Variation de l'intensité de la facilitation avec la salinité et l'aridité dans les dépressions salines continentales de Tunisie.

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Variation de l'intensité de la facilitation avec la salinité et l'aridité dans les dépressions salines continentales de Tunisie.

Sous la direction de Richard MICHALET
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Titre : Variation de l'intensité de la facilitation avec la salinité et l'aridité dans les dépressions salines continentales de Tunisie.

Résumé :

L'objectif de ce travail de thèse est de clarifier le débat de la littérature d'écologie des communautés sur les variations d'interactions plante-plante le long de gradients de stress hydrique. Nous nous sommes focalisés sur l'importance du type de stress (ressources vs. non-ressources) et la méthode utilisée (observationnelle vs. expérimentale) pour quantifier les interactions biotiques. Les dépressions salines continentales (Sebkhas) de Tunisie se caractérisant par l'existence d'un gradient marqué de salinité dans des contextes climatiques contrastés est un excellent système modèle pour clarifier ce débat notamment en séparant les effets de la salinité de ceux du stress hydrique.

Dans une première étape, nous avons effectué une étude observationnelle à l'échelle de la zone aride tunisienne afin d'identifier les conséquences des interactions possibles existant entre la topographie et le climat et déterminant les variations de stress salin et hydrique et donc la structure, la composition des communautés végétales et le fonctionnement des écosystèmes. Nous avons mis en place un dispositif de terrain croisant un traitement de position topographique (avec quatre habitats) et un traitement de stress hydrique (avec deux situations climatiques, le climat faiblement aride et le climat fortement aride) avec quatre répétitions à l'échelle régionale. Nous avons également effectué deux expérimentations, une première sur les l'effet des voisins par la méthode observationnelle avec transplantation de trois espèces dominantes dans l'ensemble des traitements et une sur l'effet de la méthode (observationnelle vs. expérimentale) avec transplantation de trois Poaceae dans les deux habitats les moins salés.

L'étude observationnelle a clairement montré que la salinité est le facteur direct majeur déterminant la composition, la diversité et la structure des communautés, ainsi que la productivité des écosystèmes et leur fertilité. L'aridité a des effets moindres plus subtiles et son effet ne peut être comparé spatialement que dans l'habitat le moins salé entre les zones très et faiblement arides.

La première étude expérimentale a montré que le stress salin (facteur direct non de ressource) entrainait un collapse de la facilitation et que ce collapse s'accentuait avec l'aridité croissante, aussi bien temporellement que spatialement. Nous n'avons pas trouvé de retour de la compétition en situation d'aridité extrême comme le prédit la littérature. Ceci est sans doute due à la stratégie faiblement compétitrice des Chaméphytes dominants les habitats les plus salés. La seconde étude expérimentale a montré qu'avant la saison sèche estivale les interactions de court-terme mesurées par la méthode expérimentale (removal method) sont négatives alors que les interactions de long-terme, mesurées par combinaison des méthodes observationnelle et expérimentale sont positives, confirmant nos hypothèses et la littérature. Cependant, après la saison sèche estivale les interactions de court-terme deviennent positives, alors que les

interactions de long-terme collapsent par disparition de l'effet tampon du sol végétalisé sur l'humidité.

Ces résultats sont cruciaux car ils montrent que dans ce système aride et à important stress salin le collapse de la facilitation est le processus majeur expliquant la structure, la diversité et le fonctionnement des écosystèmes et ce aussi bien le long des gradients de salinité que lorsque que le stress hydrique augmente. D'autre part la combinaison des méthodes observationnelle et expérimentale nous a permis de démontrer que l'augmentation de la facilitation prédite par le SGH lors d'une augmentation modérée de stress hydrique n'est qu'une réponse des plantes à l'effet négatif croissant de l'environnement abiotique, contrairement à l'augmentation de la compétition dans les environnements non stressés et celui de la facilitation des environnements très à moyennement stressés, qui sont des processus d'origine biotique.

Mots clés: Climat méditerranéen aride, écosystèmes salins, interactions biotiques, collapse de la facilitation, stress hydrique

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Title: Changes in facilitation intensity with salinity and aridity in continental saline depressions of Tunisia.

Abstract:

We aim to clarify the debate of the community ecology literature on changes in plant-plant interaction along water stress gradients. We focused on the importance of the type of stress (resources vs. non-resources) and the method used (observational vs. experimental) to quantify biotic interactions. The continental saline depressions (Sebkhas) of Tunisia, characterized by the existence of a strong gradient of salinity in contrasting climatic conditions, is an excellent model system to clarify this debate, in particular by separating the effects of salinity from water stress.

In a first step, we carried out an observational study on the scale of the Tunisian arid zone in order to identify the consequences of the possible interactions existing between topography and climate and determining variations in salinity and water stress and ultimately the structure, composition of plant communities and ecosystem functioning. We set up a field design combining a topographic position treatment (with four habitats) and a water stress treatment (with two climate conditions: the wet arid climate and the dry arid climate) with four replicates at the regional scale. We also carried out two experiments, one on the effect of neighbors using the observational method with transplants of three dominant species in all treatments and a second on

the effect of the method (observational vs. experimental) with transplantation of three Poaceae in the two least saline habitats.

The observational study clearly showed that salinity was the major direct factor determining the composition, diversity and structure of communities, as well as the productivity of ecosystems and their fertility. Aridity has less, more subtle effects, which can only be spatially compared in the least saline habitat between the low and high arid climates.

The first experimental study showed that salinty stress (a direct, non-resource factor) induced a facilitation collapse that increased with increasing aridity, both temporally and spatially. The switch to competition in extreme conditions of aridity predicted in the literature was not found. This is very likely due to the weakly competitive strategy of Chamaephytes dominating the most saline habitats. The second experimental study showed that, before the dry summer season, the short-term interactions measured by the experimental method (removal method) were negative whereas the long-term interactions, measured by the combination of the observational and experimental methods were positive, thus, supporting our hypotheses and the literature. However, after the dry summer season, the short-term interactions turned to positive, whereas the long-term interactions collapsed due to vanishing the buffering effect of the vegetated soil on humidity.

These results are crucial because they showed that in this arid and saline system, the collapse of facilitation is the major process explaining the structure, diversity and functioning of ecosystems, both along salinity gradients and when water stress increases. On the other hand, the combination of the observational and experimental methods was crucial to show that the increase in facilitation predicted by SGH with increasing water stress is only a response of plants to the increasing negative effect of abiotic environment (environmental-severity effect). This contrasts with the increased competition in unstressed environments and increased facilitation from highly stressed to intermediate environments, both being neighbor-trait effects.

Keywords: Arid climate, saline ecosystems plant-plant interaction, plant facilitation

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Nous avons trois moyens principaux: l'observation de la nature, la réflexion et l'expérience. L'observation recueille les faits ; la réflexion les combine, l'expérience vérifie les résultats de la combinaison…

Denis Diderot

Dédicaces

***

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I. INTRODUCTION GÉNÉRALE

La facilitation est un mécanisme important de la structuration des communautés. Elle est définie comme étant l'effet positif d'un organisme sur un autre au sein d'un même niveau trophique (Callaway, 2007). Elle est largement reconnue comme étant une interaction biotique fréquemment observée dans les conditions environnementales contraignantes des écosystèmes terrestres et marins côtiers (Bruno et al., 2003; He et al., 2013; Soliveres & Maestre, 2014; Michalet & Pugnaire, 2016; Bulleri et al., 2018). La facilitation est le résultat de l'amélioration directe des conditions abiotiques (froid, salinité, sécheresse, etc…), ou indirecte de protection contre l'action des herbivores ou liée à la diminution de la compétition entre trois partenaires (Callaway, 2007). La facilitation est cruciale dans les environnements sévères, car elle améliore la diversité locale, en permettant aux espèces végétales non tolérantes au stress de survivre dans des habitats contraignants (Bruno et al., 2003; Liancourt et al., 2005; Michalet et al., 2006 ; Gavini et al. 2020 JVS). En outre la facilitation améliore le fonctionnement des écosystèmes (Soliveres et al., 2015; Wright et al., 2017) et leur stabilité (Kéfi et al., 2007). De plus, la facilitation peut être utilisée comme un outil d'ingénierie écologique, pour la restauration des habitats dégradés (Gomez-Aparicio et al., 2004; Padilla & Pugnaire, 2006).

A l'inverse de la facilitation, la compétition est définie par l'effet négatif d'un organisme sur un autre. Elle est considérée depuis longtemps comme un processus crucial dans de nombreuses théories fondamentales d'écologie des communautés (Connell & Slatyer, 1977; Grime, 1979; Tilman, 1982). Elle est largement reconnue comme étant un facteur majeur, déterminant la diversité et la dominance des espèces au sein des communautés végétales (Grime 1973), pouvant réduire la diversité spécifique suite à la raréfaction, voire l'extinction des espèces (Hautier et al., 2009).

La compétition est couramment invoquée comme étant un processus déterminant la réponse des communautés végétales aux changements environnementaux, tels que les stress, les perturbations, les espèces exotiques envahissantes, et le changement climatique (Brooker, 2006).

Il est à signaler que la compétition a généralement lieu pour les ressources, comme l'eau, les nutriments et la lumière, mais également est de type interférence sans impliquer directement la consommation de ressources au sein des communautés.

1. Interactions biotiques le long des gradients environnementaux dans les écosystèmes contraints hydriquement

Les changements d'intensité et d'importance de la compétition et de la facilitation le long des gradients de stress dans les écosystèmes contraints hydriquement est un sujet très débattu dans la littérature (Maestre et al., 2005, 2009; Michalet, 2007; He & Bertness, 2014; Michalet et al., 2014; Soliveres et al., 2015). L'hypothèse du gradient de stress (SGH) considère que la compétition diminue et la facilitation augmente lorsque la sévérité environnementale s'accroit (Bertness & Callaway, 1994). Bien que ce modèle ait été confirmé par plusieurs expérimentations (Pugnaire & Luque, 2001 ; Gomez-Aparicio et al., 2004 ; Liancourt et al., 2005; Sthultz et al., 2007; Muhamed et al., 2013), d'autres études ont montré que la compétition pouvait s'accroitre lorsque le stress hydrique augmentait (Davis et al., 1998; Tielbörger et Kadmon, 2000; Maestre et Cortina, 2004; Armas & Pugnaire, 2005).

Il existe à ce propos dans la littérature, une interrogation majeure sur l'importance relative de la compétition et de la facilitation en milieu aride (Maestre et al. 2005 & 2009, Lortie & Callaway 2006, Michalet 2006 & 2007, Michalet et al. 2014, He & Bertness 2014). En situation de stress hydrique sévère, certaines études ont montré que la compétition pour l'eau, pouvait augmenter (Davis et al. 1998, Tielbörger & Kadmon 2000, Maestre & Cortina 2004), alors que d'autres études démontraient expérimentalement dans les mêmes conditions de stress, que la facilitation pouvait disparaitre (Le Bagousse-Pinguet et al. 2014b, Michalet et al. 2015b, Noumi et al. 2016), un processus appelé le collapse de la facilitation (Michalet et al. 2006). Holmgren & Scheffer (2010) et Verwijmeren et al. (2013) ont proposé que la relation entre les interactions biotiques et les contraintes environnementales n'était pas linéaire, contrairement à la proposition du modèle initial SGH (Bertness & Callaway 1994), mais plutôt unimodale, avec un maximum de facilitation dans les situations intermédiaires, due soit au retour de la compétition ou au collapse de la facilitation. Par ailleurs, Michalet et al. (2014) ont suggéré l'intérêt de séparer les deux alternatives au SGH, à savoir, le collapse de la facilitation et le retour à la compétition.

Le passage de la facilitation à la compétition s'observerait en conditions de stress, lorsque les espèces seraient en concurrence pour une ressource comme l'eau du sol (Michalet 2007; Maestre et al., 2009; Saccone et al., 2009). Cette alternative ne s'appliquerait pas aux gradients environnementaux dominés par des facteurs non liés à une ressource, tel que la salinité ou la

température (Michalet 2007; Maestre et al,. 2009; Holmgren & Scheffer, 2010). Ainsi le long de ce type de gradient mais également le long de gradients de perturbations par pâturage (Brooker et al. 2006 ; Baraza et al., 2006 ; Smit et al., 2007 ; Le Bagousse-Pinguet et al., 2012) ou perturbation physique excessifs (Forey et al., 2010) le collapse de la facilitation serait l'interaction dominante (Michalet et al., 2006). Toutefois, ces hypothèses sont encore controversées, notamment avec la publication d'une méta-analyse, montrant l'augmentation généralisée de la facilitation avec le stress (He et al. 2013, He & Bertness 2014).

La séparation des facteurs directs entre gradients de ressources ou de non-ressources nécessitent une bonne compréhension de la variation des facteurs directs le long des gradients environnementaux complexes. La distinction entre les facteurs complexes et les facteurs directs constitue un progrès conceptuel et méthodologique clé en écologie permettant de séparer la répartition des espèces végétales, au sein des différents espaces géographiques et écologiques (Whittaker, 1965 & 1978; Naveh & Whittaker, 1980; Austin & Smith, 1989). Divers exemples illustrant cette distinction ont été fournis par des études relative à la répartition écologique des espèces le long des gradients latitudinaux ou aussi, la variation des processus écologiques le long des gradients altitudinaux (Ozenda, 1975; Ohsawa, 1995; Körner, 2003; Cavieres et al., 2006).

Les facteurs climatiques, la nature de la roche mère et la topographie interagissent également dans l'espace géographique pour déterminer la variation des facteurs directs, telles que la température ou la disponibilité en eau pour les espèces végétales, en particulier dans les étages alpin et subalpin (Bamberg & Major, 1968; Gibson & Kirkpatrick, 1985; Michalet et al., 2001). Les études sur les écosystèmes benthiques des zones intertidales ont également montré l'importance des interactions existant entre les facteurs climatiques et topographiques pour façonner la distribution des espèces le long des gradients directs de stress physique (salinité et stress hydrique) (Pennings & Callaway, 1992; Fariña et al., 2017).

Dans les climats humides, il a été montré, que le stress salin diminuait en remontant le long du gradient topographique de par la diminution du temps d'inondation par l'eau salée. Ainsi, à la limite inférieure du gradient topographique, le stress salin détermine la zonation des espèces végétales, tandis qu'à sa limite supérieure, c'est plutôt la compétition qui conditionne cette répartition (Bertness, 1991; Bertness & Pennings, 2002). Dans leurs travaux sur les marais salins au Chili, Fariña et al. (2017) ont étudié la répartition de la végétation le long d'un gradient

latitudinal. Ils ont ainsi constaté que la zonation des espèces végétales selon la topographie est significativement visible sous climats semi-aride et hyper aride. En revanche, cette zonation est absente sous climat humide et hyper-humide. Afin d'expliquer cette différence, les mêmes auteurs ont constaté la présence d'un gradient plus fort de salinité et de stress hydrique dans les marais salins de basse latitude (climat semi-aride et hyper aride). Le climat engendre dans ces conditions l'augmentation du stress hydrique et du stress salin (accumulation du sel par évaporation ; Duchaufours….). En régions humides et hyper-humides, le climat semble donc avoir moins d'effets diminuant ainsi la zonation de la végétation.

2. Importance des stratégies fonctionnelles des espèces

La direction et l'intensité des interactions biotiques dépend en outre des stratégie fonctionnelles des espèces végétales impliquées (Goldberg et al., 1999). En effet, au sein d'une communauté végétale donnée, la manifestation de la facilitation ou de la compétition dépend de la capacité des espèces considérées à tolérer le stress (Grime, 1974 ; Gaudet & Keddy, 1988; Michalet, 2007; Maestre et al., 2009), ou aussi de leur ontogenèse (Butterfield, 2009). Les espèces intolérantes au stress sont susceptibles d'être plus facilitées que les espèces tolérantes, du fait qu'elles sont plus sensibles à l'amélioration des conditions environnementales (Liancourt et al., 2005; Graff et Aguiar, 2017). Au sein des écosystèmes arides et désertiques, les interactions biotiques sont spécifiques à la nature de l'espèce végétale en question (Lortie et Callaway, 2006). Cette relation est liée à la distribution géographique des espèces et à leur stratégie fonctionnelle, (espèces compétitives/espèces stress tolérantes), qui peuvent engendrer des réponses différentes à l'effet du voisinage (Liancourt et al., 2005; Albert et al., 2010; Liancourt et al., 2017). He et al. (2013) suggèrent aussi l'importance des traits fonctionnels des espèces cibles et ceux de leur voisinage, puisque les cibles annuelles sont d'après ces auteurs davantage plus compétitives que des cibles pérennes.

L'ontogénèse des espèces intervient en outre dans la nature des interactions biotiques. Par exemple les espèces cibles au stade juvénile, sont à ce propos plus vulnérables au stress environnemental, et tentent de bénéficier davantage de la facilitation que les cibles adultes (Callaway & Walker, 1997; Miriti, 2006).

3. Méthode utilisée dans l'étude des interactions biotiques

L'utilisation de la méthode (observationnelle et expérimentale) dans les interactions biotiques est cruciale pour évaluer l'effet du voisinage sur les espèces cibles (Michalet 2006). En effet, avec la méthode observationnelle (comparaison des performances des cibles en présence et en absence naturelle de voisins), le voisinage a plutôt un effet positif dominant sur les cibles. En revanche, avec la méthode expérimentale (comparaison des performances avec et sans voisins éliminés expérimentalement), le voisinage a souvent un effet négatif (Maestre et al. 2003 & 2005, Michalet 2006). Michalet (2006) proposa que la facilitation était plus fréquemment observée avec la méthode observationnelle parce que dans les écosystèmes arides le stress hydrique est plus important au niveau des milieux ouverts naturellement que dans les micro-habitats occupés par de la végétation. A l'inverse, la méthode expérimentale montre plus fréquemment de la compétition de par le prélèvement de ressources par les voisins (Maestre et al., 2003 ; Michalet, 2006). Néanmoins, en appliquant les deux méthodes Sthultz et al. (2007) ont montré un effet positif des arbustes sur le pin (*Pinus edulis*) dans les écosystèmes semi-arides de l'Arizona. Inversement, Noumi et al. (2015) ont trouvé avec les deux méthodes un effet négatif des voisins sur *Acacia tortilis* dans les écosystèmes arides de Tunisie.

Michalet et al. (2015) et Noumi et al. (2016) ont proposé de combiner les deux méthodes pour obtenir deux indices permettant la séparation des effets à court et long termes des voisins. L'effet à court terme ou effet de la canopée, défini par Michalet et al. (2015), est évalué en utilisant la méthode expérimentale, par le calcul de la différence de performance entre le traitement avec et sans voisins éliminés expérimentalement. L'effet à long terme est évalué par la différence de performance entre le sol du voisinage et le sol nu sans voisinage (Noumi et al. 2016). L'effet total du voisinage, qui est la somme des effets à court et à long terme, est lui évalué par la méthode observationnelle. Les études effectuées dans les écosystèmes semi-arides en Espagne ont d'ailleurs montré l'existence d'un effet négatif de court terme et un effet positif de long terme du voisinage sur les graminées dominantes de ces écosystèmes (Maestre et al., 2005 ; Schöb et al., 2012; Michalet et al., 2015). De même, Noumi et al. 2016, signalent des résultats similaires sous climat aride en Tunisie. Michalet, (2006) prédit l'augmentation des effets à court et à long terme avec l'accentuation de la sécheresse. Toutefois, Michalet et al. (2015) ont remarqué un collapse de ces deux effets avec l'augmentation du stress hydrique ; alors que dans

ces mêmes conditions, Noumi et al. (2016) ont observé un effet négatif de court terme et une diminution de l'effet à long terme. Il est important aussi de signaler que la direction et l'intensité des effets à court et à long terme, peuvent dépendre plus tôt du phénotype compétitif de l'espèce que du niveau de stress, auquel elle est exposée (Michalet et al., 2017; Piston et al., 2018).

