3.1 to 3.3 billion m^3 per year. Furthermore, water consumption of the same plant species in Northern Cape (South Africa) was estimated at 70 m^3/month, using the Penman–Monteith methodology. Corroborating findings were reported by Dzikiti et al. (2018) in South Africa, where the water consumption of *P. juliflora* plants was about 1.5 to 2.5 billion m^3 per year. Recently, Howari et al. (2022) calculated the water consumption of *P. juliflora* through remote sensing technology. They estimated the amount of water lost through evapotranspiration lose to about 22.22 million m^3/year in the three studied region (near Sharjah Airport, Umm Fannan, and Al Talla). However, the studied that was conducted on the native *P. cineraria* indicated that, its water consumption is very low. For example, Al Yamani et al. (2018) calculated the water consumption of two native trees (*P. cineraria* and *Ziziphus spina-christi*) in Abu Dhabi, UAE, and found very low water consumption (0.043 m3/day) for the two species. The overall results of Howari et al (2022) indicated that the groundwater depletion by *P. juliflora*, especially on sand dunes, will threaten the xerophytic scarce vegetation with the main focused on the native keystone *P. cineraria*. The high water consumption of *P. juliflora* necessitates more research about water use efficiency and photosynthetic rate. A comparison between the exotic invasive *P. juliflora* and the native *P. cineraria* in these important physiological functions is important to understand the causes of the successful invasion of the *P. juliflora*.

6.3. On soil quality

Biotic and abiotic components interact together to maintain the balance of ecosystem structure and functioning. Therefore, any noticeable alteration occurring in these two components of the soil ecosystem would strongly affect the expectable function of that ecosystem. For example, acidophiles microorganisms are efficient in the pH ranging from 3 to 4 (Sharma et al., 2016), while neutrophils show better growth in the pH 6 to 8, or neutral pH, and the alkaliphiles are more adapted in the pH values exceeding 9 (Preiss et al., 2015). Therefore, any change associated with the pH would significantly affect the ecology of these microorganisms that inhabit these environments. The change in the soil microbial community would affect the nutrient content and decomposition, affecting the types and abundance of the aboveground flora.

Globally, the historical taxonomy of soils greatly depends on the environmental factors that play an important function in their formation. United Arab Emirates (UAE) presents an alternation of the seasons, with the hottest in summer and the coolest in winter. Drought and salt content are the two main environmental factors controlling any fundamental processes in UAE, from soil-to-plants. Accordingly, Emirates soils are broadly diversified. Shahid and Abdelfatttah (2008) categorized the soils of UAE as sandy, sandy calcareous, saline, hardpan, etc. These soils structure, texture, and chemical properties strongly reflect local weathering processes. Both Higher drought and salt significantly alter the quality of soils. Effects of extreme climate on soil quality were reported by Anjali and Dhananjaya (2019). In addition to the effects of drought and salt on the soil quality, anthropological activities may considerably impact the soil ecosystem. To protect soil degradation and control desertification processes, several exotics plants were transported and introduced in many countries throughout the world and especially in arid systems. However, regrettably, some of those plants species have become a serious problem in their introduced range. In most cases, alien invasive plants have important growth rate with monoculture stands. Impacts of alien invasive plants on the soil quality were documented by Dassonville et al. (2008).

Invasive *Prosopis* species are well-known today to be an important cause of many habitats degradation globally (Shackleton et al., 2015; Wakie et al., 2016; Tadros et al., 2020; Slate et al., 2020). The infestation of mesquite plants has led to the alteration of the soils properties locally. Earlier studies assessed the impact of the invasive and native *Prosopis* species on the physiochemical properties of the soil of UAE (El-Keblawy and Al-Rawai. 2007; El-Keblawy and Abdelfatah, 2015). Analogical data were obtained by Oludare and Muoghahalu (2014) in *Tithonia diversifolia* (Hemlsy). Recent findings reported by Gemeda et al. (2021) demonstrated that the invasion associated with mesquite palnts increased the soil pH. According to the same authors, exchangeable cations, exchangeable sodium and water-soluble Ca, and other elements percentages decreased in the areas infested by *P. juliflora* compared to the non-infested places. Moreover, clay content in the stands of exotics *Prosopis* was importantly higher than the non-invaded lands. On other hand, Saadoun et al. (2014) reported the depressive effects of mesquite plants on the soil microbial activities in UAE. Consistent and analogical findings were addressed by Wang et al. (2015) in *Lantana camara*.

The growth of *P. juliflora* has been shown to improve soil physical and chemical properties in the UAE, which might positively affect the associated species (El-Keblawy and Abdelfatah, 2015). The canopies of *P. juliflora* increased the most important macro-nutrients, such as potassium, nitrogen and phosphorous, and the organic matter contents. The increase in organic content could increase the water holding capacity, improving soil texture and moisture (El-Keblawy and Abdelfatah, 2015). As the harmful and beneficial mechanisms of plant-plant interactions do not act in isolation from each other in nature, the relative importance of these two processes determines the structure of the plant community under and around the native and exotic trees (Callaway and Walker, 1997). In the case of *P. juliflora*, it seems that the allelopathic effect may override its facilitative effect and consequently result in an overall depressive effect on the associated flora. Phenolic compounds have been reported to present in high concentrations in *P. juliflora* (Inderjit et al. et al., 2008; Goel et al., 1989; Nakano et al., 2003), could reduce the water and nutrients uptake of the associated plants. For example, the net uptake of phosphorous, potassium, and water by cucumber seedlings was reduced by 57, 75, and 29%, respectively, when the whole root system was exposed to ferulic acid, an allelopathic phenolic acid. In addition, plant transpiration was reduced in a linear manner as the fraction of the cucumber roots in contact with ferulic acid increased (Lyu and Blum, 1990).

7. *Prosopis* species description

The genus *Prosopis* belongs to the *Fabaceae* family, including 44 species native to the Americas and Asia (Landeras et al., 2006).

7.1. *Prosopis juliflora (*Sw.) DC.