Un autre concept méthodologique important au niveau des études des interactions biotiques, et permettant d'apprécier le mécanisme de la variation de la compétition et de la facilitation, est de scinder l'effet total du voisinage en deux sous-effets, l'effet des traits des voisins et l'effet de la sévérité environnementale (Michalet et al., 2014b). Les expériences réalisées en vue d'étudier les interactions biotiques se basent sur l'utilisation des indices comme le RII (Armas et al., 2004) qui permettent de calculer l'effet du voisinage sur l'espèce cible. Cependant, ces indices ne permettent pas de séparer l'effet réel du voisin de celui de l'environnement. Ainsi, l'effet neighbour-trait permet de comprendre l'effet du voisinage sur la cible, alors que l'effet de la sévérité environnementale évalue l'effet d'un gradient de stress sur les cibles isolées sans voisinage. Par exemple, dans les écosystèmes alpins, Michalet et al. (2014b) ont constaté qu'à l'étage subalpin, l'augmentation de la compétition liée à la diminution du froid était due à un effet du voisinage. En revanche, dans l'alpin l'augmentation de la facilitation avec l'augmentation du froid est engendrée par l'effet de la sévérité environnementale. L'étude de ces deux effets est cruciale pour prédire la réponse des espèces végétales aux changements globaux, étant donné que ceux-ci peuvent affecter soit l'espèce cible ou ses voisins (Alexander et al. 2015).

OBJECTIFS DE LA THESE :

L'objectif de cette thèse est d'utiliser les milieux salins arides de Tunisie comme système modèle pour clarifier le débat sur les variations d'interactions biotiques le long des gradients de stress dans les milieux contraints hydriquement. Nous nous concentrerons en particulier sur l'importance du type de stress (ressources vs non-ressources), de la méthode utilisée pour quantifier les interactions et des stratégies des espèces cibles. La Tunisie aride comprend un nombre important de dépressions continentales salines (appelées localement Sebkhas) au sein desquelles se succèdent différentes communautés d'halophytes le long de gradients topographiques complexes intégrant des gradients directs de salinité et de stress hydrique. Étant donné que ces dépressions salines sont observées dans des conditions bioclimatiques relativement

variées, depuis le climat saharien jusqu'au climat semi-aride, ce système est particulièrement adapté pour séparer l'influence respective de la salinité et du stress hydrique sur les variations d'interactions biotiques le long des gradients de stress. Ce fut donc l'objet d'une première expérimentation sur les interactions biotiques le long des gradients de salinité dans différentes conditions d'aridité qui fait l'objet du chapitre 2. Dans cette expérimentation nous n'avons utilisé que la méthode dite observationnelle (utilisation des patchs naturellement sans voisins pour éliminer l'effet des voisins). En préalable nous avons effectué une première étude observationnelle à l'échelle de l'ensemble de la zone aride de Tunisie pour identifier les interactions éventuelles existantes entre les variations de salinité et de stress hydrique (facteurs directs) et leurs relations avec la distribution des espèces et le fonctionnement des écosystèmes (productivité et décomposition de litières) le long des gradients (complexes) topographique et climatique. Ce sera l'objet du chapitre 1. Dans un troisième chapitre nous nous concentrerons sur l'importance de la méthode utilisée et donc de l'échelle temporelle des interactions biotiques (effets de court et long termes). Ce chapitre concerne donc une seconde expérimentation sur les interactions biotiques où nous avons utilisé à la fois la méthode observationnelle et la méthode expérimentale (élimination de voisins) dans les habitats les moins salés des Sebkhas. Dans cette deuxième expérimentation nous nous sommes également intéressés à l'influence respective des déterminismes environnementaux et biotiques des variations d'interactions biotiques (environmental-severity vs. neighbour-trait effects, sensu Michalet et al. 2014). Dans ces deux expérimentations nous avons utilisé plusieurs espèces cibles pour aborder l'effet de la stratégie des espèces cibles dans leur réponse aux effets des voisins.

Les questions principales posées dans cette thèse sont les suivantes :

1. Quelles sont les influences du climat, de la topographie et de leur interaction sur les variations de stress hydrique et de salinité et à terme sur la composition floristique et le fonctionnement des écosystèmes salins des dépressions salines de Tunisie ?
2. Quelles sont les effets respectifs de la salinité et du stress hydrique sur les variations d'interactions biotiques au sein des dépressions salines de Tunisie ?
3. Comment évoluent les interactions de courts et long-termes le long des gradients de stress hydrique et de salinité dans les dépressions salines de Tunisie ?

CHAPITRE I. MATERIELS ET METHODES

1. CARACTÉRISTIQUES DES SITES D'ÉTUDES

1.1. Principales caractéristiques du climat aride en Tunisie

En Tunisie, le climat Méditerranéen aride occupe la partie centrale et méridionale du pays. Il couvre environ les ¾ de la surface totale de la Tunisie (Floret & Pontanier, 1982). Dans cette région méditerranéenne également connue sous le nom de Tunisie présaharienne, l'hiver est caractérisé par des moyennes de 19°c et l'été par des températures moyennes de l'ordre de 35°c. L'évapotranspiration potentielle (ETP) est très importante (1500 mm). La moyenne annuelle des précipitations sous climat Méditerranéen aride est comprise entre 100 et 300 mm (Le Houérou, 1959). Ce climat aride est subdivisé en deux sous climats, appelés sous-étages par Emberger (1955), l'aride supérieur et l'aride inférieur. Dans l'aride supérieur, les précipitations moyennes annuelles sont comprises entre 200 et 300 mm (Slimani et al., 2007) et dans l'aride inférieur, elles sont de l'ordre de 200 à 100 mm (Hanafi & Jauffret, 2008; Jeddi et al., 2009). L'aride supérieur est habituellement marqué par une saison pluvieuse hivernale d'environ quatre mois et une saison sèche d'environ 8 mois, alors que pour l'aride inférieur, la saison hivernale est plus courte (environ 1 mois) et la saison sèche très longue (environ 11 mois) (Bagnouls & Gaussen 1954, voir figure 15).

1.2. Distribution géographique des sols salins en Tunisie aride

Les sols salins sont repartis sur environ 10% du territoire tunisien. Leur importance sous climat aride est remarquable, puisqu'ils y couvrent environ 1,5 million d'hectares. Selon leur niveau de salinité, ces sols halomorphes sont subdivisés en deux catégories, à savoir, les sols très salés, connus sous le nom vernaculaire de Sebkha, et les sols moyennement salés, connus sous le nom vernaculaire de Garât.

1.3. Typologie des sols salins en Tunisie aride (Sebkhas)

Généralement en Tunisie, les Sebkhas se présentent sous forme de larges dépressions, plus ou moins circulaires, avec une superficie variant entre 10 à 300 km^2 (Fig.1). Une Sebkha est

globalement structurée en deux zones principales. Une première zone centrale couvre environ 70% de la surface de la Sebkha (Fig. 2) avec un sol dépourvu de végétation et une couche superficielle de sel. La seconde zone occupe environ 30% de la surface restante de la Sebkha. Il s'agit de la zone colonisée par la végétation halophile, dont la physionomie et la zonation suivent un gradient topographique, allant du bord de la zone centrale (la plus basse, et sans végétation) vers la partie périphérique (la plus haute et la moins salée) (Fig. 3).

La zone de végétation halophile est bordée de cultures (arboriculture, oléiculture ou céréaliculture en sec) ou de friches (Fig. 4). Le dénivelé entre la zone centrale de la Sebkha et sa périphérie est d'environ 1 à 2 m (Floret & Pontanier, 1982).

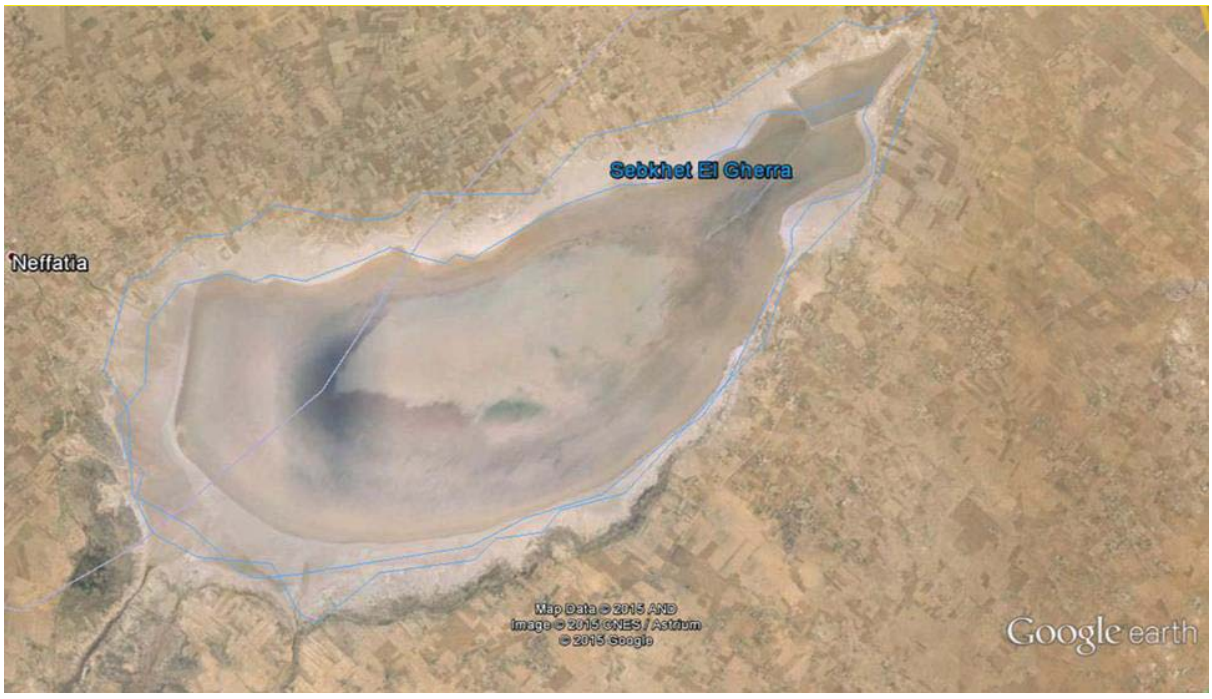

Figure 1: Sebkha d'El Ghorra (El Djem), vue par image satellitaire (source: Google).

Figure 2: Zone centrale de la Sebkha de Noual (Mezzouna), dépourvue de végétation.

Figure 3: Sebkha de Hchichina (La Skhira), avec localisation des zones 1 et 2.

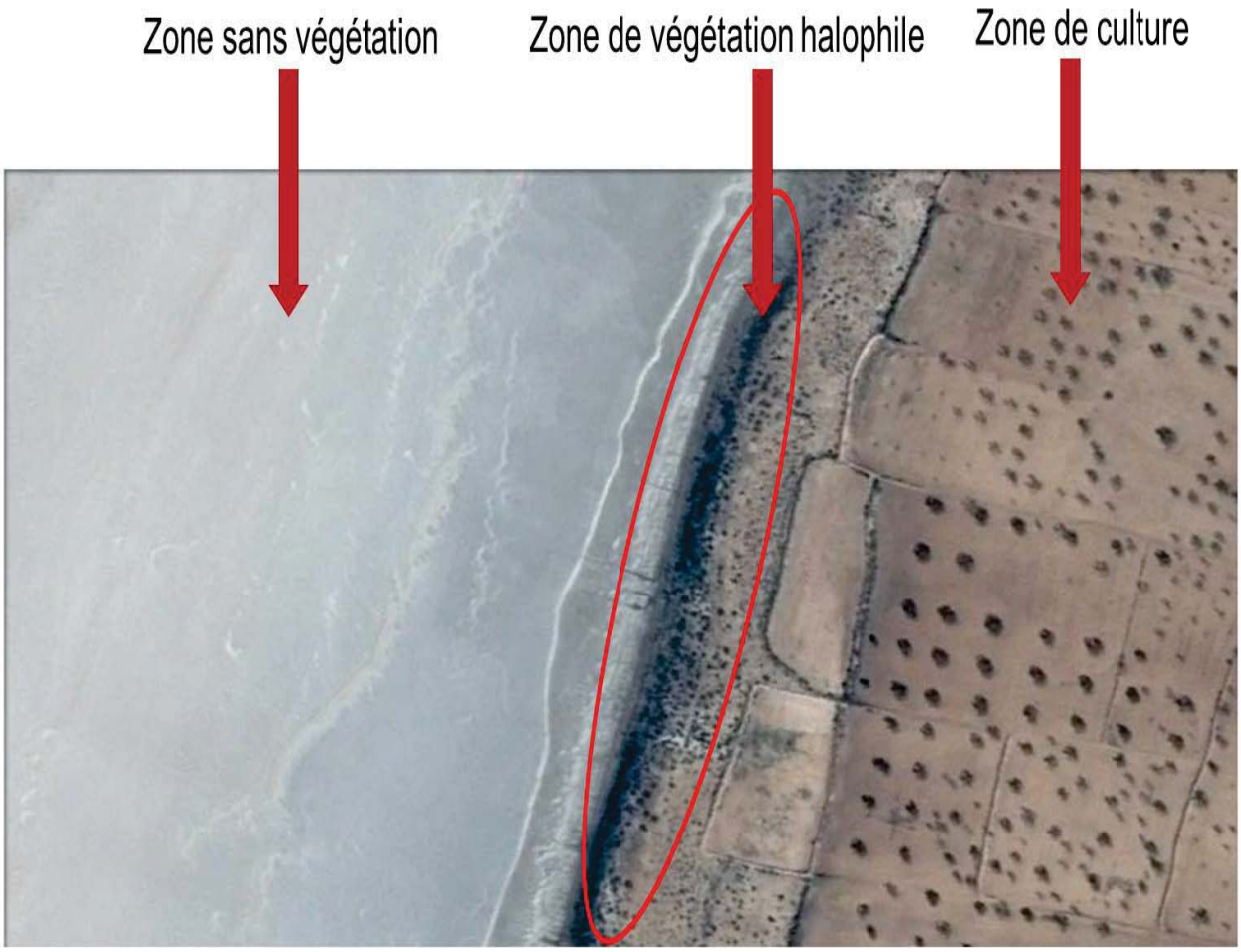

Figure 4: Zone centrale, zone de végétation halophile et zone de cultures (oliveraie) au niveau de la Sebkha de Boujmel (Sfax).

La zonation de la végétation halophile le long du gradient topographique des Sebkhas est fortement corrélée à la salinité du sol. Pour mieux connaître cette relation, nous avons mis en place un protocole d'une étude observationnelle, à l'échelle des Sebkhas de la Tunisie centrale et méridionale.

2. MÉTHODES

2.1. Étude observationnelle et définition des habitats au sein des Sebkhas retenues

L'étude observationnelle réalisée au niveau des différentes Sebkhas, constitue une étape préliminaire de notre travail de thèse. Les expérimentations ont été réalisées le long d'un gradient géographique de 400 km au sein de la zone aride tunisienne (depuis le centre du pays, jusqu'à proximité de la frontière libyenne.

Dans ce contexte, nous avons mis en place un dispositif d'échantillonnage tenant compte les deux facteurs complexes principaux de ce système: l'aridité climatique et la position le long du gradient topographique). Nous avons sélectionné huit Sebkhas sous climat aride supérieur et aride inférieur (soit quatre Sebkhas dans chacun de ces deux zones climatiques). Ensuite, au sein de chaque Sebkha retenue, nous avons délimité le long du gradient topographique cinq parcelles, ayant chacune une superficie de 1000 m^2.

A une distance de 10 m de la limite avec la zone centrale dépourvue de végétation, nous avons défini le premier habitat (H1), qui est donc l'habitat le plus bas du gradient topographique. A la limite supérieure de la Sebkha, c'est-à-dire à l'écotone avec les zones de cultures, bordant la Sebkha, nous avons délimité l'habitat 5 (H5).

La parcelle située en position intermédiaire (mi- altitude) entre les habitats H1 et H5, correspond ainsi à l'habitat 3 (H3).

Enfin, les deux dernières parcelles correspondent respectivement à l'habitat 2 (H2), qui est situé à mi-chemin entre H1 et H3, et l'habitat 4 (H4), entre H3 et H5 (Fig. 5 et Fig. 6).

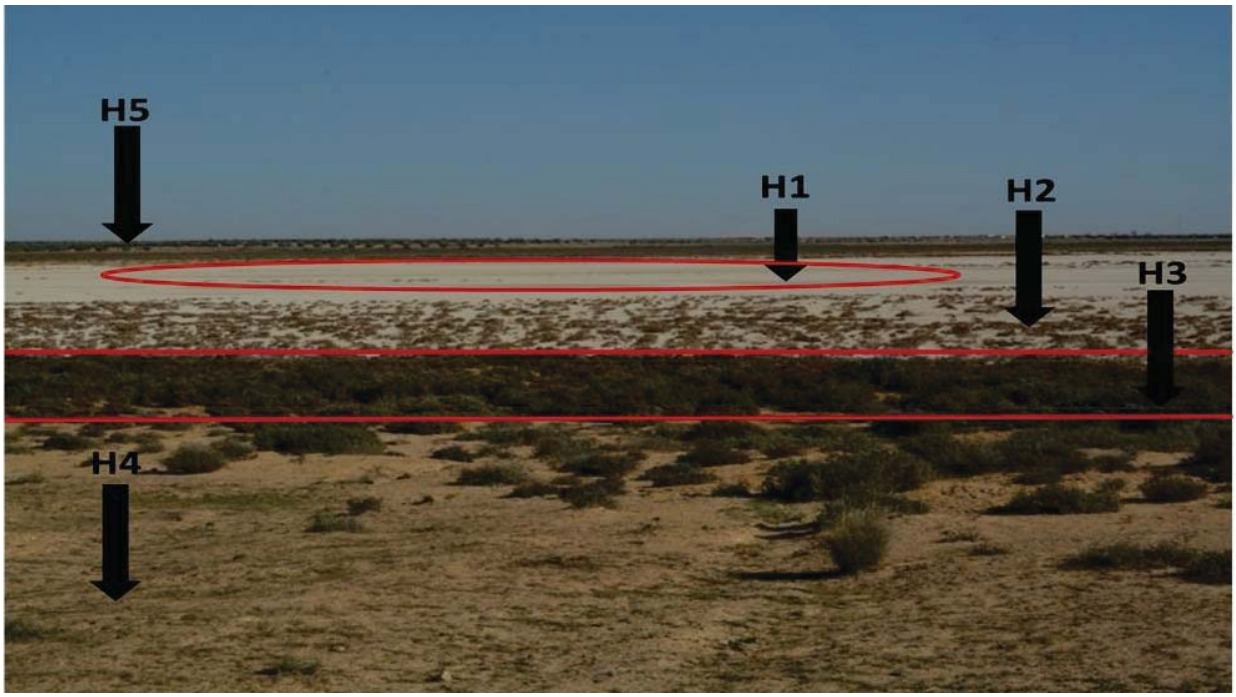

Figure 5 : Distribution des différents habitats au cours de l'étude observationnelle au niveau de la Sebkha de Hchichina (La Skhira).