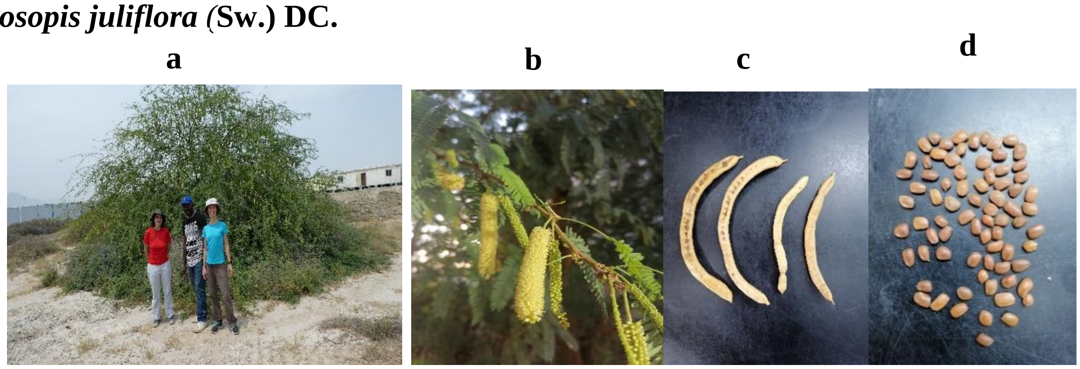

Figure 7: Adult plant (**a**), flowers (**b**), pods (**c**), and seeds (**d**) of *Prosopis juliflora*.

P. juliflora is well adapted to tolerate extreme environmental conditions. This species is native to the Americas and is habitually known as Mesquite (Tewari et al., 2013). It grows fast, can fix atmospheric nitrogen, and is an evergreen species. There are higher morphological, anatomical, and molecular variabilities observed in this species compared to the other species of the same genus. Both tap and lateral roots extremely differ from the other species of the same genus, and the species of other plant taxa. In most cases, the length is significantly higher than the other species of the same genus, and the surrounding plant species.

Burkart (1976) described *P. juliflora* to grow to about 15 m in height with many thorns observed in the above plant part; the thorn length is around 3 to 5 cm. Tree bark is a particularly thick and rough. In most cases, the tree of *P. juliflora* presents several stems with significant leaf organization variations. Mesquite shrubs has compound and paripinnate leaves with important variability in the number of pairs per compound leaf. Flowers are particularly attractive to the surrounding environment, ranging from 5 to 10 cm. Important variabilities also exist in the fruits of mesquite. Different fruit shapes were observed; fruits may be slightly straight or curved, and their color depends on their physiological maturity. The leaves are fully green at the early stage but turn yellowish when they mature. Fruit length varies significantly; it may range from 10 to 20 cm. Variability is also noticed in mesquite seeds; every fruit contains approximately 10 to 20 seeds with different shapes, and the seed length is about 2.5 to 7 mm (Figure 7).

7.2. *Prosopis cineraria* (L.) Druce

P. cineraria is native to the UAE region and other parts of Asia, and it is locally known as "Ghaf tree". Recently, *P. cineraria* was declared locally as a national tree in the UAE due to its higher cultural significance for the Emirati population. Compared to mesquite tree, this latter has a slower growth rate. Both tap and lateral roots lengths are relatively less compared to that of mesquite. It also has the ability to fix atmospheric nitrogen as its exotic congener, but its environmental conditions' tolerance is more than the invasive *Prosopis* species. This plant species grows to about 6.5 m height only. Contrary to *P. juliflora* tree, *P. cineraria* does not have several stems; it has a main trunk of about 30 cm. The crown is open from the lower part to the first branches with around 2 m height. Branches and sub-branches are thorny with around 5 mm thorn length. Its tree bark is thick with many fissures. The leaves are also compound and paripinnate. Each pod contains about 10 to 25 seeds with brownish color (Pasiecznik et al., 2004) (Figure 8).

A B C D

Figure 8: Plant (**A**)**,** flowers (**B**)**,** pods (**C**), and seeds (D) of *Prosopis cineraria*

8. Hypothesis

Exotics *Prosopis* species are a key factor with adverse impacts on the United Arab Emirates (UAE) biodiversity, water table, and human health. The main objective of introducing this species in UAE was to control the desertification process and stabilize the soil against natural erosion. Regrettably, they escaped the cultivation areas and invaded many natural habitats, displacing the native diversity. The exotics *Prosopis* invasion affects biodiversity and significantly impacts on the water table. Recently, it was associated with climate change. In addition to *P. juliflora*, *P. pallida* was also identified in UAE. So, invaders *P. juliflora*, *P. pallida,* and the native *P. cineraria* are co-occurring in the different habitats of UAE. However, the different *Prosopis* species affect the native flora, soils, and water table differently. Overall, *P. juliflora* is documented to be the worst one with greater depressive effects associated with its invasion. However, the other exotic invasive *P. pallida* has lower depressive impacts than *P. juliflora*. A harmonious association is observed between *P. cineraria* and the native diversity. Therefore, the occurrence of the three *Prosopis* species in UAE gives a chance to study and to understand how exotics *Prosopis* have evolved over the native *P. cineraria*.

Exotics *Prosopis* species are opportunist and strategic since they present exceptional adaptive evolutionary features that allow them to invade wide ranges of climates and soils. Furthermore, the exotic species have greater competitive ability than the native *P. cineraria*. So, we hypothesized that native plants growth and abundance under and around the canopies of the three *Prosopis* species depend on the competitive ability of each of the three species. Furthermore, it hypothesized that allelochemicals of the invasive *Prosopis* have higher detrimental effects on the associated flora, whereas the native *P. cineraria* has more facilitative or neutral effects. Moreover, the exotic *Prosopis* species are both heat and drought resistant than the native *P. cineraria.* Therefore, we hypothesize that the exotic *Prosopis* species have more water use and photosynthesis efficiencies than the native *P. cineraria*. These hypotheses are linked to the study overall objective.

In addition, the associated plants with *Prosopis* species are natives and non-natives (referred to as agricultural weeds). We hypothesized that exotic invasive *P. juliflora* encourages and accommodates more agricultural weeds, but the native *P. cineraria* facilitate the growth of the native flora. Besides, we also hypothesized that soil fertility under the canopies of the *Prosopis* species depends on the chemical composition of the leaves and shallow later roots under the canopy of the different species. Furthermore, we hypothesized that lateral root length, fine root biomass, and litter accumulated under the canopy are greater under the exotic *Prosopis* than in the native one. These hypotheses are linked to the first objective presented in the first chapter of this PhD Memory.

Allelopathy is a major key to the exotic *Prosopis* species success (El-Keblawy and Mahmoud, 2014; Tsombou et al., 2021). Allelopathic plants metabolize and release substances (i.e., allelochemicals) that might be beneficial or detrimental to their surrounding environment. Allelochemicals affect both soil quality, plant growth, and development, and their impacts might be correlated with the recipient plant stage. In most published allelopathic studies, the depressive effects of the allelochemicals were more pronounced on the seed germination than the plant growth. To test the congeneric approaches in explaining the role of allelopathy in the invasive process, we also hypothesized that the allelochemicals released from the exotic *Prosopis* species litters have more detrimental effects on the germination of associated species than litters of the native *P. cineraria* species. Besides, as most previous studies tested the allelopathy effects in Petri-dishes, we hypothesized that using potting soils would give more realistic results on the role of allelopathy in the invasion process than using Petri dishes. These hypotheses are linked to the second objective presented in the second chapter of this PhD Memory.

Water deficit, temperature, and light are the major environmental factors that limit desert plants growth and development. Therefore, many desert plants have strategically evolved to cope with these stressful environmental conditions. Invasive plants developed important evolutionary adaptive traits that enable them to tolerate high temperatures and drought in the hot arid environment of the UAE. Exotic *Prosopis* species are drought, heat and light resistant. So, we also hypothesized that alien *Prosopis* are more water use efficient than the native *P. cineraria*. This hypothesis is linked with the third objective presented in chapter three of this PhD Memory.

Plants convert the sunlight into chemical energy during the photosynthetic process, and some of the light energy is fixed and converted into chemical energy during photosynthesis. However, still, some cannot be fully utilized and might cause potential damage. This situation is more serious when plants grow under extreme environments, such as hyper-arid desert conditions. Therefore, plants have evolved photoprotective mechanisms to counteract the damaging effects of excess light in hyper-arid desert environments. We hypothesized that the invasive fast-growing *Prosopis* species utilize light more efficiently, i.e., reduce the damaging effect of high light radiation in hot deserts than the slow-growing native *P. cineraria*. This hypothesis is linked with the fourth objective presented in chapter four of this PhD Memory.

9. Objectives

An invasive plant is a species that is both non-native and able to establish in a wide range of environmental conditions, grow faster, and spread to the point of altering plant communities and ecosystems. The exotic *P. juliflora* is considered as the most dangerous invasive plant in UAE and other places worldwide. Its invasion affects the local diversity in addition to underground water, and more recently, *P. juliflora* invasion was considered as a key component of climate change. Invasive *P. juliflora*, *P. pallida*, and the native *P. cineraria* are co-occurring in UAE. The depressive impacts of the exotic *P. juliflora* are more pronounced than the other species of the same genus, especially the native *P. cineraria*. Therefore, the occurrence of exotic and native *P. cineraria* provides a good chance to evaluate the congeneric approach for understanding mechanisms for the higher detrimental effect of the exotic than native plants. This is especially important as none of the previous studies tested the impact of the exotic and native species on the associated native and non-native plants. Also, none of the previous studies assessed the impact of the allelochemicals of the exotic and native *Prosopis* in potting soils, which reflects the challenge facing seeds in natural environments. Furthermore, few studies assessed functional traits, such as water use and photosynthesis efficiency, of native and exotic plants under the hot hyper-arid deserts. Therefore, the overall aim of the current study was to quantify the impacts of native and exotic *Prosopis* species on native and non-native flora and soil properties, in addition, to assessing some functional traits of *Prosopis* species that help understand the invasive ability of *Prosopis* species in the hyper-arid desert of UAE.

The specific objectives of the study are to:

1. Make congeneric comparisons of the impacts of *P. juliflora* and its congener *P. cineraria* on aboveground diversity of weedy and non-weedy plants in the UAE
2. Elucidate allelopathy as a mechanism of invasion success of *P. juliflora* in its introduced ranges. This will be through assessing the impact of allelochemicals from the litters on germination of associated plants in conventional controlled conditions (i.e., in Petri-dishes in growth chambers) and challenging conditions (i.e., potting soils)
3. Assess the intrinsic water use efficiency of invasive and native *Prosopis* congeners
4. Assess the thermal energy dissipation, photosynthetic efficiency, carbon gain, and nitrogen partitioning in invasive and native *Prosopis* congeners

10. Importance of This Study for the United Arab Emirates (UAE)

UAE is commonly known to be among the hottest places in the world. UAE climate is mostly dry, with less than 100 mm overall average precipitation per year, and temperatures vary between very hot in summer and warm in winter. Therefore, species diversity and abundance are low in these environments. Besides the harsh climatic conditions in the UAE, the invasive *P. juliflora* adversely affects the native biodiversity of the UAE. It produces allelochemicals that significantly reduce diversity and abundance. The invasive *P. juliflora* has currently formed dense monocultures in some UAE areas. These dense plantations of *P. juliflora* resulted in deterioration of the biodiversity; most native plants under and around the canopy of the *P. juliflora* are killed. Among those affected plants is the native *P. cineraria*. Therefore, understanding the mechanisms of *P. juliflora* invasion would help control this invasive species. Besides, defining some native plants that might be adapted to grow in the allelochemicals produced by *P. juliflora* would help in using plants of this species in the reclamation of lands ruined by this species.

Among the other serious impacts of the invasion of *P. juliflora* are great amounts of pollen grains that cause allergies to sensitive people. *Prosopis juliflora* flowers in two periods: from November to January and March to June. The length of the flowering period and the amount of pollen generated per reproduction time associated with this invasive plant are higher than that of the local species. Therefore, the reproduction rate and the sizable pollen mass can greatly increase the risk of some sickness or allergies. It has been reported that the airborne pollens of this species can be inhaled through the nose and/or mouth, resulting in sensitization of susceptible people and subsequent elicitation of symptoms of respiratory allergic diseases. For example, it was estimated that 45% of the test patients in the UAE were sensitive to the pollens of *Prosopis* (Bener et al., 2002). Therefore, understanding the biology and ecology of the invasive *Prosopis* species could help control this species, reducing the risk associated with animal and human health.