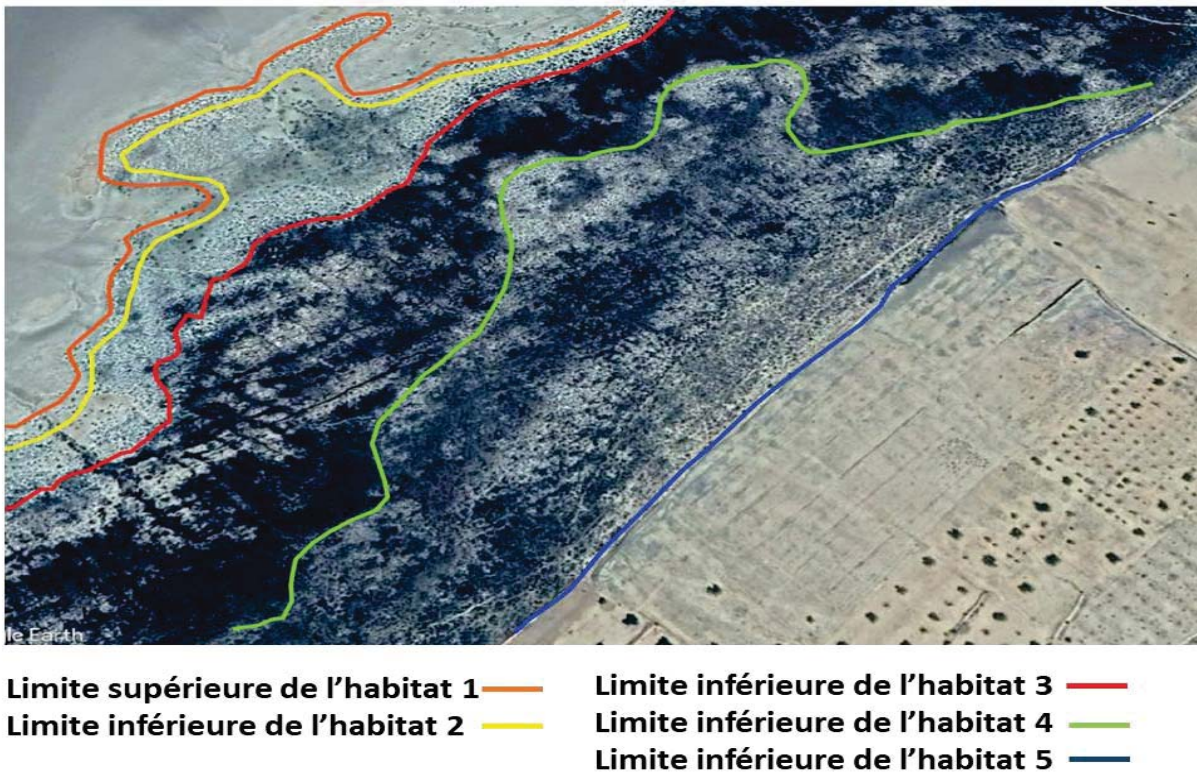

Figure 6 : Limites des différents habitats au cours de l'étude observationnelle

2.2. Échantillonnage des paramètres environnementaux et floristiques

Dans les huit Sebkhas retenues sous climat aride supérieur et aride inférieur, nous avons donc mis en place un total de 40 parcelles (2 climats X 4 réplicas X 5 habitats), qui ont tous fait l'objet de mesures environnementales. Pour les mesures floristiques, seuls 32 habitats (2 climats X 4 habitats X 4 réplicas) ont été considérés. Les huit habitats restants, correspondant aux zones dépourvues de végétation, n'ont pas été échantillonnés de par l'absence de végétation.

Au cours du printemps (mois de mars) 2015, soit après les dernières pluies hivernales, nous avons mesuré à deux profondeurs (0-20 cm et 20-40 cm), et à l'aide d'un humidimètre type HH2 (Delta-T Devices, Cambridge, UK), la salinité du sol (conductivité électrique, exprimée en $mS.cm^{-1}$), la teneur en eau du sol (exprimée en %) et la température du sol (exprimée en °C). Le pH du sol a été mesuré avec un pH-mètre de terrain (type HANNA, HI. 9921) (Fig. 7).

En raison de la couverture discontinue de la végétation, les différentes mesures ont toujours été effectuées de façon aléatoire dans des zones ouvertes entre les touffes de végétation. Pour chaque paramètre environnemental mesuré cinq répétitions ont été effectuées dans chacun des 40 parcelles sélectionnées.

Figure 7: Mesures des paramètres environnementaux au sein des Sebkhas, et équipements scientifiques utilisés.

Durant la même période, nous avons effectué des relevés de végétation (Fig. 8). Les paramètres retenus ont été la densité des espèces (richesse spécifique), leur abondance, ainsi que le couvert végétal total et le type biologique (Raunkiær 1934). La densité en espèces, exprimée en nombre d'espèces/m^2, a été échantillonnée sur des quadras de 1mX1m, avec 3 répétitions par parcelle. L'abondance des espèces, exprimée en nombre d'individus/espèce a été notée dans un quadra de 10mX10m, à raison d'une seule répétition par plot. Pour le couvert végétal total et le couvert végétal des espèces, classées selon leurs types biologiques, et exprimés en %, nous avons adopté la méthode de Daget & Poissonnet (1971). Cette méthode est basée sur des transects linéaires de 10 m de longueur, avec usage d'une aiguille métallique positionnée à des points d'observations situés tous les 10 cm, soit au total 100 points par transect, et à raison de 3 répétitions par parcelle.

Figure 8: Mesures des paramètres floristiques dans la Sebkha El Melah (Zarzis).

2.3. Expérimentation

2.3.1. Habitats sélectionnés pour l'expérimentation

Rappelons que les habitats sont répartis au niveau de chaque Sebkha étudiée, dans différentes positions en fonction de la topographie. Bien que la notion d'habitat adoptée dans l'étude expérimentale (quatre habitats), soit la même que celle adoptée dans l'étude observationnelle (5 habitats), pour la première expérimentation, nous avons subdivisé l'habitat 2 (H2) de l'étude observationnelle en deux habitats différents, à savoir l'Habitat H1, à l'interface avec la zone centrale (H1 de l'étude observationnelle) et l'Habitat H2 proprement dit correspondant au H2 de l'étude observationnelle. Ce choix a été motivé par la question scientifique, notre objectif dans cette expérimentation étant de tester le modèle du collapse de la facilitation le long du gradient de salinité et donc il nous fallait échantillonner particulièrement à la limite de la végétation. Les habitats 3 et 4 sont les mêmes que ceux de l'étude observationnelle (Fig. 9). Enfin, l'habitat 5 (H5), de l'étude observationnelle, n'a pas été sélectionné pour l'étude expérimentale de par l'importance de la perturbation humaine.

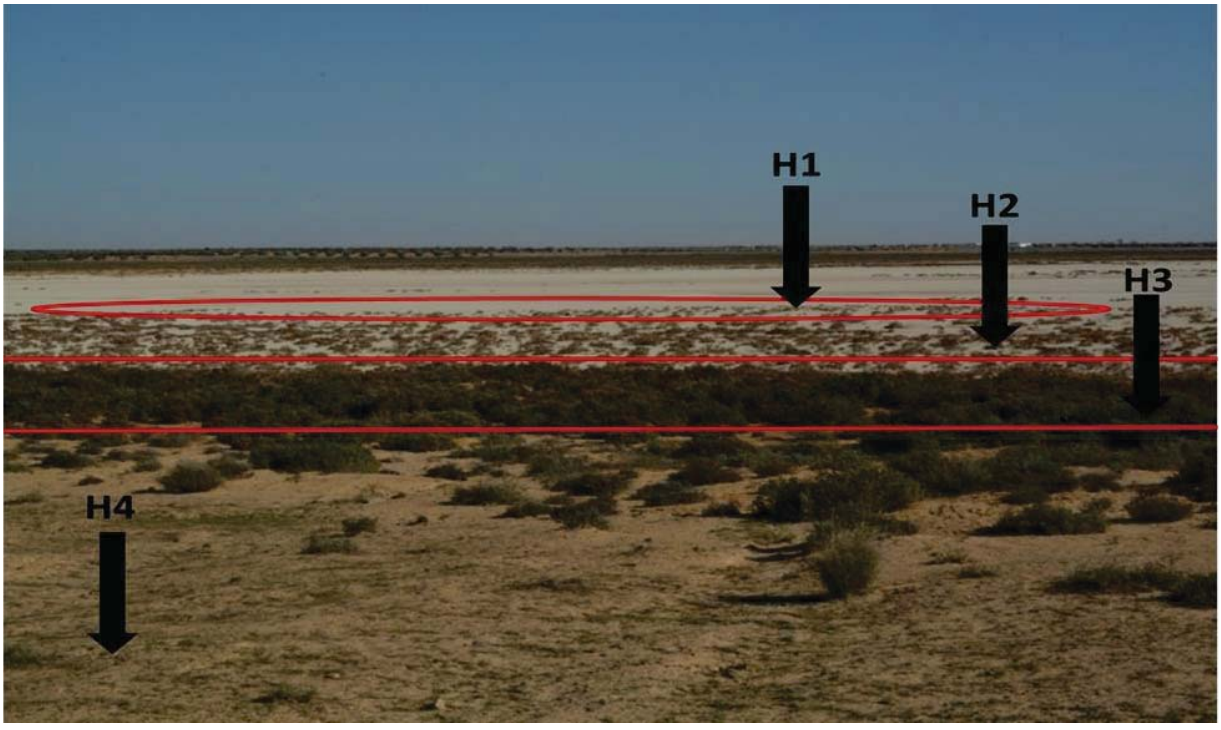

Figure 9: Localisation des différents habitats la première expérimentation (Sebkha de Boujmel).

2.3.2. Zonation de la végétation au niveau des Sebkhas étudiées

Les espèces végétales dominantes au niveau des Sebkhas sont des ligneuses basses halophiles, et des graminées pérennes, présentes le long du gradient topographique en relation avec la salinité du sol. Ainsi, l'habitat 1 (H1) dont le couvert végétal est plus le faible (<20%) (Fig.10), comporte une seule espèce qui est *Halocnemum strobilaceum* (*Amaranthaceae*). Cette espèce de type biochimique de photosynthèse en C_3 est présente dans toute la région méditerranéenne et jusqu'en Asie occidentale (Liu, 1985). Il s'agit d'une espèce très tolérante à la salinité (Redondo-Gomez et al., 2010). L'habitat 2 (H2) est également uniquement occupé par *Halocnemum strobilaceum,* mais avec un couvert végétal plus élevé (20-50%) que celui du H1(Fig.11). L'habitat 3 est dominé par *Arthrocnemum macrostachyum* (*Amaranthaceae*), également espèce de type biochimique en C_3 (Fig. 12 & 13). Cette espèce est connue comme étant accumulatrice de sel (Redondo-Gomez et al., 2010). Elle est dans cet habitat associée à d'autres espèces, telles que *Suaeda mollis*, *Limoniastrum monopetalum* et *Atriplex halimus*. Enfin, l'habitat 4 est dominé par *Lygeum spartum (Poaceae)*, graminée pérenne rhizomateuse, très répandue dans la région méditerranéenne et connue pour sa tolérance de la salinité (Fig.14) et du surpâturage. Au sein de cet habitat, *L. spartum* est associée à d'autres espèces, principalement ligneuse comme *Salsola tetrandra, Zygophyllum album, Reaumuria vermiculata* et *Nitraria retusa.*

Figure 10: Habitat 1, uniquement peuplé par *Halocnemum strobilaceum.*

Figure 11 : Habitat 2, uniquement peuplé par *Halocnemum strobilaceum.*

Figure 12: Habitat 3, dominé par *Arthrocnemum macrostachyum*.

Figure 13: Un individu adulte d'*Arthrocnemum macrostachyum.*

Figure 14: Habitat 4, dominé par *Lygeum spartum.*

2.3.3. Collecte et analyse des précipitations dans les sites d'études, durant les expérimentations

Les expérimentations se sont déroulées de novembre 2016 à septembre 2017 pour la première expérimentation et de novembre 2017 à septembre 2018 pour la deuxième. Durant ces expérimentations, nous avons collecté avec un pluviomètre totalisateur, installé dans chaque site d'étude, les quantités mensuelles de précipitations. En revanche, les températures sont celles des stations météorologiques les plus proches de ces Sebkhas.

Ainsi, pour une meilleure analyse de la répartition des précipitations durant chacune de nos deux années études, nous avons effectué une comparaison entre ces quantités observées sur nos sites d'études par rapport aux précipitations moyennes habituelles, caractérisant cette région de Tunisie.

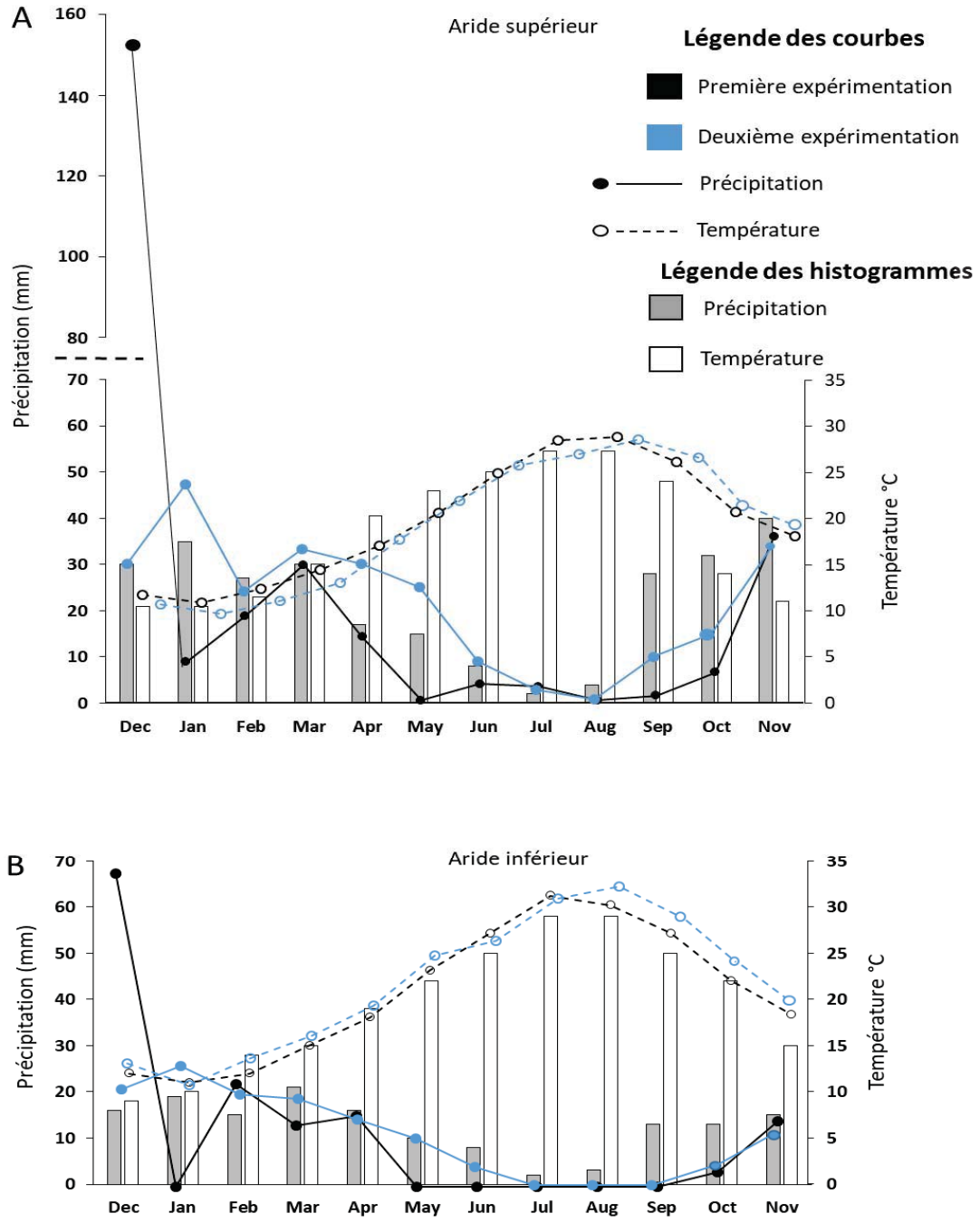

Figure 15. Précipitations et températures enregistrées durant les deux années d'expérimentation, comparées avec les données moyennes diagramme ombrothermique de Bagnouls & Gaussen, (Le Houérou, 1995), établi sur la base des précipitations, relevées par le service météorologique de Tunisie (de 1921 à 1995).

2.3.3.1. Répartition des précipitations durant l'année 2016-2017 (première expérimentation)

Nous avons calculé pour les trois saisons de chaque expérimentation (hiver, printemps et été) l'anomalie de précipitations entre l'année de l'expérimentation et les valeurs moyennes de cette région de Tunisie (Tableau 1). Lors de la première expérimentation le climat fut plus humide en hiver, et moins arrosé au printemps et en été par rapport à la moyenne. Ces anomalies ont été assez similaires (mis à part au printemps qui fut plus sec la deuxième année) dans les climats aride supérieur et aride inférieur (respectivement : hiver + 92% et + 78%, printemps + 31% et - 41% et été -53% et -100%). Ainsi, la pluviosité observée lors de notre expérience peut être considérée comme étant représentative des différences moyennes d'aridité, survenant en Tunisie entre ces deux zones climatiques, au moins pendant l'hiver et l'été (la différence fut plus accentuée entre les deux zones climatiques au printemps). Par contre, pour ces deux zones arides, les différences d'humidité entre les saisons hivernales et estivales furent plus élevées durant l'année de notre expérience que la moyenne habituelle.

En ce qui concerne la température, nous avons observé une légère hausse de la température moyenne mensuelle, durant l'année 2016-2017, par rapport à la température moyenne.

Tableau 1: Variation des précipitations observées durant l'année 2016-2017, par rapport à la moyenne habituelle de la région (Le Houérou 1995).

	Précipitations moyennes habituelle (mm) (Le Houérou 1995).		Variation durant l'année 2016-2017 (par rapport aux précipitations habituelles).	
Type de climat / Saison	Aride sup.	Aride inf.	Aride sup.	Aride inf.
Hiver	93	70	+ 92%	+ 78%
Printemps	64	48	+ 31%	- 41%
Été	14	12	- 53%	- 100%

2.3.3.2. Répartition des précipitations durant l'année 2017-2018 (deuxième expérimentation)

Concernant les précipitations, durant la seconde année de notre expérience, le climat fut légèrement plus humide en hiver et plus sec au printemps et en été pour l'aride inférieur (l'aride supérieur. étant plus humide) que la moyenne habituelle. Ces différences pour l'aride supérieur et inférieur sont respectivement de l'ordre de + 31% + 6.5% pour l'hiver, + 37,1% et - 9,6% pour le printemps et - 40% et - 69,2 % pour l'été. A l'inverse donc de la première année, les différences de précipitations entre les deux zones arides a été beaucoup moins marqué en hiver que durant les autres années. D'autre part, l'été a été particulièrement plus sec que la moyenne dans les deux zones arides.

Pour cette seconde année d'expérimentation, la température moyenne mensuelle, est également légèrement supérieure aux moyennes habituelles.

Tableau 2: variation des précipitations observées durant l'année 2017-2018, par rapport à la moyenne habituelle de la région (Le Houérou 1995).