In addition, many farms have been invaded by *P. juliflora* and already ruined. Furthermore, the very deep roots system of *P. juliflora* extracts the precious limited water resources in the UAE. Therefore, it is very important to understand the possible mechanisms enabling *P. juliflora* to invade different habitats in the UAE. This would help propose a proper management plan for *P. juliflora* populations in the UAE.

The study would help us to understand why some exotic invasive species form mono-dominant communities in introduced ranges and disproportionately suppress local plant species. We will gain knowledge on drivers of the invasion success of exotic species. The results would also allow us to evaluate the future probabilistic competitiveness of *P. juliflora* and its success or failure under altered hydrologic regimes due to over withdrawal of groundwater and climate change and to evaluate *P. juliflora* future projections. More specifically, results will allow us to establish a relationship between *P. juliflora* and hydrological variables to determine.

11. Structure of PhD Memory

This PhD Memory is structured in four chapters which correspond to the four articles published in scientific journals included in the ISI web knowledge. Below are the names of the co-authors, the titles of the publication, the reference of the journal, the DOI and a brief summary in English and Spanish.

Chapter 1: Slate, M., Tsombou, F. M., Callaway, R. M., Inderjit, El-Keblawy, A. A., 2020. Exotic *Prosopis juliflora* suppresses understory diversity and promotes agricultural weeds more than a native congener. Plant Ecology 221, 659-669. https://doi.org./10.1007/s11258-020-01040-1

Exotic invasive plant species alter ecosystems and locally extirpate native species, and by doing so alter community structure. Changes in community structure may be particularly important if invaders promote species with certain traits. For example, the positive effects of most invaders on soil fertility may promote species with weedy traits, whether native or not. We examined the effects of two co-occurring *Prosopis* congeners, the native *P. cineraria* and the exotic *P. juliflora*, on species identified as “agricultural weeds” and species that were not agricultural weeds in the United Arab Emirates. When compared to plots in the open, *P. cineraria* canopies were associated with lower richness and density of non-weeds while having no impact on agricultural weed species. In contrast, there was lower richness and densities of non-weeds under canopies of *P. juliflora*, but higher densities of agricultural weeds than in the open surrounding the canopies. These patterns associated with *Prosopis* congeners and understory plant community composition might be due to the much higher litter decomposition, if litter is inhibitory, and shallow root biomass under *P. juliflora*, or the different soil properties that corresponded with the two *Prosopis* canopies. In general, soils contained more nitrogen under *P. juliflora* than *P. cineraria*, and both understories were more fertile than soil in the open. Our results suggest that evolutionary history may play a role in how exotic invasive species may select for some traits over others in plant communities, with an exotic invader potentially creating reservoirs of agricultural weeds.

Las especies exóticas de plantas invasoras alteran los ecosistemas y desplazan las especies nativas locales y, al hacerlo, alteran la estructura de la comunidad evegetal. Los cambios en la estructura de la comunidad pueden ser particularmente importantes si las especies invasoras promueven especies con ciertos caracteres espcificos. Por ejemplo, los efectos positivos de la mayoría de los invasores sobre la fertilidad del suelo pueden promover especies de malezas, ya sean nativas o no. Examinamos los efectos de dos congéneres de Prosopis concurrentes, la nativa P. cineraria y la exótica P. juliflora, en especies identificadas como "malezas agrícolas" y especies que no son malezas agrícolas en los Emiratos Árabes Unidos. En comparación con las parcelas sin cobertura de ambas especies, el dosel de los árboles de P. cineraria se asocia con una menor riqueza y densidad de no malezas sin afectar a las especies de malezas agrícolas. En contraste, hubo menor riqueza y densidad de no malezas debajo del dosel de P. juliflora, pero mayores densidades de malezas agrícolas que en parcelas sin cobertura. Estos patrones asociados con los congéneres de Prosopis y la composición de la comunidad de plantas bajo sus doseles podrían deberse a la una mayor descomposición de la hojarasca, si la hojarasca es inhibidora, y a la biomasa de raíces poco profundas bajo P. juliflora, o a las diferentes propiedades del suelo bajo los dos doseles de Prosopis. En general, los suelos contenían más nitrógeno bajo P. juliflora que bajo P. cineraria, y ambos suelos eran más fértiles que el suelo de las parcelas sin cobertura. Nuestros resultados sugieren que la historia evolutiva puede desempeñar un papel en cómo las especies invasoras exóticas pueden seleccionar algunos caracteres sobre otros en las *comunidades de plantas y con una invasora exótica podría promover reservorios de malezas agrícolas.*

Chapter 2: Tsombou, F. M., El-Keblawy, A. A., Elsheikh, E. A., AbuQamar, S. F., El-Tarabily, K. A., 2022. Allelopathic effects of native and exotic *Prosopis* congeners in Petri dishes and potting soils: assessment of the congeneric approach. Botany 100 (3), 329-339. https://doi.org/10.1139/cjb-2021-0064

The congeneric approach assesses the relative role of exotic invasive plants compared to native plants on associated species. However, most studies on seed germination have been conducted in Petri dishes that do not reflect natural soil conditions. Here, we compared the effects of different litter extracts of the exotics *Prosopis juliflora* (Sw.) DC. and *P. pallida* (Willd.) Kunth, as well as native *P. cineraria* (L.) Druce, on seed germination and seedling dry weight of two weedy plants (*Amaranthus graecizans* L. and *Sisymbrium irio* L.) and the native *Senecio flavus* (Decne.) Sch.Bip. in both Petri dishes and potted soil experiments. The results indicate that non-treated seeds (control) of the three species attained more than 95% germination in the Petri dishes (*in vitro*). The increase in the litter concentrations of both invasive *Prosopis* species inhibited the native *Senecio flavus* germination and significantly reduced germination and seedling weight of the weedy *A. graecizans* and *S. irio*. Nevertheless, the native P. cineraria extracts had significant depressive effects on seed germination and seedling growth of the native *Senecio flavus* but limited effects on the weedy *A. graecizans* and *S. irio*. The results support a greater impact of exotic than native congener on native plants. To better assess allelopathic effects, it is recommended to not rely on germination in Petri dishes.