	Précipitations moyennes habituelle (mm) (Le Houérou 1995).		Variation durant l'année 2017-2018 (par rapport aux précipitations habituelles).	
Type de bioclimat / Saison	Aride sup.	Aride inf.	Aride sup.	Aride inf.
Hiver	93	70	+ 31%	+ 6.52%
Printemps	64	48	+ 37.09%	- 9.57%
Été	14	12	- 40%	- 69.23%

2.3.4. Description des expérimentations effectuées

2.3.4.1. Étude de l'influence de la salinité et de l'aridité sur les interactions biotiques le long du gradient topographique (expérimentation réalisée en 2016-2017) :

L'objectif principal de cette étude est de comprendre le rôle du stress salin et celui de la sécheresse sur la variation des interactions biotiques le long de gradients complexes topographies et climatiques au niveau des écosystèmes arides. Sachant que les stress de salinité et de sécheresse interagissent à travers des gradients topographiques et climatiques complexes, nous avons mis en place un plan expérimental à l'échelle régionale, où nous avons évalué l'effet de la salinité sur les interactions biotiques, le long des gradients topographiques en conditions climatiques différentes. Pour cela, nous avons sélectionné huit Sebkhas au niveau des climats, aride supérieur et inférieur du centre et du sud de la Tunisie.

Dans la première expérience réalisée durant l'année 2016-2017, pour les deux types de climats (aride supérieur et aride inférieur), nous avons cherché à quantifier les interactions biotiques par la méthode observationnelle, le long d'un gradient de salinité. Pour chaque type de climat, quatre Sebkhas ont été retenues. Cette expérience a débuté au mois de novembre 2016, et s'est achevée en septembre 2017. Des transplantations réciproques de trois espèces dominantes ont été effectuées dans les huit Sebkhas étudiées, avec deux niveaux de voisinage (avec sans voisinage). Au total, 576 cibles (2 climats X 4 répétitions de Sebkha X 4 habitats X 3 espèces X 2 niveau de voisinage X 3 individus) ont été transplantées. Les espèces de voisinage retenues sont: *Halocnemum strobilaceum* dans les habitats 1 et 2, *Arthrocnemum macrostachyum* dans l'habitat 3, et *Salsola tetrandra* dans l'habitat 4.

Les espèces cibles transplantées avec et sans voisinage sont: *Halocnemum strobilaceum* (Fig.16), *Arthrocnemum macrostachyum* (Fig. 17 &Fig. 18) et *Lygeum spartum* (Fig.19).

Figure 16: Individu cible d'*Halocnemum strobilaceum,* transplanté au sein de l'espèce de voisinage *Arthrocnemum macrostachyum.*

Figure 17: Individu cible d'*Arthrocnemum macrostachyum,* transplanté au sein de l'espèce de voisinage *Salsola tetrandra*.

Figure 18: Individu cible d'*Arthrocnemum macrostachyum*, transplanté sans voisinage.

Figure 19: Individu cible de *Lygeum spartum*, transplanté au sein de l'espèce de voisinage *Halocnemum strobilaceum*

Préparation des transplants

Les transplants ont été préparés à partir de boutures enracinées pour *H. strobilaceum* et *A. macrostachyum* et par éclats de touffes en talles pour *L. spartum*. Ainsi, pour les *Amaranthaceae*, des boutures d'environ 10 à 20 cm de longueur et environ 1 cm de diamètre, furent prélevées au début du mois de septembre 2016. Pour la *Poaceae*, des talles de 3 à 4 feuilles, ont été prélevés à partir des touffes adultes, et transplantés dans les sachets, en vue de la rhizogenèse et l'émergence de nouvelles feuilles. Le site de prélèvement des boutures et des talles fut la Sebkha d'El Djem (Chaieb & al., 2019). Les boutures d'*H. strobilaceum*, et *A. macrostachyum* et les éclats de touffes de *L. spartum* ont été prélevés avec leur sol. Ces boutures et ces talles ont été ensuite transplantées dans des sachets en plastique de 20 cm de longueur et 5 cm de diamètre (Fig. 20). Ces sachets étaient perforés afin de garantir le drainage. Ils ont ensuite été installés durant 3 mois (septembre à novembre 2016), dans la pépinière forestière de Sfax, afin de provoquer la rhizogenèse (Fig. 20). Des irrigations modérées, ont été effectuées tous les 15 jours, à une dose de 20 mm pour chaque irrigation. La quantité totale d'eau d'irrigation des boutures et des talles, fut l'équivalent de 120 mm, quantité nécessaire pour enclencher l'apparition des racines sur les boutures et les talles.

Figure 20 : Vue des transplants des espèces cibles dans la pépinière.

D'autre part, cette quantité d'eau d'irrigation est apparue également suffisante pour provoquer la lixiviation totale du sel, contenu dans le sol de tous les transplants. Cette lixiviation a permis tel qu'on voit sur la figure 21, d'avoir à l'issue de la phase pépinière, des transplants pour les trois espèces cibles, ayant une salinité du sol, quasi-identique, puisqu'elle est voisine de celle du sol de la pépinière (inférieure à 1,5 $mS.cm^{-1}$).

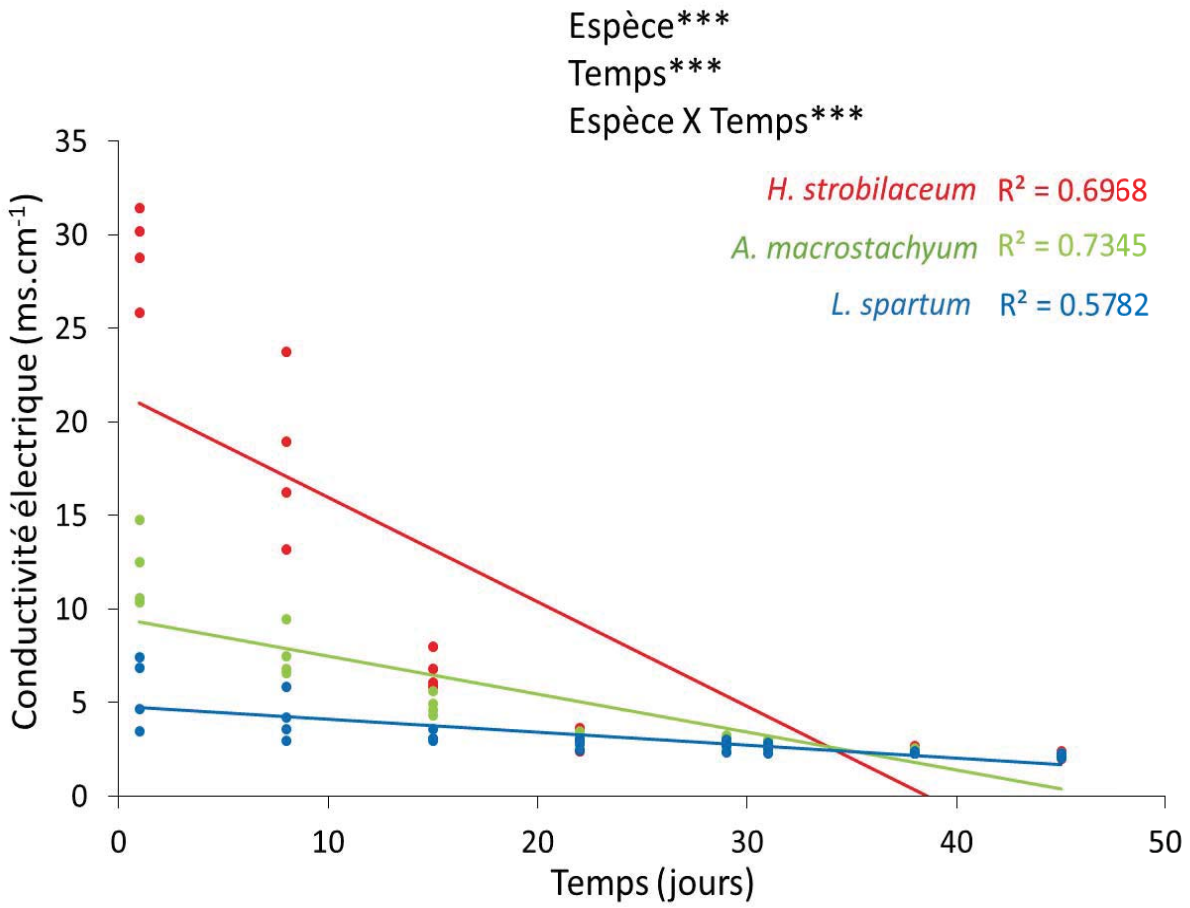

Figure 21: Chute de la salinité du sol des transplants des trois espèces cibles en fonction du temps

A l'issue de la phase de pépinière, et avec le démarrage des expérimentations, les transplants ayant développé des racines, ont été transplantés dans les sites expérimentaux.

2.3.4.2. Séparation des effets des voisins de court et long termes et des déterminants environnementaux et biotiques de ces interactions.

L'objectif principal de cette étude est d'évaluer les changements dans les effets à court et à long terme des arbustes dominants sur trois espèces de graminées cibles avec des stress croissants de sécheresse et de salinité, dans les dépressions salines continentales du climat méditerranéen aride du centre de la Tunisie.

L'effet du stress dû à la sécheresse a été évalué dans le temps, du printemps humide à la saison estivale sèche, alors que l'effet du stress salin a été évalué spatialement, en comparant les effets des voisins le long du gradient topographique de l'habitat 4 à l'habitat 3.

Cette expérience a débuté au mois de novembre 2017, et s'est achevée en septembre 2018. Des transplantations de trois espèces de *Poaceae* pérennes, ont été effectuées dans les huit Sebkhas étudiées, et uniquement dans les habitats H3 et H4 (H1 et H2, n'ont pas été considérés dans cette expérimentation, en raison de leur forte salinité), avec trois niveaux de voisinage (avec voisins, sans voisins arrachés et microhabitat naturellement sans voisins). Au total, 432 cibles (2 climats X 4 réplicas X 2 habitats X 3 espèces X 3 niveaux de voisinage X 3 individus) ont été transplantées. Les espèces de voisinage retenues furent :*Arthrocnemum macrostachyum* (H3) et *Salsola tetrandra* (H4).

Les cibles utilisées au cours de cette expérience, sont des espèces de *Poaceae* pérennes, naturellement présentes dans l'habitat 4, *Lygeum spartum* (Fig. 22), *Hyparrhenia hirta* (Fig. 23) et *Aristida adscensionis* (Fig. 24). Les transplants utilisés dans cette expérience, sont issus des touffes adultes des trois espèces de *Poaceae* pérennes. Nous avons effectué des éclats de touffes, comportant des feuilles et des racines. Ces éclats de touffes ont été immédiatement transplantés dans les différentes Sebkhas.

Figure 22: Cible *Lygeum spartum*.

Figure 23: Cible *Hyparrhenia hirta*.

Figure 24: Cible *Aristida adscensionis*.

2.3.4.3. Étude du Fonctionnement des écosystèmes

Durant cette étude, nous avons échantillonné la biomasse de chaque communauté végétale occupant les habitats H1 à H4 sous les deux types de climats et, à deux périodes de l'année, à savoir l'automne (début de la croissance végétale) et en été (fin de la croissance végétale). Parallèlement, nous avons quantifié la vitesse de décomposition des litières des espèces dominantes étudiées (*Halocnemum strobilaceum, Arthrocnemum macrostachyum* et *Lygeum spartum*).

- **Mesures de la biomasse des communautés**

Au cours de nos expérimentations, la biomasse a été échantillonnée durant deux périodes, soit au cours du mois de mai 2018 et du mois de septembre 2018. Ainsi, pour les habitats H1, H2, H3 & H4, nous avons mesuré par des coupes totales de la partie aérienne, la biomasse produite, par *Halocnemum strobilaceum (*en H1 et H2*)*, et l'ensemble des Chamaephytes de l'habitat H3 et aussi ceux de l'habitat H4 avec trois répétitions par parcelle de 100m^2, soit au total 192 échantillons récoltés. Pour chaque répétition la biomasse récoltée a été placée dans un sachet en plastique à part, scellé et numéroté, avant d'être lavée à l'eau de robinet, et placée à l'étuve à une température de 65°c, durant 3 jours. La biomasse sèche des échantillons a ensuite été pesée avec une balance de précision, de marque Mettler Toledo, Modèle XPR504S, avec 0,1mg de précision.

- **Étude de la décomposition de la matière organique des espèces**

Les espèces concernées par cette expérience sont: *Halocnemum strobilaceum*, *Arthrocnemum macrostachyum* et *Lygeum spartum.* Dans les quatre habitats (H1 à H4) des quatre Sebkhas de chaque climat, nous avons pour chacune de ces trois espèces, mis la litière dans une étuve à une température de 48°c. Ensuite, nous avons inséré une quantité de 50 gr de matière sèche foliaire dans des sacs de litière (Litter bag) à très petites mailles (1.5 x 1.5 mm). Ces sacs de litière de 10 X 7 cm de dimension, et au nombre de 576 (2 climats X 4 réplicas X 4 habitats X 3 espèces X 2 niveaux de voisinage X 3 répétitions de mesures), ont été enterrés en mars 2018 (début du printemps), à une profondeur d'environ 5 cm, dans des microsites ouverts, et sous les arbustes dominants dans chaque plot. En fin de saison de l'été (septembre 2018), tous les sacs de litière enterrés, ont été récupérés, puis nettoyés à l'eau, en vue de récupérer la fraction de la matière organique non décomposée. Celle-ci a été ensuite placée à l'étuve, à une température de 48°c durant 5 jours avant d'être pesée avec une balance de précision.

CHAPITRE II. EFFETS DES FACTEURS COMPLEXES SUR LES GRADIENTS ECOLOGIQUES, LA REPARTITION DE LA VEGETATION ET LE FONCTIONNEMENT DES ECOSYSTEMES.

1. EFFETS DES FACTEURS COMPLEXES SUR LES GRADIENTS ECOLOGIQUES & LA RÉPARTITION DE LA VÉGÉTATION

Cette partie a fait l'objet d'un article publié au *Journal of Vegetation Science* ,sous la référence suivante :

Chaieb G, Abdelly C, Michalet R .2019. Interactive effects of climate and topography on soil salinity and vegetation zonation in North-African continental saline depressions. *J Veg Sci*.; 30:312–321. https://doi. org/10.1111/jvs.12693.

Introduction

Dans ce premier chapitre nous présenterons les résultats de deux études observationnelles réalisées à l'échelle de l'ensemble de la zone aride de Tunisie pour identifier les interactions éventuelles existantes entre les variations de salinité et de stress hydrique (facteurs directs) et leurs relations avec la distribution des espèces et le fonctionnement des écosystèmes (productivité et décomposition de litières) le long des gradients (complexes) topographique et climatique (aride supérieur et aride inférieur).

La séparation entre facteurs complexes et facteurs directs corrélés à la distribution des espèces végétales s'est avérée cruciale en écologie théorique pour bien comprendre leur répartition dans respectivement les espaces géographique et écologique. Ceci permet notamment de comprendre comment les facteurs complexes interagissent pour déterminer la distribution écologique des espèces. Dans ce contexte, nous avons voulu comprendre comment l'aridité climatique croissante influence les gradients directs d'eau et de salinité du sol et de façon ultime la structure et la composition des communautés, le long du gradient topographique dans les Sebkhas.

Résultats principaux

Nous avons montré dans cette étude que l'aridité croissante modifiait le gradient de salinité, le long du gradient topographique. En effet, avec l'augmentation de l'aridité, la salinité du sol augmente dans les niveaux inférieurs du gradient topographique. En revanche, celle-ci décroit dans les niveaux supérieurs de ce même gradient complexe. L'augmentation de la salinité au niveau des habitats inférieurs s'explique par la diminution des précipitations et l'augmentation des températures avec l'aridité croissante, impliquant une augmentation de l'évaporation et par conséquent une importante concentration en sel dans les horizons supérieurs du sol. La diminution de la salinité dans les habitats supérieurs s'explique elle par le moins fort débordement de l'eau salé en hiver en climat aride inférieur.

Nous avons constaté que les deux facteurs écologiques complexes, à savoir, la topographie et le climat, interagissent significativement pour engendrer une variation au sein de l'espace géographique en termes de facteurs écologiques directs tels que la salinité, d'humidité du sol et d'une éventuelle perturbation anthropique. L'ensemble de ces facteurs écologiques directs interviennent dans la zonation de la végétation dans les dépressions salines continentales.

Le climat modifie les gradients de salinité et de structure de la végétation. Par contre, il n'intervient pas dans la composition de la végétation, en raison de sa faible variation dans le cas de notre étude. Ce constat se justifie d'ailleurs par les analyses multivariées, qui révèlent un important effet des espèces abondantes. De plus, nous avons constaté dans l'aride inférieur, que la salinité collapse au niveau de la limite supérieure du gradient topographique. Ce collapse est probablement dû au faible flux d'eau dans les situations de contrainte hydrique.

Parallèlement, en allant de l'aride inférieur vers l'aride supérieur, nous avons constaté que le couvert végétal total et l'abondance relative des Thérophytes sont importants à l'extrémité la plus élevée du gradient topographique. Ce constat est principalement lié à l'humidité croissante dans l'aride supérieur, et l'augmentation de la perturbation anthropique (Labour & pâturage) dans les habitats supérieurs (généralement fertiles) des Sebkhas.

Ces résultats montrent qu'il est nécessaire de séparer les facteurs directs, salinité (gradient direct non de ressource) et l'eau du sol (gradient de ressource) pour mieux comprendre les variation d'interactions biotiques le long des gradients complexes.

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RESEARCH ARTICLE

Journal of Vegetation Science IAVS

Interactive effects of climate and topography on soil salinity and vegetation zonation in North-African continental saline depressions

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Abstract

Questions: Complex distal factors such as climate and topography can interact to drive direct proximal ecological gradients and vegetation zonation in geographical and ecological space, in particular salinity and soil moisture in arid climates. We pose the following questions: (a) Does increasing climate aridity alter direct water and salinity gradients along topography gradients in saline depressions in arid climates? (b) Do these effects of increasing climate aridity in turn alter vegetation life-form zonation? (c) Does increasing climate aridity alter community composition along the zonation?

Study site: Continental saline depressions of the Mediterranean arid climate of central and southern Tunisia.

Methods: We sampled vegetation structure, diversity, and composition and environmental variables at five positions along the topography gradient of continental saline depressions in wet and dry conditions.

Results: Climate aridity altered salinity gradients and vegetation structure but not diversity and community composition. Salinity increased with increasing aridity at the lowest positions of the depressions but decreased with increasing aridity at their highest positions. Total vegetation cover and relative abundance of therophytes decreased, whereas relative abundance of chamaephytes increased with increasing climate aridity at the upper habitats.

Conclusions: Ecological factors acting at a regional scale can alter the spatial variation of other ecological factors acting at smaller spatial scales, ultimately explaining vegetation zonation in continental saline depressions. Salinity collapses with increasing aridity.

KEYWORDS

aridity, chamaephytes, complex gradients, continental saline depressions, direct gradients, salinity, therophytes

1 | INTRODUCTION

One key conceptual and methodological progress in ecology has certainly been achieved with the distinction between complex and direct factors correlated to species distribution in the geographical and ecological spaces, respectively (Austin & Smith, 1989; Naveh & Whittaker, 1980; Whittaker, 1965, 1978). The most striking examples illustrating the importance of this distinction have been provided by studies assessing variation across latitudinal gradients of the ecological distribution of species or of ecological processes along elevation gradients (Cavieres, Badano, Sierra-Almeida, Gómez-González, & Molina- Montenegro, 2006; Körner, 2003; Ohsawa, 1995; Ozenda, 1975).

Additionally, it is crucial to assess how complex factors, such as climate, rock type and topography, interact with each other for shaping direct ecological gradients and plant species distributions in geographical space. Examples of striking variation in plant species zonation along topography, snow cover or soil depth gradients across climates or rock types have been provided in particular in alpine systems (Bamberg & Major, 1968; Gibson & Kirkpatrick, 1985), highlighting for example the overlooked role of water availability and plant–plant interactions in alpine systems (Michalet, Gandoy, Joud, Pages, & Choler, 2002).

Coastal salt marshes are another well-studied system for understanding how large-scale climate factors interact with local topography for shaping direct gradients of physical disturbance, waterlogging, water availability and salinity, and ultimately vegetation distribution (Fariña, He, Silliman, & Bertness, 2017; Pennings & Callaway, 1992). It has been shown, in particular in northern Atlantic marshes, that physical stresses, such as waterlogging and salinity, decrease with increasing elevation along topography gradients and that the lower limits of plants are more determined by physical stress, while their upper limits are determined by competition (Bertness, 1991; Bertness & Pennings, 2002). However, Pennings and Callaway (1992) showed in drier Mediterranean marshes from California that the least stressful position with important competition between species was rather at mid-position along the topography gradient, whereas physical stress was the highest at the two extremes of the gradient, because of waterlogging at its lowest end and drought and salinity stresses at its highest end. In an important comparison of salt marsh zonation along topography gradients across latitudes in Chile, Fariña et al. (2017) showed that intertidal plant species zonation was present in hyper-arid and semi-arid climates, but not in humid and hyper-humid climates. Low-latitude salt marshes were shown to have steeper soil salinity and moisture gradients, because hotter climates increased soil salinity at high elevations due to evaporative salt accumulation (Pennings, Selig, Houser, & Bertness, 2003). In contrast, in more humid high latitudes of Chile, water availability and soil salinity were not limiting factors for plants at the highest end of the topographic gradient (Bertness & Pennings, 2002; Fariña et al., 2017).

Salinity is known also to be an important driving factor of vegetation zonation along local topography gradients in continental saline depressions from arid climates. However, to our knowledge, there has been no attempt to assess how large-scale climate factors might interact with local topography to alter vegetation zonation in saline depressions. Continental saline soils have been widely studied, in particular in agronomy and soil science, due to the negative effect of salinity on crop productivity and water quality (Mahajan & Tuteja, 2005; Metternicht & Zinck, 2003; Rengasamy, 2006; Zhu, 2001). It is often assumed that the importance of salinity for soil processes, crop yield and, thus, wild plant distribution, should increase with increasing drought in arid and semi-arid climates because of lower water drainage, as in coastal salt marshes (Chaves, Flexas, & Pinheiro, 2009). Indeed, saline soils are increasingly frequent in upper slopes as water drainage decreases with increasing drought because decreasing rainfall and increasing potential evapotranspiration enhances salt concentration in soils (Duchaufour, 1997). In contrast, in wet climates saline soils are only present in concave topography close to saline sources. However, extreme aridity may alternatively decrease the frequency of saline soils, due to lower salt transfer in the slopes with water scarcity. Therefore, the effect of salinity on natural and human-managed ecosystems might collapse in desert climates.

Thus, our knowledge of the interactive effects between climate and topography on direct ecological gradients, in particular salinity, and ultimately plant species distribution in continental saline depressions, is still limited. In order to address this issue, we conducted an observational study in arid central Tunisia (North Africa), a country known for its abundance of continental saline depressions (locally named sebkhas). In continental saline depressions, along a climatic drought gradient expanding from central to southern Tunisia, we assessed the interactive effects of climate and topography on water and salinity gradients and plant species distribution. We aim to answer the following questions:

1. Does increasing climate aridity directly alter water and salinity gradients occurring along complex topography gradients in saline depressions of arid Tunisia?
2. Do these effects of increasing climate aridity in turn alter vegetation life-form zonation?
3. Does increasing climate aridity alter community composition along the zonation?

2 | METHODS

2.1 | Materials

This study was conducted in continental saline depressions along a 400-km-long climate gradient expanding from central to southern Tunisia, at the border with Libya. In this part of Tunisia, climate is Mediterranean arid following Emberger's classification (Emberger, 1955). Mean annual precipitation in the arid climate is included

between 100 and 250 mm and the mean temperature is 19.0°C, with a minimum of 4.6°C in winter and a maximum of 37.0°C in summer (Le Houérou, 2008). As for other Mediterranean climates, summer is the driest season, but due to the high aridity induced by rain shadow effects, rainfall during other seasons is low and very unpredictable among years (Michalet, 1991). Saline soils are very abundant, covering ~1.5 million of hectares and, thus, 10% of the surface of the country, likely due to the important occurrence of low-elevation plains in an arid Mediterranean climate (Hachicha, 2007). Most saline soils are observed in large depressions named sebkhas, with sizes varying between 10 and 300 km^2 and with rounded or lentil-like shapes. They are always composed of an important central part with no vegetation, irregularly inundated during the wetter cold season and surrounded by a narrow string (<200 m) of saline-tolerant vegetation on the edge of the depressions. The surrounding vegetated zone is formed of several distinct vegetation belts distributed in relation to elevation along the topography gradient from the central zone of the sebkhas to the ploughed fields at the edge of the depression (Supporting information Appendix S1). The difference in elevation between the central zone without vegetation and the ploughed fields at the edge of the sebkhas is always very low (<1 m) (Floret & Pontanier, 1982), but sufficient to induce strong gradients in salinity and waterlogging that are likely to drive the zonation of the halophytic vegetation (Floret & Pontanier, 1982). Dominant species are shrubs, mostly from the Chenopodiaceae family (*Halocnemum strobilaceum*, *Arthrocnemum macrostachyum*, *Salsola tetrandra Suaeda mollis* and *Atriplex halimus*), but also from the Zygophyllaceae (*Zygophyllum album*), Tamaricaceae (*Reaumuria vermiculata*) families and the grass *Lygeum spartum*. Finally, at the external limit of the sebkhas, shrubs are replaced by therophytes, such as *Diplotaxis harra*, *Diplotaxis simplex*. and *Erodium glaucophyllum*, at the ecotone with ploughed fields (Chaieb, 2015). Species were identified using the Flora Med-Checklist (Greuter, Burdet, & Long, 1984; –1989) and the Index synonymique de la Flore d'Afrique du Nord (Dobignard & Chatelain, 2010–2013).

2.2 | Experimental design

In order to assess how increasing aridity may affect direct gradients of water and salinity, and vegetation zonation along topography gradients in the Tunisian saline depressions, we set up an experimental design including two main parameters, climate aridity and habitat (i.e., topographic positions). We first randomly selected as main plots eight sebkhas in two conditions of climate aridity (four in each) within the arid Mediterranean climate of Tunisia (Supporting information Appendix S2) and then five subplots in each sebkha for the habitat. We chose to select our sites within the arid Mediterranean climate because this climate covers approximately two thirds of the country, mostly in southern and central Tunisia, and includes most of the saline soils of the country (~75%; Chaieb, 2015). Following the bioclimatic classification of Emberger, the Mediterranean arid climate has been divided in two subclimates, the upper arid climate and the lower arid climate (Emberger, 1958). Mean annual precipitation is 200–300 mm in the upper arid climate and 100–200 mm in the lower arid climate. Thus, for our climate aridity parameter we selected four sebkhas within the upper arid climate and four sebkhas within the lower arid climate. However, to avoid confusion and for simplicity, throughout the paper upper arid was replaced by wet and lower arid by dry. Those eight sebkhas were located in a 400-km-long plain with a similar management. Thus, climate was the main driver of vegetation change along this latitudinal gradient with no other likely confounding environmental variation (Le Houérou, 2008). The De Martonne aridity index (I_m) was in the range between 7.4 and 10.5 for the four sites from the wet climate and between 5.2 and 6.1 for the four sites from the dry climate (Supporting information Appendix S2) (De Martonne, 1923).

For the habitat, we selected in each sebkha five 1,000-m^2-large subplots that were located at different positions along the topography gradient. We randomly located a transect within the sebkhas and selected a first subplot in the central zone with no vegetation, at a distance of at least 10 m from the first growing plants (center-habitat H1), and a second subplot at the upper edge of the sebkhas, i.e., the ecotone with the ploughed fields surrounding the sebkhas (edge-habitat H5). Then, we positioned a third subplot at an intermediate spatial and elevation position between the two extreme subplots H1 and H5 (intermediate habitat H3). The two last subplots (second-lowest H2 and second-highest H4) were similarly positioned at intermediate positions between H1 and H3 and between H3 and H5, respectively. We chose not to position subplots at fixed distances along transects in all sebkhas, because the width of the vegetation zones varied between sebkhas, depending on the slopes of the local topography gradient.

2.3 | Sampling

In each of the 40 subplots (2 climates × 5 habitats × 4 replicates), we sampled environmental conditions, but vegetation structure and composition were only sampled in 32 of the 40 subplots (2 climates × 4 habitats × 4 sebkhas), because we did not sample habitat 1 for vegetation due to its absence. In mid-March 2015 (two months after the last rain event), we measured soil salinity (electrical conductivity), soil water content, soil temperature, and soil pH at two soil depths (0–20 cm) and (20–40 cm), using a HH2 moisture meter (Delta-T Devices, Cambridge, UK) for the three former variables and a field pH-meter (type Hana) for the latter. Due to the patchy structure of the vegetation in all habitats, measurements were always made randomly in open areas between vegetation patches, with five repetition measurements of each environmental variable in each of the 40 subplots. The five repetition measurements of environmental variables per subplot were pooled before statistical analyses.

In mid-March 2015, we assessed vegetation structure, species density and species abundance, three complementary metrics of plant communities. We used three different sampling procedures,

each adapted to each response variable. For vegetation structure, we used the line intercept method to quantify the total vegetation cover and cover of the different Raunkiaer life forms (Raunkiær, 1934). Following Daget and Poissonet (1971), we randomly located three 10-m-long transects in each of the 32 subplots, recording every contact of plant individuals of each Raunkiaer life-form group with a rod positioned within the vegetation every 10 cm along the transects. Due to the overwhelming dominance of therophytes and chamaephytes in all habitats, other groups (geophytes and hemicryptophytes) were pooled in a third group before statistical analysis. Since there were very few species in most habitats, species density was measured by counting the number of species in three 1-m^2-large quadrats randomly located in each of 32 subplots. Thus, a total of 96 (2 climates × 4 habitats × 4 sites × 3 repetition measurements) values of life-form group cover, total vegetation cover and species density were collected, but the three values of each replicate of each parameter combination were pooled before statistical analyses per subplot for each of these response variables. Additionally, the abundance of each species (i.e., number of individuals of each species) was quantified in one 100-m^2-large quadrat, randomly located in each of the 32 subplots, in order to have representative abundance values.

2.4 | Data analysis

We first used a split-plot ANOVA model using R package agricolae (R Core Team, R Foundation for Statistical Computing, Vienna, Austria) for randomized complete block design to assess the effects of the climate and habitat and their interaction on soil electrical conductivity and soil moisture at each soil depth, with climate as main factor and habitat as subfactor, sebkhas as blocks, and electrical conductivity and soil moisture as response variables. Since salinity was highly correlated to topography positions (habitat factor), we then chose to assess how total vegetation cover and species density varied according to salinity depending on climate conditions. For this, we used a split-plot mixed analysis of covariance (ANCOVA) with climate as main factor, soil salinity (soil electrical conductivity) as continuous subfactor, sebkhas as blocks and total vegetation cover and species density as response variables. We used two expressions of salinity (salinity and salinity^2) to potentially detect non-linear relationships (Maalouf, Le Bagousse-Pinguet, Marchand, Touzard, & Michalet, 2012). Data on relative cover of Raunkiaer life-form groups (chamaephytes, therophytes, two other forms pooled) were analyzed using a split-split-plot mixed analysis of covariance (ANCOVA) with climate as main factor, salinity (or salinity^2) as continuous subfactor, and life form as subsubfactor.

Additionally, we conducted separate multivariate analyses on environmental variables and vegetation composition data since habitat 1 was only sampled for environmental variables due to the absence of vegetation. We conducted a Principal Component Analysis (PCA) on a table including for the 40 subplots (2 climates × 5 habitats × 4 replicates) the eight environmental variables (salinity, soil moisture, soil temperature and soil pH, all sampled at two soil depths) measured at the subplot level and the three climate variables recorded at the (plot) sebkhas level (min temperature, max temperature and precipitation). Data on species abundances recorded in the 32 subplots including vegetation (2 climates × 4 habitats × 4 replicates) were also analyzed with a PCA. The PCA was conducted on 71 species since 59 species (out of 130) with a frequency lower than 3 in the 32 subplots were excluded from the analysis. In order to assess if our parameters had significant effects on species composition, we conducted split-plot ANOVAs on the effect of climate (main parameter) and habitat (subparameter) and their interaction on plot scores along the two first PCA axes. Dependent variables were checked for normality and log-transformed before ANOVAs. All statistical analyses were done using R.

3 | RESULTS

Salinity and soil moisture were positively correlated, both strongly increasing from the edge to the center of the sebkhas. This habitat effect was highly significant at both soil depths and in both climates (Figure 1). However, there was a significant habitat × climate interaction for both salinity and soil moisture at a depth of 20–40 cm. The slope of increasing salinity and soil moisture from the edge to the center of the sebkhas was steeper in the dry than in the wet climate (Figure 1b, d). In other words, at the edge of the sebkhas (habitats 4 and 5) salinity and soil moisture were lower in the dry than in the wet climate, but the reverse was observed at the center of the sebkhas (habitats 1 and 2).

In all climate conditions, both vegetation cover and species density decreased linearly with increasing salinity from the edge to the center of the sebkhas (Figure 2). However, and for cover only, there was a significant climate × salinity interaction, because the slope of decreasing vegetation cover with increasing salinity was steeper in the wet than in the dry climate (Figure 2a). In other words, for low salinity values (i.e., at the edge of the sebkhas), vegetation cover was higher in the wet than in the dry climate, whereas the reverse was observed at high salinity values (i.e., at the center of the sebkhas).

There was a highly significant life-form effect on life form relative cover in Figure 3, due to the much higher relative abundance of chamaephytes and therophytes as compared to other life forms (two other groups pooled) all along the salinity gradient and in both climates. However, there was a highly significant salinity × life-form interaction because in both climates therophytes dominated at low salinity levels and chamaephytes at high salinity levels. Additionally, there was a significant salinity × climate × life-form interaction, because the switch in dominance between therophytes and chamaephytes with increasing salinity was stronger in the wet than in the dry climate. In other words, in the wet climate there were both more therophytes at low salinity levels and more chamaephytes at high salinity levels than in the dry climate.

The first axis of the PCA conducted on species abundances was highly significantly related to the topography gradient, with the highly saline habitats 2 of the center of the sebkhas on the positive

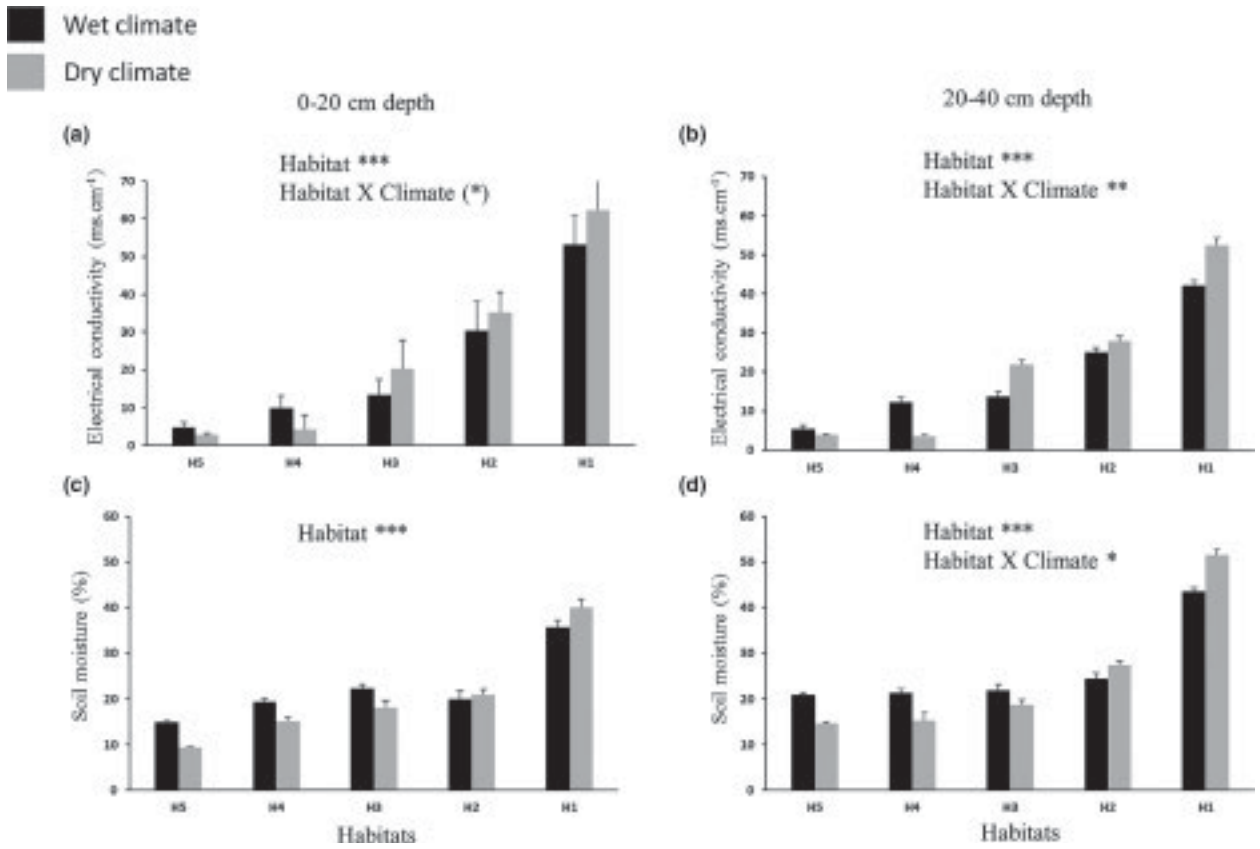

FIGURE 1 Mean (N = 40, ±SE) of soil electrical conductivity (upper panels [a] and [b]) and soil moisture (lower panels [c] and [d]) at 0–20 cm depth (left panels [a] and [c]) and 20–40 cm depth (right panel [b] and [d]) in the five habitats and the two climate conditions. Significant results of the split-plot ANOVAs on the effects of the habitat, climate and their interaction on each response variable are shown above each panel: *p < 0.1; *p < 0.05; **p < 0.01; ***p < 0.001

side of the axis opposite to the low-salinity habitats 4 and 5 of the edge of the sebkhas in the negative side of the axis (Figure 4a). Habitats 3, characterized by intermediate salinity values, were located at intermediate position between these two extreme habitats, although much closer to the latter. Axis 2 was weakly explained by habitat position, with mainly habitats 3 on the positive side of the axis opposite to habitats 5 on its negative side. The first axis of the PCA conducted on environmental variables was positively correlated to both salinity and soil moisture, and, thus, linked to the topography gradient, with the habitats from the edge of the sebkhas on the negative side of the axis and the habitats from the center of the sebkhas on its positive side (Figure 4b). The second PCA axis was negatively correlated with precipitation and positively correlated with soil temperature, and thus related to climate conditions, with sebkhas from the wet climate on the negative side of the axis and sebkhas from the dry climate on its positive side. There were also interesting interactions between climate and salinity occurring on both axes. On axis 1, consistent with the results of Figure 1, there were stronger differences in salinity across the topography gradient in the dry than in the wet climate. On axis 2, there were stronger climate differences (likely soil temperature) in the center than on the edge of the sebkhas.