El enfoque congenérico evalúa la función de las plantas invasoras exóticas en comparación con las plantas nativas en las especies asociadas a ellas. La mayoría de los estudios sobre la germinación de semillas se han realizado en placas de Petri las cuales no reflejan las condiciones naturales del suelo. En este estudio, comparamos los efectos de diferentes extractos de hojarasca de las especies exóticas Prosopis juliflora (Sw.) DC. y P. pallida (Willd.) Kunth, así como la nativa P. cineraria (L.) Druce, sobre la germinación de semillas y el peso seco de las plántulas de dos malezas (Amaranthus graecizans L. y Sisymbrium irio L.) y la nativa Senecio flavus (Decne.) Sch. Bip. tanto en placas de Petri como en experimentos con tierra en macetas. Los resultados indican que las semillas no tratadas (control) de las tres especies alcanzaron más *del 95% de germinación en las cajas de Petri (in vitro). El aumento en las concentraciones de hojarasca de ambas especies invasoras de Prosopis inhibió la germinación de la nativa S. flavus y redujo significativamente la germinación y el peso de las plántulas de las malas hierbas A. graecizans y S. irio. Sin embargo, los extractos de la nativa P. cineraria tuvieron efectos depresores significativos sobre la germinación de semillas y el crecimiento de plántulas de S. flavus, pero efectos limitados sobre las malezas A. graecizans y S. irio. Los resultados respaldan un mayor impacto de los congéneres exóticos respect a los nativos en las plantas nativas. Para evaluar mejor los efectos alelopáticos, se recomienda no depender de la germinación en placas de Petri.*

Chapter 3: Hussain, M. I., El-Keblawy, A. A. and Tsombou, F. M., 2019. Leaf age, canopy position, and habitat affect the carbon isotope discrimination and water-use efficiency in three C_3 leguminous *Prosopis* species from a hyper-arid climate. Plant 8 (10), 1-11. https://doi.org/10.3390/plants8100402

The present study involved measurements of the stable carbon isotope composition ($\delta^{13}C$) and intrinsic water-use efficiency (iWUE) of three C_3 leguminous (*Prospis juliflora*, *P. cineraria*, and *P. pallida*) foliage at different canopy positions (east and west) from saline (SLH) and non-saline habitats (NSH). Integrated measurements of the stable carbon isotope composition ($\delta^{13}C$) of plant tissue were broadly used to study iWUE, taking into consideration the effect of leaf age and canopy position on C isotope discrimination. Mature foliage of *P. pallida* from an SLH with a west canopy position had significantly higher $\delta^{13}C$ (less negative) than that from NSH. On the west side, $\Delta^{13}C$ values ranged from 17.8% (*P. pallida*) to 22.31% (*P. juliflora*) for a west canopy position, while they varied from 18.05% (*P. pallida*) to 22.4% (*P. cineraria*) on the east canopy side. Because the patterns are similar for the three *Prosopis* species, the difference in carbon isotope discrimination ($\Delta^{13}C$) between the canopy position (west and east) is relatively consistent among species and sites, ranging between 17.8 ± 4.43% for the young foliage in the west and 18.05 ± 4.35% for the east canopy position. The iWUE of *P. pallida* was twice that of *P. cineraria*. The iWUE of *P. juliflora* was higher from NSH than SLH. Mature leaves possessed a higher iWUE than the young leaves. We concluded that exotic *P. juliflora* and *P. pallida* have higher iWUE values than the native *P. cineraria*, which might be due to the rapid below-ground development of plant roots in the Arabian deserts of the United Arab Emirates (UAE). This could enable the alien species access to deeper humid soil layers or water resources.

El presente estudio se basa en mediciones de la composición de isótopos de carbono estables (δ13C) y la eficiencia intrínseca del uso del agua (iWUE) de tres leguminosas C3 (Prosopis juliflora, P. cineraria y P. pallida) hojas en diferentes posiciones del dosel (este y oeste) de hábitats salinos (SLH) y no salinos (NSH). Las mediciones integradas de la composición de isótopos de carbono estables (δ13C) del tejido vegetal se utilizaron ampliamente para estudiar iWUE, teniendo en cuenta el efecto de la edad de la hoja y la posición del dosel en la discriminación de isótopos de C. Las hojas maduras de P. pallida de un SLH con una posición de dosel occidental tienen un δ13C significativamente mayor (menos negativo) que el de NSH. En el lado oeste, los valores de Δ13C oscilaron entre 17,8 % (P. pallida) y 22,31 % (P. juliflora) para una posición de dosel occidental, mientras que variaron entre 18,05 % (P. pallida) y 22,4 % (P. cineraria) en el lado este del dosel. Debido a que los patrones son similares para las tres especies de Prosopis, la diferencia en la discriminación de isótopos de carbono (Δ13C) entre la posición del dosel (oeste y este) es relativamente consistente entre especies y sitios, variando entre 17.8 ± 4.43% para las hojas jovenes en el oeste y 18,05 ± 4,35% para la posición este del dosel. La iWUE de P. pallida fue el doble que la de P. cineraria. El iWUE de P. juliflora fue mayor en NSH que en SLH. Las hojas maduras poseen una mayor iWUE que las hojas jóvenes. Concluimos que las exóticas P. juliflora y P. pallida tienen valores de iWUE más altos que la nativa P. cineraria, lo que podría deberse al rápido desarrollo subterráneo de las raíces de las plantas en los desiertos árabes de los Emiratos Árabes Unidos (EAU). Esto podría permitir que las especies exóticas accedan a capas de suelo húmedo más profundas o a más recursos hídricos.

Chapter 4: Hussain, M. I., Tsombou, F. M. and El-Keblawy, A. A., 2020. Surface canopy position determines the photosystem II photochemistry in invasive and native *Prosopis* congeners at Sharjah desert, UAE. Forests 11 (7), 1.20. https://doi.org/10.3390/f11070740

Plants have evolved photoprotective mechanisms in order to counteract the damaging effects of excess light in hyper-arid desert environments. We evaluated the impact of surface canopy positions on the photosynthetic adjustments and chlorophyll fluorescence attributes (photosystem II photochemistry, quantum yield, fluorescence quenching, and photon energy dissipation), leaf biomass and nutrient content of sun-exposed leaves at the south east (SE canopy position) and shaded-leaves at the north west (NW canopy position) in the invasive *Prosopis juliflora* and native *P. cineraria* in the extreme environment (hyper-arid desert area, United Arab Emirates (UAE)). The main aim of this research was to study the photoprotection mechanism in invasive and native *Prosopis* congeners via the safe removal—as thermal energy—of excess solar energy absorbed by the light collecting system, which counteracts the formation of reactive oxygen species. Maximum photosynthetic efficiency (F_v/F_m) from dark-adapted leaves in *P. juliflora* and *P. cineraria* was higher on NW than SE canopy position while insignificant difference was observed within the two *Prosopis* congeners. Greater quantum yield was observed in *P. juliflora* than *P. cineraria* on the NW canopy position than SE. With the change of canopy positions from NW to SE, the reduction of the PSII reaction center activity in the leaves of both *Prosopis* congeners was accelerated. On the SE canopy position, a significant decline in the electron transport rate (ETR) of in the leaves of both *Prosopis* congeners occurred, which might be due to the blockage of electron transfer from *Q*A to *Q*B on the PSII acceptor side. On the SE canopy position; *Prosopis* leaves dissipated excess light energy by increasing non-photochemical quenching (NPQ). However, in *P. cineraria*, the protective ability of NPQ decreased, which led to the accumulation of excess excitation energy (1 − qP)/NPQ and the aggravation of photoinhibition. The results also explain the role of different physiological attributes contributing to invasiveness of *P. juliflora* and to evaluate its liaison between plasticity of these characters and invasiveness.

Las plantas han desarrollado mecanismos fotoprotectores para contrarrestar los efectos dañinos del exceso de luz en ambientes desérticos hiperáridos. Evaluamos el impacto de las posiciones de la superficie del dosel sobre los ajustes fotosintéticos y los atributos de fluorescencia de la clorofila (fotoquímica del fotosistema II, rendimiento cuántico, extinción de la fluorescencia y disipación de energía fotónica), la biomasa de las hojas y el contenido de nutrientes de las hojas expuestas al sol en el sureste (dosel SE) y hojas sombreadas en el noroeste (dosel NW) en la invasora Prosopis juliflora y la nativa P. cineraria en el ambiente extremo (área desértica hiperárida, Emiratos Árabes Unidos (EAU)). El objetivo principal de esta investigación fue estudiar el mecanismo de fotoprotección en congéneres de Prosopis invasoras y nativas a través de la eliminación segura, como energía térmica, del exceso de energía solar absorbida por el sistema de obtención de luz, que contrarresta la formación de especies reactivas de oxígeno. La eficiencia fotosintética máxima (Fv/Fm) de las hojas adaptadas a la oscuridad en P. juliflora y P. cineraria fue mayor en la posición del dosel NW que en la SE, mientras que se observó una diferencia insignificante dentro de los dos congéneres de Prosopis. Se observó un mayor rendimiento cuántico en P. juliflora que en P. cineraria en la posición de dosel NW que en SE.

Con el cambio de posición del dosel de NW a SE, se aceleró la reducción de la actividad del centro de reacción PSII en las hojas de ambos congéneres de Prosopis. En la posición del dosel SE, ocurrió una disminución significativa en la tasa de transporte de electrones (ETR) en las hojas de ambos congéneres, lo que podría deberse al bloqueo de la transferencia de electrones de QA a QB en el lado del aceptor de PSII. En la posición SE; Las hojas de Prosopis disiparon el exceso de energía luminosa al aumentar el enfriamiento no fotoquímico (NPQ). Sin embargo, en P. cineraria, la capacidad protectora de NPQ disminuyó, lo que condujo a la acumulación de un exceso de energía de excitación (1 − qP)/NPQ y al agravamiento de la fotoinhibición. Los resultados también explican el papel de diferentes atributos fisiológicos que contribuyen a la invasividad de P. juliflora y evalúan el vínculo entre la plasticidad de estos caracteres y la invasividad.

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CONCLUSIONS

CONCLUSIONS

1. Congeneric studies comparing the effects of the invasive *Prosopis juliflora* and the native *P. cineraria* on (1) richness and density of the agricultural and non-agricultural weeds and on (2) soil properties under their canopies shown that:

    (1) *P. juliflora* promotes agricultural weeds and strongly suppresses the non-agriculturals. The opposite trends were found under the canopies of the native *P. cineraria.*

    (2) The densityand richness of the non-agricultural weeds were greater at the margins of *P. cineraria*, but not underneath the canopies.

    (3) These effects might be due to the inhibitory of the decompose litter and the higher density of root biomass under *P. juliflora* compared with *P. cineraria.*

    (4) Soil fertility beneath the two species was higher compared to the open areas. In general, soils contained more nitrogen under *P. juliflora* than under *P. cineraria.*

1. Estudios congenéricos que compararon los efectos de la invasora Prosopis juliflora y la nativa P. cineraria en (1) la riqueza y densidad de las malas hierbas agrícolas y no agrícolas y en (2) las propiedades del suelo debajo de sus copas demostraron que:

(1) P. juliflora promueve las malas hierbas agrícolas y suprime fuertemente las no agrícolas. Las tendencias opuestas se encontraron bajo las copas de los árboles nativos de P. cineraria.

(2) La densidad y riqueza de malas hierbas no agrícolas fue mayor en los márgenes de las copas de P. cineraria.

(3) Estos efectos podrían deberse a la inhibición ejercida por la descomposición de la hojarasca y a la mayor densidad de biomasa de raíces bajo P. juliflora en comparación con P. cineraria.

(4) La fertilidad del suelo debajo de las dos especies fue mayor en comparación con áreas abiertas. En general, los suelos contenían más nitrógeno bajo P. juliflora que bajo P. cineraria.

2. Congeneric studies used to asses the allelochemical effects of the invasive *P. juliflora* and *P. pallida* and the native *P. cineraria* on seed germination and seedling of weedy *Amaranthus graecizans* and *Sisymbrium irio* and the native *Senecio flavus* shows that:

(1) The invasive *Prosopis* reduce seed germination and seedling growth on the weedy and native species.

(2) The native *P. cineraria* had significant depressive effects in native species and limited in the weedy.