4 | DISCUSSION

In response to our first question, we found that climate aridity altered the relationship occurring at small scales between topography and salinity in continental saline depressions. We found in particular that the gradient of salinity was wider in the dry than in the wet climate because of both higher salinity at the center and lower salinity at the edge of the sebkhas. In response to our second question, we also found that climate aridity altered the patterns of vegetation structure along the topography gradient. We found specifically that the decrease in total vegetation cover and the switch from therophytes to chamaephytes occurring with decreasing elevation were both stronger in the wet than in the dry climate. In contrast, there was a high consistency of the gradients in richness and vegetation composition since we did not find significant effects of climate aridity on these vegetation variables. This study improves our knowledge on the interactive effects of complex factors in driving direct ecological gradients and vegetation zonation in the geographical and ecological spaces. In addition, this knowledge might help our prediction of the effects of increasing climate aridity on salinity gradients and vegetation zonation with climate change in arid ecosystems.

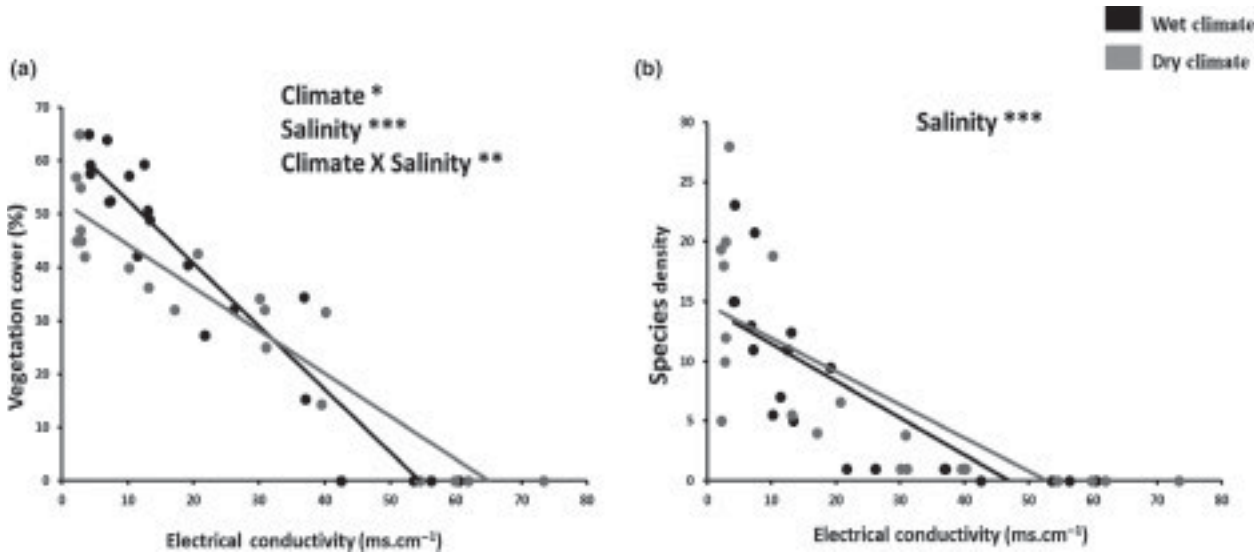

FIGURE 2 The relationships between salinity and total vegetation cover (a) and species density (b) under wet and dry climate conditions. Significant results of the split-plot ANCOVAs on the effect of salinity, climate and their interaction are shown above each panel: $*p < 0.05$; $**p < 0.01$; $***p < 0.001$

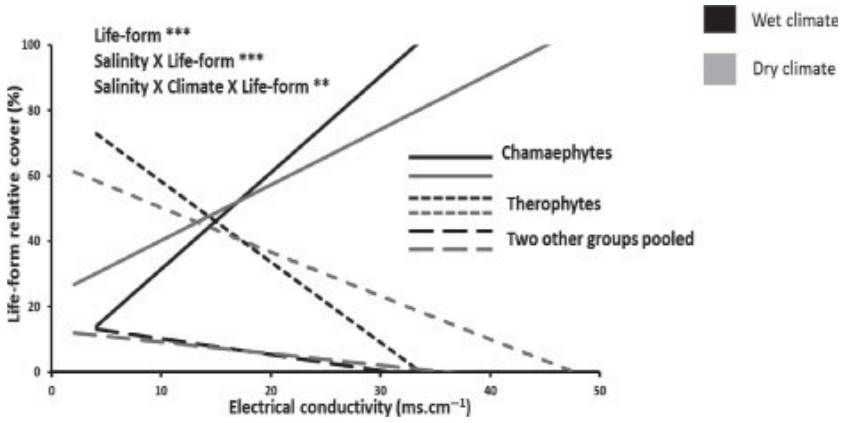

FIGURE 3 The relationships between relative vegetation cover and salinity for three Raunkiaer groups (chamaephytes, therophytes, three other groups pooled) under wet and dry climate conditions. Significant results of the split-split-plot ANCOVA on the effects of salinity, life form, climate and their interactions are shown above the graph: $**p < 0.01$; $***p < 0.001$

4.1 | The alteration of the salinity gradient along the topography gradient

In the three habitats (H1, H2 and H3) of the center of the saline depressions, salinity was higher in the dry than in the wet climate, whereas the opposite pattern was observed in the two habitats from their edge (H4 and H5). The highest salinity of the center habitats can very likely be explained by the lower rainfall and higher temperatures of the dry climate enhancing salt concentration through the increase in evaporative demand (Duchaufour, 1997). However, the converse patterns observed at the edge of the sebkhas may seem inconsistent with our knowledge from salt marshes, or agronomy and soil science studies. Indeed, in intertidal salt marshes increasing climate aridity in dry Mediterranean climates has been shown to increase both salinity and drought at the upper end of the marshes as compared to wet marshes from temperate climates (Fariña et al., 2017; Pennings & Callaway, 1992). Salinity increases there because hotter climates increase soil salinity at high marsh elevations due to evaporative salt accumulation (Pennings et al., 2003). Interestingly, the relationship between salinity and soil moisture was opposite in our study, as compared to dry coastal salt marshes from Mediterranean and subtropical climates. In our study, salinity and soil moisture were tightly positively correlated, with the lowest salinity and soil moisture occurring at the edge of the sebkhas and the highest salinity and soil moisture at their center, in particular in the dry climate. In contrast, in dry coastal marshes salinity decreases but soil moisture increases from the higher to the lower end of the intertidal gradient. This difference is likely due to the high dependency of soil salinity on water transfer. Indeed, topography patterns of soil moisture and soil salinity might differ between continental and coastal systems because water transfer in the upper coastal marshes is independent of climate, being only influenced by the tides, whereas climate aridity only drives water transfer in continental saline depressions. In other words, in coastal marshes salt accumulates more at the upper end of the topography gradient in dry than in wet climates because salt

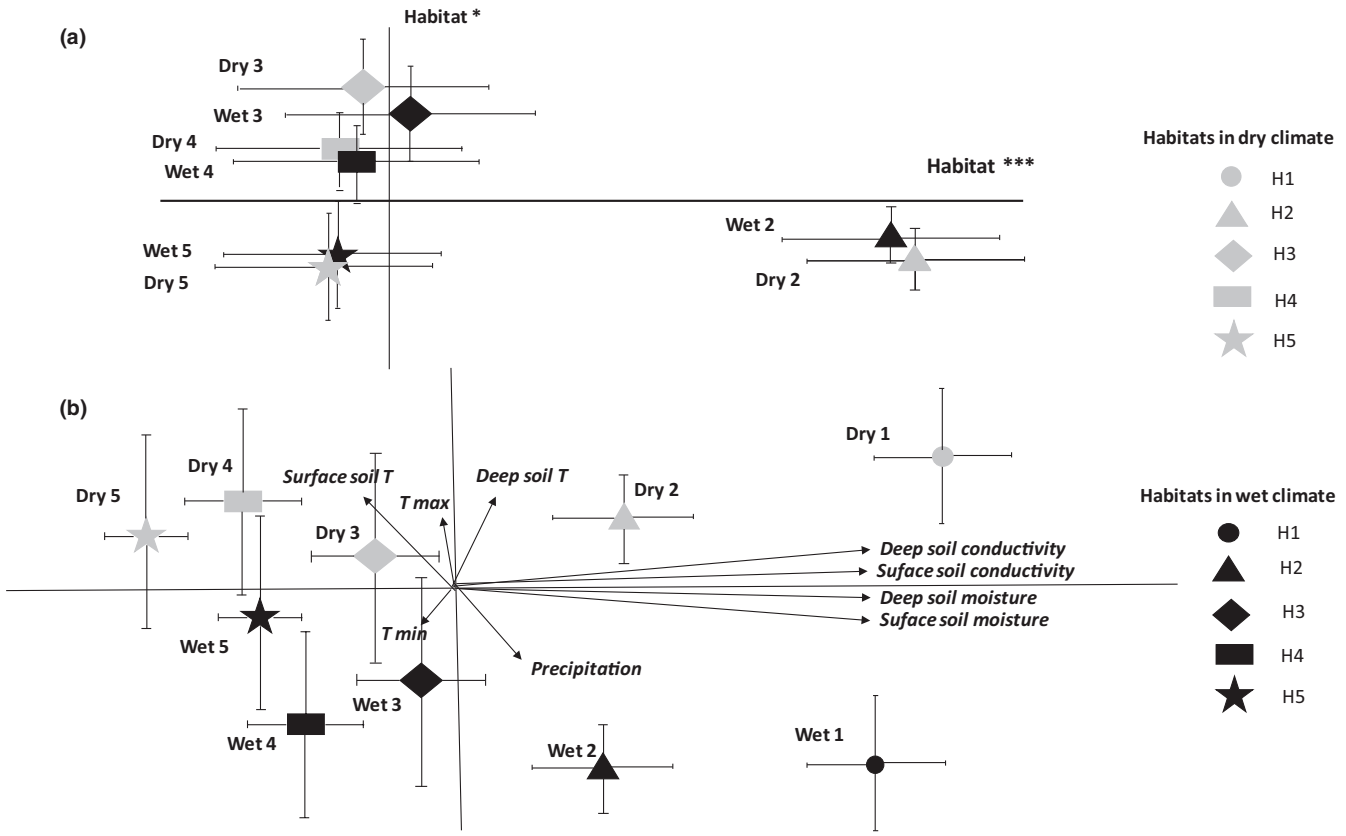

FIGURE 4 (a) Diagram of the Principal Component Analysis (PCA) conducted on vegetation abundance data with means (±*SE*) of plot scores for the four habitats in each climate condition. Results of the split-plot ANOVAs conducted on the effects of the climate and habitat and their interaction on PCA scores on each axis are shown near axes labels, (b) diagram of the PCA conducted on environmental variables. Symbols represent the mean scores (±*SE*) of the five habitats in each climate condition

is always transferred by the ocean at this elevation during the high tides and the increasing evaporative demand with increasing aridity increases salinity while decreasing soil moisture. In contrast, in continental saline depressions, with increasing climate aridity there is likely a decrease in salt transfer towards the edge of the sebkhas because of the decrease in water drainage. Indeed, during exceptionally wet winters it is very common to see the saline depressions fully inundated in the wet climate, whereas in those from the dry climate inundation is more limited to the center of the depressions (G. Chaieb, personal observation, January, 15, 2015). In other words, at the upper end of the depressions salinity and soil moisture were lower in the dry than in the wet (arid) climate, likely because saline water very rarely reaches this elevation in the former climate. Thus, salinity collapses (sensu Michalet et al., 2006) at the extreme end of aridity gradients in our study, whereas salinity never collapses at the upper end of the topography gradient in intertidal salt marshes even in the driest climates (He & Bertness, 2014) because salty water brought by the tide still reaches this habitat while continental water fluxes have stopped.

These contrasting results observed between continental and coastal intertidal saline ecosystems suggest that the classic pattern of increasing soil salinity with increasing aridity described in agronomy and soil science might be explained by the irrigation of arid soils by salty water to enhance crop production (Hu & Schmidhalter, 2005; Rengasamy, 2006). Indeed, our results showed that in natural arid ecosystems like those from our study, in the absence of irrigation, salinity decreases with increasing aridity at the edge of the saline depressions due to the decrease in salt transfer induced by decreasing water fluxes. Thus, the opposite pattern observed in agronomy and soil science might be induced by soil irrigation maintaining water transfer in soils of dry climates, enhancing salt concentrations with increasing potential evapotranspiration. This finding is important for managing arid soils and water quality in agriculture, in particular in a climate change context with predictions of increasing drought in low-latitude countries such as Tunisia (IPCC, 2015).

4.2 | The alteration of vegetation zonation along the topography gradient

At the center of the sebkhas, we found a lower total vegetation cover in the wet than in the dry climate. In contrast, there was a higher total vegetation cover at the edge habitats and thus, a steeper decrease in total vegetation cover with decreasing elevation in the dry than in the wet climate. The lower vegetation cover of the center habitats of the wet climate cannot be due to higher soil salinity or lower soil moisture than in the dry climate because both variables

showed opposite patterns of variation across climate conditions in these habitats. Thus, the likely explanation is the highest frequency and duration of inundation occurring in the wet rather than in the dry climate, due to higher winter rainfall and lower potential evapotranspiration with decreasing aridity (see Supporting information Appendix S2). Waterlogging stress and physical disturbances are known to be the main direct ecological factors driving marsh vegetation limits at the lowest intertidal levels in coastal salt marshes (Bertness, 1991; Bertness & Pennings, 2002; Pennings & Callaway, 1992). In coastal marshes, the frequency and duration of inundation driving this lower limit are regulated by sea level and tidal rhythm, whereas in continental saline depressions the driving factor of inundation, and thus of this lower limit, is likely climate humidity. Similarly, at the edge habitats the increase in total vegetation cover occurring with increasing climate humidity cannot be driven by salinity, because in the two highest habitats salinity was higher in the wet than in the dry climate. Thus, the most likely explanation is the lower drought stress occurring in the wet than in the dry climate (Grime, 1973; Maestre et al., 2012).

There was a clear shift in relative abundance of vegetation life forms along the topography gradient in both climates, with a large dominance of therophytes at the edge of the sebkhas and of chamaephytes at their center. This pattern has been observed in many arid climates and was explained by both the higher salt tolerance of chamaephytes and the higher tolerance for disturbance (due to grazing and ploughing) of therophytes (Callaway, 1994; Castro, Lehsten, Lavorel, & Freitas, 2010; Grime, 1974; Jauffret & Lavorel, 2003; McIntyre, Lavorel, & Tremont, 1995; Noe & Zedler, 2001). Interestingly, this shift was more important in the wet than in the dry climate, due in particular to a much higher dominance of therophytes at the edge of the sebkhas. This higher relative abundance of therophytes in the wet than in the dry climate cannot be due to lower salinity in the wet climate because salinity conversely increased with increasing humidity in the edge habitats. Thus, the increase in disturbance due to grazing and ploughing with increasing humidity is very likely to drive this variation in life-form dominance across climate conditions. This result also suggests that variation in vegetation structure across climate conditions at the edge of the saline depressions is not driven by salinity, which certainly reaches levels too low to have any important effect on community structure. Indeed, salinity of the habitats of the center of sebkhas from both climates reaches very high values that impede the germination and growth of therophytes. In contrast, the low salinity of the edge habitats is suitable for therophytes. Thus, edge habitats are likely more disturbed through overgrazing and cultivation, in the wet than in the dry climate. However, additional measurements of disturbance are necessary before conclusions can be drawn. In addition, the variation from topography to salinity shown in Figures 1, 2, 3 indicates that this gradient alteration is more steeper in wet arid than in dry arid because of decreasing aridity.

We found no significant effect of climate on species composition. There are two main reasons for this absence. To begin, multivariate analyses are known to be highly sensitive to the abundance of dominant species and most of the habitats (in particular habitats 2 and 3) of the saline depressions in wet arid and dry arid; are occupied by Chenopodiaceae communities exhibiting often 80%–100% of the community biomass and species abundances. So this similarity of Chenopodiaceae dominance in wet arid and dry arid show no differences between the two climates. The other reason is that our climate factor was likely not strong enough to have induced effects on species composition, the most important biotic responses being changes in abundance of dominant species. Indeed, there was only a maximum of 50% more rainfall in the wet than in the dry climate in our study, which was much lower than the differences occurring in other studies, such as in the coastal salt marshes of Chile (Fariña et al., 2017).

5 | CONCLUSION

We found that two complex ecological factors, topography and climate, significantly interacted to drive variation in the geographical space in salinity, soil moisture and likely disturbance, i.e., the ecological factors directly explaining vegetation zonation in continental saline depressions. Climate altered salinity gradients and vegetation structure but not vegetation composition, likely due to the weak variation in climate in our study and the overwhelming influence of abundant species in multivariate analyses. Interestingly, we found that salinity collapsed in the dry climate at the edge of the continental saline depressions, likely because of a collapse of water fluxes in extremely dry conditions. This contrasts what has been described in agronomy, soil science and coastal salt marshes, likely because of constant irrigation by farmers in the two former cases and by the ocean at high tide in the latter. We also found that total vegetation cover and the relative abundance of therophytes increased at the highest end of the topography gradient from dry to wet climate, primarily because of decreasing water stress and thus increasing disturbance by grazing and ploughing in the arid climate.

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AUTHOR CONTRIBUTIONS

G. C. & A. C. designed the experiment; G. C. & A. C. did the fieldwork; G. C. and R. M. analyzed the data; R. M. and G. C. wrote the paper; all authors contributed to the correction of the manuscript.

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REFERENCES

Austin, M. P., & Smith, T. M. (1989). A new model for the continuum concept. *Vegetatio*, *83*, 35–47. https://doi.org/10.1007/978-94-009-1934-1_4

Bamberg, S. A., & Major, J. (1968). Ecology of the vegetation and soils associated with calcareous parent materials in three alpine regions of Montana. *Ecological Monographs*, *38*, 127–167. https://doi.org/10.2307/1942290

Bertness, M. D. (1991). Zonation of *Spartina patens* and *Spartina alterniflora* in New England salt marsh. *Ecology*, *72*, 138–148. https://doi.org/10.2307/1938909

Bertness, M. D., & Pennings, S. C. (Eds.) (2002). Spatial variation in process and pattern in salt marsh plant communities in eastern North America. In M. P. Weinstein & D. A. Kreeger (Eds.), *Concepts and controversies in tidal marsh ecology* (pp. 39–57). Dordrecht, the Netherlands: Springer.

Callaway, R. M. (1994). Facilitative and interfering effects of *Arthrocnemum subterminale* on winter annuals. *Ecology*, *75*, 681–686. https://doi.org/10.2307/1941726

Castro, H., Lehsten, V., Lavorel, S., & Freitas, H. (2010). Functional response traits in relation to land use change in the Montado. *Agriculture, Ecosystems & Environment*, *137*, 183–191. https://doi.org/10.1016/j.agee.2010.02.002

Cavieres, L. A., Badano, E. I., Sierra-Almeida, A., Gómez-González, S., & Molina- Montenegro, M. A. (2006). Positive interactions between alpine plant species and the nurse cushion plant *Laretia acaulis* do not increase with elevation in the Andes of central Chile. *New Phytologist*, *169*, 59–69. https://doi.org/10.1111/j.1469-8137.2005.01573.x

Chaieb, G. (2015). *Relation plante–sol en milieu salin sous bioclimat aride: Mise en évidence d'un modèle*. [Plant–soil relationship in saline soils under arid climate: Highlighting a model]. Master Dissertation, Marseille, France: Aix-Marseille University.

Chaves, M. M., Flexas, J., & Pinheiro, C. (2009). Photosynthesis under drought and salt stress: Regulation mechanisms from whole plant to cell. *Annals of Botany*, *103*, 551–560. https://doi.org/10.1093/aob/mcn125

Daget, P., & Poissonet, J. (1971). Une méthode d'analyse phytosociologique des prairies [Application of method of phytosociology in grassland]. *Critères d'application. Annales Agronomiques*, *22*, 41–45.

De Martonne, E. (1923). Aridité et indices d'aridité [Aridity and aridity indices]. *Académie des Sciences. Comptes Rendus*, *182*, 1935–1938.

Dobignard, A., & Chatelain, C. (2010–2013). *An index of synonyms for the flora of North Africa*. Genève, Switzerland: Conservatoire et Jardin Botaniques.

Duchaufour, P. (Ed.) (1997). *Abrégé de pédologie. Sol, végétation, environnement* [Abstracts of pedology. Soil, vegetation environment]. Paris, France: Masson.

Emberger, L. (1955). Une classification biogéographique des climats [Biogeography classification of climats]. *Travaux de l'Institut Botanique de Montpellier*, *7*, 3–43.

Emberger, L. (1958). Afrique du Nord et Australie méditerranéenne [North Africa and Mediterranean Australia]. *Climatologie et microclimatologie* [Climatology and microclimatology] (pp. 141–146). Paris, France: UNESCO.

Fariña, J. M., He, Q., Silliman, B. R., & Bertness, M. D. (2017). Biogeography of salt marsh plant zonation on the Pacific coast of South America. *Journal of Biogeography*, *45*, 238–247. https://doi.org/10.1111/jbi.13109

Floret, C., & Pontanier, R. (1982). *L'aridité en Tunisie présaharienne: Climat, sol, végétation et aménagement*. [Aridity in pre-desertic region of Tunisia: Climate, soil and vegetation arrangement]. Montpellier, France: Orstom.

Gibson, N., & Kirkpatrick, J. B. (1985). Vegetation and flora associated with localised snow accumulation at Mount Field West Tasmania. *Australian Journal of Ecology*, *10*, 91–99. https://doi.org/10.1111/j.1442-9993.1985.tb00869.x

Greuter, W., Burdet, H. M., & Long, C. (Eds.) (1984). *Med-check list*. Genève, Switzerland: Conservatoire et Jardin Botaniques.

Grime, J. P. (1973). Competitive exclusion in herbaceous vegetation. *Nature*, *242*, 344–347. https://doi.org/10.1038/242344a0

Grime, J. P. (1974). Vegetation classification by reference to strategies. *Nature*, *250*, 26–31. https://doi.org/10.1038/250026a0

Hachicha, M. (2007). Les sols salés et leur mise en valeur en Tunisie. [Saline soils and their enhancement in Tunisia]. *Sécheresse*, *18*, 45–50.

He, Q., & Bertness, M. D. (2014). Extreme stresses, niches, and positive species interactions along stress gradients. *Ecology*, *95*, 1437–1443. https://doi.org/10.1890/13-2226.1

Hu, Y., & Schmidhalter, U. (2005). Drought and salinity: A comparison of their effects on mineral nutrition of plants. *Journal of Plant Nutrition and Soil Science*, *168*, 541–549. https://doi.org/10.1002/jpln.200420516

IPCC (2015). *Climate change (2014): Mitigation of climate change. Summary for policymakers and technical summary*. Cambridge, UK: Cambridge University Press.

Jauffret, S., & Lavorel, S. (2003). Are plant functional types relevant to describe degradation in arid, southern Tunisian steppes. *Journal of Vegetation Science*, *14*, 399–408. https://doi.org/10.1111/j.1654-1103.2003.tb02165.x

Körner, C. (Ed.) (2003). *Alpine plant life—Functional plant ecology of high mountain ecosystems*, 2nd ed. Heidelberg, Germany: Springer.

Le Houérou, H. N. (Ed.) (2008). *Bioclimatology and biogeography of Africa*. Berlin/Heidelberg, Germany: Springer-Verlag.

Maalouf, J.-P., Le Bagousse-Pinguet, Y., Marchand, L., Touzard, B., & Michalet, R. (2012). The interplay of stress and mowing disturbance for the intensity and importance of plant interactions in dry calcareous grasslands. *Annals of Botany*, *110*, 821–828. https://doi.org/10.1093/aob/mcs152

Maestre, F. T., Quero, J. L., Gotelli, N. J., Escudero, A., Ochoa, V., Delgado-Baquerizo, M., … Zaadi, E. (2012). Plant species richness and ecosystem multifunctionality in global drylands. *Science*, *335*, 214–218. https://doi.org/10.1126/science.1215442

Mahajan, S., & Tuteja, N. (2005). Cold, salinity and drought stresses: An overview. *Archives of Biochemistry and Biophysics*, *444*, 139–158. https://doi.org/10.1016/j.abb.2005.10.018

McIntyre, S., Lavorel, S., & Tremont, R. M. (1995). Plant life-history attributes: Their relationship to disturbance response in herbaceous vegetation. *Journal of Ecology*, *83*, 31–44. https://doi.org/10.2307/2261148

Metternicht, G. I., & Zinck, J. A. (2003). Remote sensing of soil salinity: Potentials and constraints. *Remote Sensing of Environment*, *85*, 1–20. https://doi.org/10.1016/S0034-4257(02)00188-8

Michalet, R. (1991). Nouvelle synthèse bioclimatique des milieux méditerranéens. Application au Maroc septentrional [New bioclimatic synthesis of Mediterranean environments. Application in northern Morocco]. *Revue d'Écologie Alpine*, *1*, 59–80.

Michalet, R., Brooker, R. W., Cavieres, L. A., Kikvidze, Z., Lortie, C. J., Pugnaire, F. I., & Callaway, R. M. (2006). Do biotic interactions shape both sides of the humped-back model of species richness in plant communities. *Ecology Letters*, *9*, 767–773. https://doi.org/10.1111/j.1461-0248.2006.00935.x

Michalet, R., Gandoy, C., Joud, D., Pages, J.-P., & Choler, P. (2002). Plant community composition and biomass on calcareous and siliceous substrates in the northern French Alps: Comparative effects of soil chemistry and water status. *Arctic, Antarctic, and Alpine Research*, *34*, 102–113. https://doi.org/10.1080/15230430.2002.12003474

Naveh, Z., & Whittaker, R. H. (1980). Structural and floristic diversity of shrublands and woodlands in northern Israel and other Mediterranean areas. *Vegetatio*, *41*, 171–190. https://doi.org/10.1007/BF00052445

Noe, G. B., & Zedler, J. B. (2001). Spatio-temporal variation of salt marsh seedling establishment in relation to the abiotic and biotic environment. *Journal of Vegetation Science*, *12*, 61–74. https://doi.org/10.1111/j.1654-1103.2001.tb02617.x

Ohsawa, M. (1995). Latitudinal comparison of altitudinal changes in forest structure, leaf-type, and species richness in humid monsoon Asia. *Vegetatio*, *131*, 3–10. https://doi.org/10.1007/978-94-011-0343-5_1

Ozenda, P. (1975). Sur les étages de végétation dans les montagnes du bassin méditerranéen [On the vegetation stages in the mountains of the Mediterranean basin]. *Documents de Cartographie Écologique*, *16*, 1–32.

Pennings, S. C., & Callaway, R. M. (1992). Salt marsh plant zonation: The relative importance of competition and physical factors. *Ecology*, *73*, 681–690. https://doi.org/10.2307/1940774

Pennings, S. C., Selig, E. R., Houser, L. T., & Bertness, M. D. (2003). Geographic variation in positive and negative interactions among salt marsh plants. *Ecology*, *84*, 1527–1538. https://doi.org/10.1890/0012-9658(2003) 084[1527:GVIPAN]2.0.CO;2

Raunkiær, C. (Ed.) (1934). *The life forms of plants and statistical plant geography*. Oxford, UK: Oxford University Press.

Rengasamy, P. (2006). World salinization with emphasis on Australia. *Journal of Experimental botany*, *57*, 1017–1023. https://doi.org/10.1093/jxb/erj108

Whittaker, R. H. (1965). Dominance and diversity in land plant communities: Numerical relations of species express the importance of competition in community function and evolution. *Science*, *147*, 250–260. https://doi.org/10.1126/science.147.3655.250

Whittaker, R. H. (Ed.) (1978). *Classification of plant communities (Handbook of vegetation science)*. Boston, MA: Kluwer Academic Publishers.

Zhu, J. K. (2001). Plant salt tolerance. *Trends in Plant Science*, *2*, 66–71. https://doi.org/10.1016/S1360-1385(00)01838-0

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

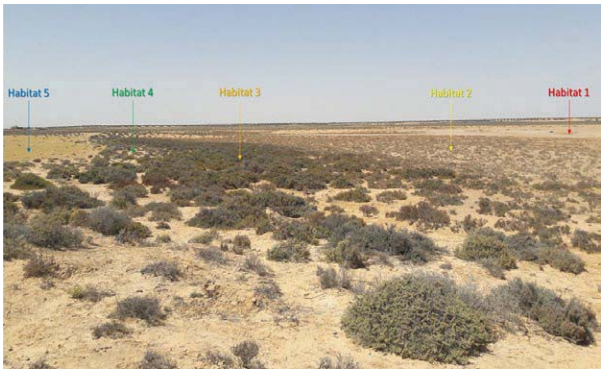
APPENDIX S1 Vegetation zonation in the sebkhas of Hachichina in Tunisia (dry climate)

APPENDIX S2 Location, area and climate conditions (Centre de Météorologie de Tunis) of the eight saline depressions (sebkhas) selected for the climate parameter

How to cite this article: Chaieb G, Abdelly C, Michalet R . Interactive effects of climate and topography on soil salinity and vegetation zonation in North-African continental saline depressions. *J Veg Sci*. 2019;00:1–10. https://doi.org/10.1111/jvs.12693

Graphical Abstract

The contents of this page will be used as part of the graphical abstract of html only.
It will not be published as part of main article.



We assessed how increasing climate aridity alters direct water and salinity gradients and vegetation zonation along topography gradients in saline depressions.

2. EFFETS DES FACTEURS COMPLEXES SUR LE FONCTIONNEMENT DE L'ÉCOSYSTÈME SALIN AU NIVEAU DES SEBKHAS CONTINENTALES

Introduction

Durant cette étude, nous avons quantifié la production et la productivité de chaque communauté végétale, aux seins des différents habitats des Sebkhas étudiées. Dans ce contexte, nous avons au préalable mesuré la biomasse des communautés dans chaque habitat, et ce, sous les deux types de climats. La biomasse a été échantillonnée à deux dates, soit en mai 2018 et en septembre 2018.

Parallèlement, nous avons quantifié la vitesse de la décomposition des espèces étudiées (*Halocnemum strobilaceum, Arthrocnemum macrostachyum* et *Lygeum spartum*). La décomposition a été quantifiée dans chaque habitat et sous les deux climats. Cette expérimentation a duré de mars 2018 à septembre 2018.

Résultats principaux

L'effet de l'habitat sur la biomasse de printemps est très significatif, avec une augmentation depuis l'habitat 1 jusqu'aux habitats 3 et 4 où la biomasse n'est pas significativement différente, bien que légèrement inférieure dans le dernier (figure 25). L'effet du climat est faiblement significatif avec une biomasse légèrement supérieur dans l'aride supérieur que l'aride inférieur. Il y'a aussi un effet très significatif de l'habitat sur la productivité (figure 26). Celle-ci augmente en allant de l'habitat 1 vers les habitats 3 et 4. L'effet de l'habitat est aussi significatif sur la décomposition de la matière organique (figure 27), qui est plus importante dans l'habitat 4 que dans l'habitat 1 (test de Tukey à donner pour appuyer cette assertion). Le climat a un effet moyennement significatif avec une décomposition plus importante en aride inférieur que en aride supérieur (résultats test de tukey: **A** pour aride inférieur et **B** pour aride supérieur) Le voisinage a aussi un effet est significatif, avec une décomposition plus importante dans les situations avec voisinage que sans voisinage (résultats test de tukey: **A** avec voisinage et **B** sans voisinage). La décomposition est ainsi plus importante pour *A. macrostachyum* et *H. strobilaceum* que pour *L. spartum* (résultats test de tukey: **A** pour *A. macrostchyum & H. strobilaceum* et **B** pour *L. spartum*). Enfin, il y a un effet significatif de l'interaction climat X espèce en raison d'une

décomposition de *H. strobilaceum* et *A. macrostachyum* plus importante dans l'aride inférieur que dans l'aride supérieur et l'inverse pour *L. spartum*..

La productivité et la décomposition s'accroissent en allant de l'habitat H1 vers l'habitat H4. Cet accroissement est corrélé avec la diminution de la salinité. En outre, la productivité est maximale dans l'habitat H4, en raison de la fertilité du sol. De plus, la décomposition est aussi maximale dans ce même habitat, suite à la faible salinité, et la qualité de litière émanant particulièrement des espèces herbacées. La biomasse est croissante de l'habitat H1 vers l'habitat H3. Cependant, elle diminue faiblement au niveau de l'habitat H4, sans doute de part l'augmentation de la perturbation induite par le pâturage étant donné que le stress salin y est le plus faible comme en témoigne la forte productivité. D'autre part, les herbivores domestiques se mettent plutôt à la recherche des espèces herbacées annuelles (*Plantago albicans, Cutandia dichotoma, schismus barbatus*), plus appétantes que les espèces halophiles arbustives.

La décomposition des litières varie en fonction de leur qualité biochimique (Dalanda-Diallo & al., 2015). Ces caractéristiques biochimiques concernent essentiellement le rapport C/N, la cellulose, hémicellulose et la lignine. Des études ont d'ailleurs montré une corrélation positive entre le rapport C/N et la perte de masse des litières (Arunachalam & al., 1998). En effet, *Arthrocnemum macrostachyum* et *Halocnemum strobilaceum*, étant des espèces en C_3 (famille des *Amaranthaceae*) sont des pérennes fortement halophiles et succulentes. *Lygeum spartum*, également espèce en C_3, est une *Poaceae* pérenne, résistante à la sécheresse, et tolérante à la salinité. N'ayant pas effectué l'analyse des caractéristiques biochimiques de ces trois espèces étudiées, nous constatons d'après la figure 27 ci-dessous des différences au niveau de leur décomposition, dans la mesure où les deux halophytes, se décomposent plus vite que la Graminée. Ainsi, en plus de sa faible teneur en eau, par comparaison aux espèces halophiles succulentes, *L .spartum* est très riches en fibres, à un point où il pourrait être valorisé dans l'industrie de papier, sachant qu'il est couramment utilisé en Afrique du Nord dans l'artisanat. La rigidité de ses feuilles, très riches en cellulose (qui est qualifié parfois comme étant un « acier végétal », pourrait expliquer sa lente décomposition par rapport aux espèces succulentes. Les fibres de cellulose sont insolubles dans l'eau, et sont très résistantes et très rigides. D'ailleurs, selon Belouadah & al. (2015), les fibres de cellulose de *Lygeum spartum* sont thermostables jusqu' à 220°c, ce qui explique sa rigidité foliaire, et la difficulté de sa décomposition. En

revanche, la décomposition plus rapide d'*Halocnemum strobilaceum* et *Arthrocnemum macrostachyum*, pourrait s'expliquer par leur forte succulence, donc leur forte teneur en eau, favorable à l'activité des micro-organismes détritivores. Ainsi, la faible teneur en matière sèche de ces deux espèces succulentes, et leur faible teneur en fibres, par comparaison au *L. spartum*, pourrait expliquer leur décomposition plus rapide.

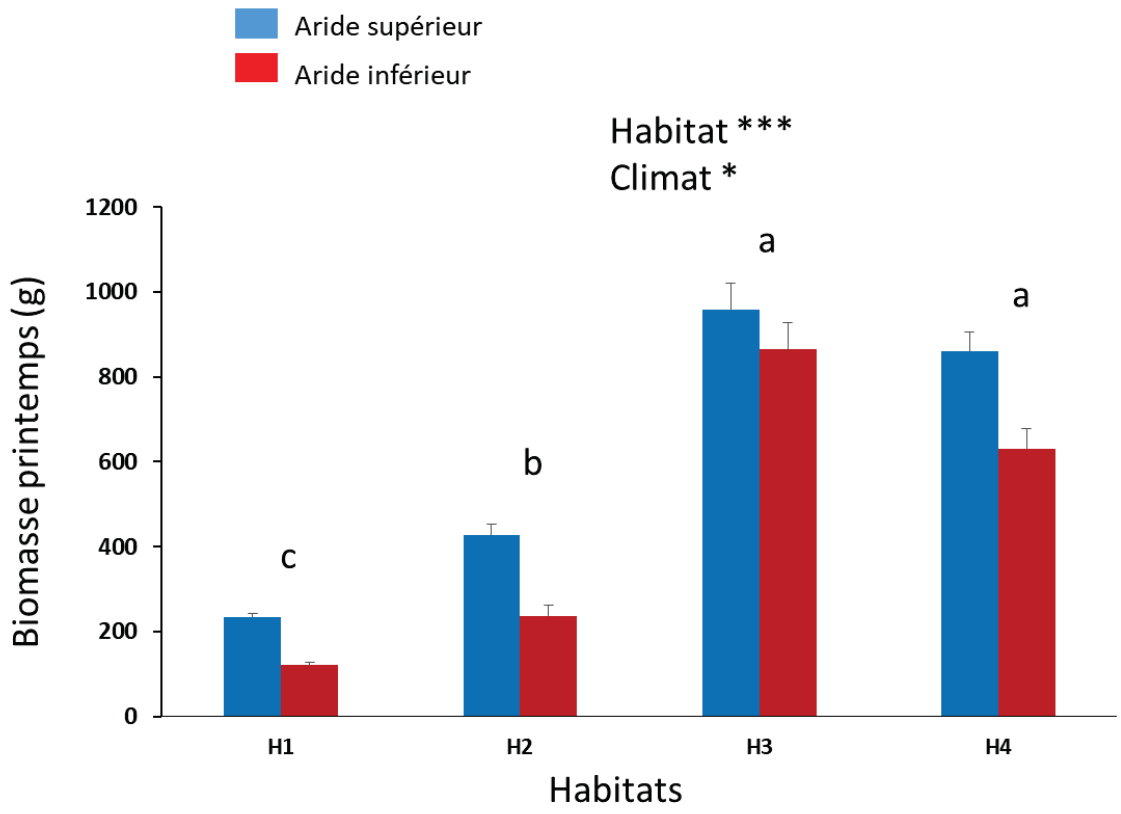


Figure 25: Moyenne (± SE, N = 4) de la biomasse dans les 4 habitats (H1, H2, H3, H4) des deux climats (aride supérieur et aride inférieur).