2. Estudios congenéricos utilizados para evaluar los efectos aleloquímicos de las invasoras P. juliflora y P. pallida y la nativa P. cineraria en la germinación de semillas y plántulas de las hierbas Amaranthus graecizans y Sisymbrium irio y la especie nativa Senecio flavus muestran que:

(1) Las especies invasoras de Prosopis reducen la germinación de las semillas y el crecimiento de las plántulas en las hierbas y en las especies nativas.

(2) La P. cineraria nativa tuvo efectos depresivos significativos en las especies nativas y limitados en las hierbas.

3. Congeneric studies comparing the intrinsic water use (iWUE) and the photosynthesis efficiency of the invasive *P. juliflora* and *P. pallida* and the native *P. cinerari* indicated that:

(1) Invasive *Prosopis* have higher iWUE values than the native *P. cineraria*, possibly due to the rapid below-ground development of invasive species roots in dry deserts. This could enable the invasive species to access deeper humid soil or water resources.

(2) The invasive *P. juliflora* maintains a slight lower but stable photosynthetic efficiency than the native *P. cineraria*, indicating that trait could not be held responsible for driving the inavasive success of *P. juliflora*.

(3) The non-photochemical fluorescence quenching value was higher in *P. juliflora* than in *P. cineraria*, indicating that the high accumulation of excess excitation energy in *P. cineraria* exacerbates the photoinhibition effects.

2. *Estudios congenéricos que compararon el uso intrínseco del agua (iWUE) y la eficiencia de la fotosíntesis de las invasoras P. juliflora y P. pallida y la nativa P. cinerari indicaron que:*

   (1) Las especies invasoras de Prosopis tienen valores de iWUE más elevados que la nativa P. cineraria, posiblemente debido al rápido desarrollo subterráneo de las raíces de las especies invasoras en los desiertos secos. Esto podría permitir que las especies invasoras accedan a suelos húmedos más profundos o a recursos hídricos.

   (2) La invasora P. juliflora mantiene una eficiencia fotosintética ligeramente más baja, pero estable que la nativa P. cineraria, lo que indica que este caracter no puede ser considerado responsable de impulsar el éxito invasivo de P. juliflora.

   (3) El valor de extinción de la fluorescencia no fotoquímica fue mayor en P. juliflora que en P. cineraria, lo que indica que la alta acumulación del exceso de energía de excitación en P. cineraria exacerba los efectos de fotoinhibición.

CHAPTER 1

Plant Ecol
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Exotic *Prosopis juliflora* suppresses understory diversity and promotes agricultural weeds more than a native congener

Mandy L. Slate · François Mitterand Tsombou · Ragan M. Callaway · Inderjit · Ali A. El-Keblawy

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Abstract Exotic invasive plant species alter ecosystems and locally extirpate native plant species, and by doing so alter community structure. Changes in community structure may be particularly important if invaders promote species with certain traits. For example, the positive effects of most invaders on soil fertility may promote species with weedy traits, whether native or not. We examined the effects of two co-occurring *Prosopis* congeners, the native *P. cineraria* and the exotic invader *P. juliflora*, on species identified as "agricultural weeds" and species that were not agricultural weeds in the United Arab Emirates. When compared to plots in the open, *P. cineraria* canopies were associated with lower richness and density of non-weeds while having no impact on agricultural weed species. In contrast, there was lower richness and densities of non-weeds under canopies of *P. juliflora*, but higher densities of agricultural weeds than in the open surrounding the canopies. These patterns associated with *Prosopis* congeners and understory plant community composition might be due to the much higher litter deposition, if litter is inhibitory, and shallow root biomass under *P. juliflora*, or the different soil properties that corresponded with the two *Prosopis* canopies. In general, soils contained more nitrogen under *P.*

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ARTICLE

Allelopathic effects of native and exotic *Prosopis* congeners in Petri dishes and potting soils: assessment of the congeneric approach

François Mitterand Tsombou, Ali El-Keblawy, Elsiddig A.E. Elsheikh, Synan F. AbuQamar, and Khaled A. El-Tarabily

Abstract: The congeneric approach assesses the relative role of exotic invasive plants compared to native plants on associated species. However, most studies on seed germination have been conducted in Petri dishes that do not reflect natural soil conditions. Here, we compared the effects of different litter extracts of the exotics *Prosopis juliflora* (Sw.) DC. and *Prosopis pallida* (Willd.) Kunth, as well as native *Prosopis cineraria* (L.) Druce, on seed germination and seedling dry weight of two weedy plants (*Amaranthus graecizans* L. and *Sisymbrium irio* L.) and the native *Senecio flavus* (Decne.) Sch.Bip. in both Petri dishes and potted soil experiments. The results indicate that non-treated seeds (control) of the three species attained more than 95% germination in the Petri dishes (in vitro). The increase in the litter concentrations of both invasive *Prosopis* species inhibited the native *Senecio flavus* germination and significantly reduced germination and seedling weight of the weedy *A. graecizans* and *Sisymbrium irio*. Nevertheless, the native *P. cineraria* extracts had significant depressive effects on seed germination and seedling growth of the native *Senecio flavus* but limited effects on the weedy *A. graecizans* and *Sisymbrium irio*. The results support a greater impact of exotic than native congener on native plants. To better assess allelopathic effects, it is recommended to not rely on germination in Petri dishes.

Key words: allelopathy, congeneric approach, exotic plants, germination, invasive species, *Prosopis* species.

Résumé : L'approche congénérique évalue le rôle relatif des plantes exotiques envahissantes comparativement aux plantes indigènes sur les espèces associées. Cependant, la plupart des études sur la germination des graines ont été réalisées dans des boîtes de Petri qui ne reflètent pas les conditions naturelles du sol. Ici, les auteurs ont comparé les effets de différents extraits de litière des espèces exotiques *Prosopis juliflora* (Sw.) DC. et *Prosopis pallida* (Willd.) Kunth et de l'espèce indigène *Prosopis cineraria* (L.) Druce sur la germination des graines et le poids sec des semis de deux espèces adventices (*Amaranthus graecizans* L. et *Sisymbrium irio* L.) et de l'espèce indigène *Senecio flavus* (Decne.) Sch.Bip. lors d'expériences en boîtes de Petri et de sol en pot. Les résultats indiquent que les graines non traitées (contrôle) des trois espèces atteignaient plus de 95 % de germination dans les boîtes de Petri (in vitro). L'augmentation des concentrations de litière des deux espèces envahissantes de *Prosopis* inhibait la germination de *Senecio flavus* indigène et réduisait de manière significative la germination et le poids des semis des espèces adventices *A. graecizans* et *Sisymbrium irio*. Néanmoins, les extraits de *P. cineraria* indigène exerçaient des effets dépressifs significatifs sur la germination des graines et la croissance des semis de *Senecio flavus* indigène, mais des effets limités sur les espèces adventices *A. graecizans* et *Sisymbrium irio*. Les résultats confirment un impact plus important des congénères exotiques que des congénères indigènes sur les plantes indigènes. Il est recommandé de ne pas se fier principalement à la germination dans des boîtes de Petri pour évaluer les effets allélopathiques. [Traduit par la Rédaction]

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CHAPTER 3

plants

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Article

Leaf Age, Canopy Position, and Habitat Affect the Carbon Isotope Discrimination and Water-Use Efficiency in Three C_3 Leguminous *Prosopis* Species from a Hyper-Arid Climate

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Abstract: The present study involved measurements of the stable carbon isotope composition ($\delta^{13}C$) and intrinsic water-use efficiency (iWUE) of three C_3 leguminous *Prosopis* spp. (*P. juliflora*, *P. cineraria*, and *P. pallida*) foliage at different canopy positions (east and west) from saline (SLH) and non-saline habitats (NSH). Integrated measurements of the stable carbon isotope composition ($\delta^{13}C$) of plant tissue were broadly used to study iWUE, taking into consideration the effect of leaf age and canopy position on C isotope discrimination. Mature foliage of *P. pallida* from an SLH with a west canopy position had significantly higher $\delta^{13}C$ (less negative) than that from NSH. On the west side, $\Delta^{13}C$ values ranged from 17.8‰ (*P. pallida*) to 22.31‰ (*P. juliflora*) for a west canopy position, while they varied from 18.05‰ (*P. pallida*) to 22.4‰ (*P. cineraria*) on the east canopy side. Because the patterns are similar for the three *Prosopis* species, the difference in carbon isotope discrimination ($\Delta^{13}C$) between the canopy position (west and east) is relatively consistent among species and sites, ranging between 17.8 ± 4.43‰ for the young foliage in the west and 18.05 ± 4.35‰ for the east canopy position. The iWUE of *P. pallida* was twice that of *P. cineraria*. The iWUE of *P. juliflora* was higher from NSH than SLH. Mature leaves possessed a higher iWUE than the young leaves. We concluded that exotic *P. juliflora* and *P. pallida* have higher iWUE values than the native *P. cineraria*, which might be due to the rapid below-ground development of plant roots in the Arabian deserts of the United Arab Emirates (UAE). This could enable the alien species access to deeper humid soil layers or water resources.

Keywords: carbon isotope composition; leaf C; leaf N; intrinsic water-use efficiency; canopy position; leaf age

1. Introduction

The element carbon possesses three naturally occurring isotopes: ^{12}C, ^{13}C, and ^{14}C. Usually, the focus is on the first two carbon forms, which are stable isotopes (^{12}C and ^{13}C), because they are differently fractionated by photosynthetic pathways. A difference in isotope assimilation into the plant structure is mainly attributed to a difference in the diffusion rates of $^{12}CO_2$ and $^{13}CO_2$ during the photosynthetic assimilation of CO_2, in conjunction with carboxylation enzyme preference for one isotopic form of carbon dioxide over another [1]. Photosynthetic assimilations of CO_2 and carboxylation enzyme preference are dependent upon the photosynthetic mechanisms that each plant uses—either C_3 or C_4 in this case. In regards to C_3 plants, Rubisco enzymes demonstrate

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CHAPTER 4

forests

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Article

Surface Canopy Position Determines the Photosystem II Photochemistry in Invasive and Native *Prosopis* Congeners at Sharjah Desert, UAE

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Abstract: Plants have evolved photoprotective mechanisms in order to counteract the damaging effects of excess light in hyper-arid desert environments. We evaluated the impact of surface canopy positions on the photosynthetic adjustments and chlorophyll fluorescence attributes (photosystem II photochemistry, quantum yield, fluorescence quenching, and photon energy dissipation), leaf biomass and nutrient content of sun-exposed leaves at the south east (SE canopy position) and shaded-leaves at the north west (NW canopy position) in the invasive *Prosopis juliflora* and native *Prosopis cineraria* in the extreme environment (hyper-arid desert area, United Arab Emirates (UAE)). The main aim of this research was to study the photoprotection mechanism in invasive and native *Prosopis congeners* via the safe removal—as thermal energy—of excess solar energy absorbed by the light collecting system, which counteracts the formation of reactive oxygen species. Maximum photosynthetic efficiency (F_v/F_m) from dark-adapted leaves in *P. juliflora* and *P. cineraria* was higher on NW than SE canopy position while insignificant difference was observed within the two *Prosopis* congeners. Greater quantum yield was observed in *P. juliflora* than *P. cineraria* on the NW canopy position than SE. With the change of canopy positions from NW to SE, the reduction of the PSII reaction center activity in the leaves of both *Prosopis* congeners was accelerated. On the SE canopy position, a significant decline in the electron transport rate (ETR) of in the leaves of both *Prosopis* congeners occurred, which might be due to the blockage of electron transfer from QA to QB on the PSII acceptor side. On the SE canopy position; *Prosopis* leaves dissipated excess light energy by increasing non-photochemical quenching (NPQ). However, in *P. cineraria*, the protective ability of NPQ decreased, which led to the accumulation of excess excitation energy (1 − qP)/NPQ and the aggravation of photoinhibition. The results also explain the role of different physiological attributes contributing to invasiveness of *P. juliflora* and to evaluate its liaison between plasticity of these characters and invasiveness.

Keywords: chlorophyll *a* fluorescence; leaf C; leaf N; thermal energy dissipation; CO_2 assimilation rate; *Prosopis* species; photosynthetic efficiency

1. Introduction

The plants convert the sunlight into chemical energy during the photosynthetic process and some of the light energy is fixed and converted into chemical energy during the photosynthesis, but still some cannot be fully utilized and might cause potential damage [1–3]. Whenever the light energy can be converted into chemical energy safely, there will be no hazard to plant metabolism. However, if sunlight