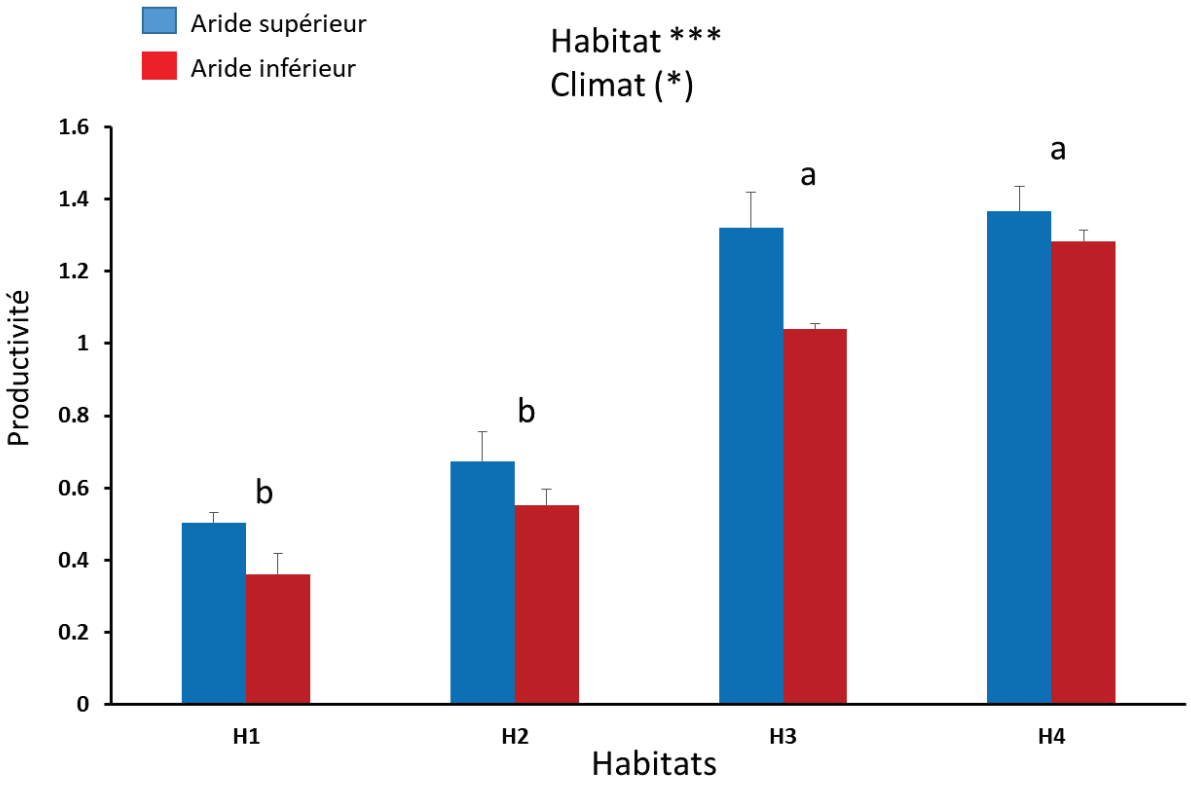


Figure 26: Moyenne (± SE, N = 4) de productivité dans les 4 habitats (H1, H2, H3, H4) des deux climats (aride supérieur et aride inférieur).

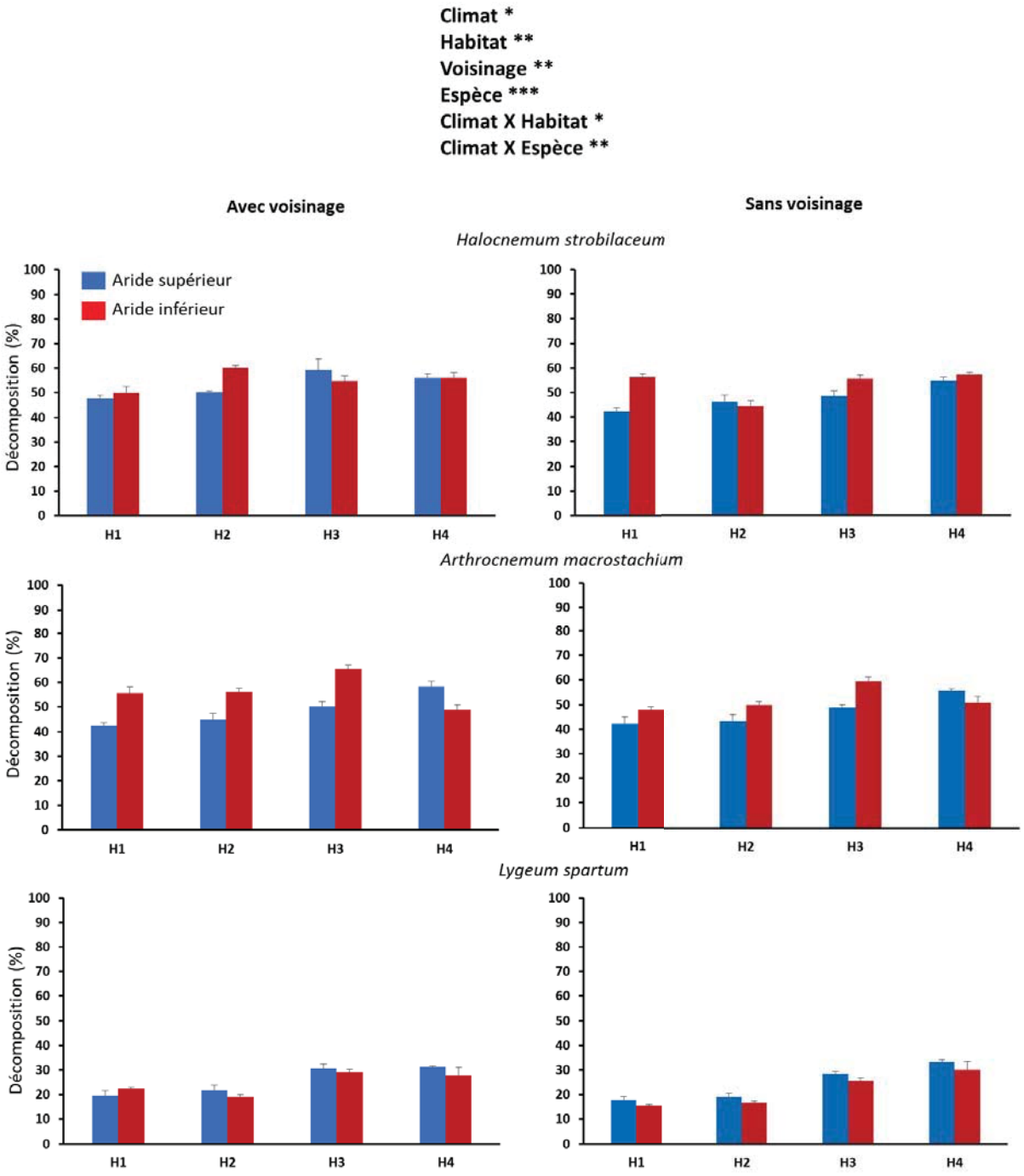


Figure 27: Moyennes (± SE, N = 4) de la décomposition des trois espèces (*H.strobilaceum, A. macrostachyum* et *L.spartum*) dans les quatre habitats (H1, H2, H3, H4) des deux climats (aride supérieur et aride inférieur).

CHAPITRE III. INTERACTIONS BIOTIQUES LE LONG DES GRADIENTS COMPLEXES ET DIRECTS

1. ÉTUDE DE L'INFLUENCE DE LA SALINITÉ & DE L'ARIDITÉ SUR LES INTERACTIONS BIOTIQUES LE LONG DU GRADIENT TOPOGRAPHIQUE

Cette partie du travail a fait l'objet d'un article publié dans la revue *Ecosystems* sous la référence suivante:

Chaieb, G., Abdelly, C. & Michalet, R. A Regional Assessment of Changes in Plant–Plant Interactions Along Topography Gradients in Tunisian Sebkhas. *Ecosystems* (2020). https://doi.org/10.1007/s10021-020-00567-8.

Introduction

Nous rappelons que l'objectif de cette expérimentation était de séparer l'influence respective de la salinité et du stress hydrique sur les variations d'interactions biotiques le long des gradients de stress, avec l'hypothèse forte que le stress salin devrait induire soit une augmentation linéaire de la facilitation, soit un collapse de cette facilitation et le stress hydrique un retour de la compétition. Nous avons voulu répondre aux questions précises suivantes : (i) comment la facilitation varie avec l'accroissement de la salinité ? (ii) comment l'aridité croissante et la réponse des espèces cibles influencent la relation existante entre la facilitation et salinité ?

Résultats principaux

Nous avons montré que la salinité entrainait un collapse de la facilitation et que ce collapse était encore plus précoce avec accroissement de l'aridité, soit spatialement soit temporellement. Ce collapse n'est pas dû au collapse de l'effet de facilitation des nurses sur la salinité mais au fait que le niveau de salinité excède la tolérance des espèces aussi bien avec que sans voisins. De plus, nous avons remarqué que les trois espèces cibles ont différemment répondu à l'effet du voisinage, au moins dans l'habitat le moins salé et en climat faiblement aride. L'espèce la moins tolérante au stress fut facilitée, alors que les espèces les plus tolérantes au stress ont été négativement affectées par le voisinage. Ces résultats ont donc globalement confirmé le modèle de collapse de la facilitation de Michalet et al. (2006) mais n'ont pas confirmé l'hypothèse de Michalet et al. (2014) que les gradients de ressources doivent montrer un retour de la compétition. Cette absence du retour à la compétition constatée dans notre étude pourrait s'expliquer par l'utilisation de la méthode observationnelle qui nous l'avons vu surestime la facilitation au dépend de la compétition. Le recourt à la méthode expérimentale pourrait fournir des résultats relatifs au retour à la compétition, ce qui a été envisagé dans notre seconde expérimentation. En outre, l'absence de la compétition peut être due à la nature des espèces nurses. Celles-ci étant des ligneuses, leur effet facilitant pourrait être supérieure à celui de nurses compétitives, telle que *Stipa tenacissima*, (Maestre et Cortina, 2004). Il est aussi probable que nos résultats aient été influencés par le faible contraste climatique utilisé dans cette étude, aride supérieur contre aride inférieur.

Ecosystems
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A Regional Assessment of Changes in Plant–Plant Interactions Along Topography Gradients in Tunisian Sebkhas

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Abstract

Facilitation among plants in dry ecosystems is crucial for diversity and ecosystem functioning and stability. However, the importance of facilitation in extremely stressful conditions is highly debated. We attempt to separate the effects of direct non-resource and resource stress factors on plant–plant interactions by assessing changes in facilitation and competition along salinity gradients at two contrasting levels of aridity. We selected eight saline depressions (hereafter sebkhas) in the wet and dry Mediterranean arid climate of North Africa, from central Tunisia to the Libyan border 500 km south-eastward. In each sebkha, we transplanted at four positions along the salinity gradient induced by topography, both in open areas and below dominant shrubs, three target species with contrasting tolerances to salinity stress. Target plant survival, soil electrical conductivity and moisture were recorded before and after the dry summer season in all treatments. Shrubs decreased salinity and drought stresses in all treatments, and facilitation was the dominant interaction. However, we found a strong collapse of facilitation along the salinity gradient, due to a dramatic mortality of the three target species both with and without neighbours above their threshold of salinity tolerance. Increasing aridity induced an earlier collapse of facilitation along the gradient. The three target species had contrasting responses to neighbours, with the least stress-tolerant species being facilitated and the two most stress-tolerant ones negatively affected by neighbours. Our study shows that disentangling resource and non-resource stresses along gradients and controlling for target species effects help understanding variation in plant–plant interactions under highly stressful conditions.

Key words: Collapse of facilitation; competition; drought; Mediterranean climate; non-resource factors; resource factors; salinity.

Highlights

- Regional experiment manipulating neighbours along salinity gradients in arid climate.
- Facilitation collapses in the most saline condi-

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Authors Contributions RM and CA designed the experiment, GC and RM conducted field work, GC analysed data and wrote the draft of the text, and the three authors corrected the manuscript.

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tions.
- Increasing aridity induces a stronger collapse of facilitation.

Introduction

Facilitation, the positive effect of an organism on another one (Callaway 2007), is widely recognized as an important biotic interaction occurring frequently in stressful environmental conditions from a variety of terrestrial and coastal marine ecosystems (Bruno and others 2003; He and others 2013; Soliveres and Maestre 2014; Michalet and Pugnaire 2016; Bulleri and others 2018). Facilitation might be due to the direct amelioration of abiotic conditions (salinity, cold, drought or oligotrophy) or to indirect positive effects, through reduced herbivory or competition (Callaway 2007). Facilitation is crucial in severe environments since it enhances local diversity by allowing stress-intolerant species to live in extreme habitats (Bruno and others 2003; Liancourt and others 2005a; Michalet and others 2006). Facilitation also affects the diversity of other organisms (Lortie and others 2016), enhances ecosystem functioning (Soliveres and others 2015; Wright and others 2017) and ecosystem stability (Kéfi and others 2007). Additionally, facilitation can be used as an engineering tool for restoring degraded habitats (Gómez-Aparicio and others 2004; Padilla and Pugnaire 2006).

However, changes in the intensity and importance of competition and facilitation along environmental gradients in water-stressed conditions are a highly debated issue (Maestre and others 2005, 2009; Michalet 2007; He and Bertness 2014; Michalet and others 2014a, b; Soliveres and others 2015). The pioneer stress-gradient hypothesis (SGH) facilitation model, considering that competition should switch to facilitation with increasing environmental severity (Bertness and Callaway 1994), was first supported by a number of experiments in water-stressed systems (Gómez-Aparicio and others 2004; Sthultz and others 2007; Muhamed and others 2013). However, other studies showed that competition may conversely increase with increasing water stress in dry systems (Tielbörger and Kadmon 2000; Maestre and Cortina 2004; Armas and Pugnaire 2005, a process now called the switchback to competition, Michalet and others 2014a, b). Additionally, facilitation may collapse (that is, decrease until neutral interactions) at the extreme of environmental gradients (Kitzberger and others. 2000). Thus, several authors have argued that the relationship between plant–plant interactions is not linear, as proposed by the pioneer SGH model, but unimodal, with a maximum of facilitation at intermediate position along environmental gradients (Michalet and others 2006; Holmgren and Scheffer 2010; Verwijmeren and others 2013). Additionally, Michalet and others (2014a) stressed the importance to separate two alternatives to the SGH, namely the collapse of facilitation and the switchback to competition, because they are likely to be due to different processes, a decrease in facilitative effects for the former and a change in the response of the target species in particular environmental conditions for the latter.

Recent research conducted since the beginning of that debate has provided conflicting results, with either support of the SGH, in particular along cold stress gradients (Cavieres and others 2014; Pugnaire and others 2015, and see the meta-analysis of He and others 2013) or of one of the other two models proposing an unimodal facilitation curve (Forey and others 2010; Le Bagousse-Pinguet and others 2014; Michalet and others 2015; Butterfield and others 2016; Noumi and others 2016; O'Brien and others 2017; Zhang and others 2018; Berdugo and others 2019). Thus, as suggested by Michalet and Pugnaire (2016), it is time considering that there is no unique model of facilitation–environment relationship and concentrating our research efforts towards assessing under which environmental and biotic conditions any of the three proposed models is expected to occur. This is crucial for understanding the role of facilitation for ecosystem functioning and stability in dry environments.

Michalet (2007) and Maestre and others (2009) proposed in particular, that non-resource direct gradients (that is, factors that are directly affecting the physiology of a plant species but that are not consumable, *sensu* Austin and Smith 1989) that should support the SGH and collapse of facilitation models (that is, only facilitation and neutral interactions in stressful and extremely stressful conditions, respectively), whereas resource gradients (for example, water availability gradients) were more likely to show a switchback to competition at the extreme of the stress gradient, consistent with the McArthur and Wilson (1967) theory. Several authors also highlighted the importance of the functional strategy of the species involved in the interactions (Liancourt and others 2005a; Michalet and others 2006; Maestre and others 2009). Indeed, stress-intolerant species are more likely to be facilitated and stress-tolerant ones more sensitive to competition (Forey and others 2010; Liancourt and others 2017; Qi and others 2018).

Another crucial point is the necessity, when possible, to assess variation in biotic interactions along direct environmental gradients and to avoid complex gradients involving several direct factors interacting with each other (He and Bertness 2014). For example, Leong and others (2019) have shown that isolating resource gradients provides SGH support in pitcher plants. Several studies have indeed shown that the interaction between drought stress and disturbance induces a collapse of facilitation (Forey and others 2010; Maalouf and others 2012; Le Bagousse-Pinguet and others 2014; Verwijmeren and others 2019). In arid ecosystems subjected to high evaporation rates, salinity stress also often interacts with water stress along complex topography or elevation gradients, since salt accumulates in soils with increasing climatic drought (Fariña and others 2017; Chaieb and others 2019). We suggest that discrepancies among studies on the shape of the facilitation–environment curve in water-stressed systems may in part be due to the occurrence of an interaction between these two direct stresses. In other words, studies conducted along salinity gradients are more likely to support the SGH or eventually the collapse of facilitation model since salinity is a non-resource direct factor, whereas studies conducted along water gradients are more likely to support the switchback to competition model because water availability is a direct resource factor.

The overall goal of our study was to disentangle the role of salinity and drought stresses in the variation in plant–plant interactions along complex environmental stress gradients in arid ecosystems. Since salinity and drought stresses interact across complex topographic and climatic gradients (Fariña and others 2017; Chaieb and others 2019), we set up an experimental design at the regional scale where we assessed the effect of salinity on plant–plant interactions along topographic gradients in different climatic conditions. We selected eight continental saline depressions (locally called sebkhas) from both the upper and lower arid climates (*sensu* Emberger 1958) of North Africa, from central Tunisia to the Libyan border, 500 km south-eastward. Within each sebkha, we transplanted along the salinity gradient induced by topography three dominant species having contrasting tolerances to salinity stress, both below the dominant shrubs and in adjacent open areas. Electrical conductivity and soil moisture were also measured in all treatments in order to identify the effects of the dominant shrubs on these two direct stress factors. We aimed to answer the following questions: (1) what is the relationship between facilitation and salinity? (2) Are changes in facilitation with increasing salinity due to changes in the effects of dominant shrubs on salinity? (3) Does increasing water stress with increasing aridity alter the relationship between facilitation and salinity? (4) Does the tolerance to salinity of the target species alter the relationship between facilitation and salinity?

Materials and Methods

Study Sites and Target Species

The study was conducted in eight sebkhas from central Tunisia in the Mediterranean arid climate (Figure 1 and Appendix 1 of ESM). The Mediterranean arid and Saharan climates occupy about 75% of the total surface of Tunisia, in the central and southern parts of the country, at the northern edge of the Sahara Desert (Figure 1). In the arid climate of Tunisia, mean annual precipitation is between 100 and 300 mm and mean annual temperature is 19.0°C with 4.6°C in winter (December to February) and 37.0°C in summer (June to August). Following the bioclimatic classification of Emberger (1958), the Mediterranean arid climate has been divided in two sub-climates, upper and lower arid (hereafter wet and dry arid, respectively), with mean annual precipitation between 200 and 300 mm and 100 and 200 mm, respectively. The year of our experiment, climate was wetter in the winter, and drier in the spring and summer than average years, but these anomalies were approximately the same in the wet and dry arid climates (winter: + 92% and + 78%, spring − 31% and − 41% and summer − 53% and − 100%, for the wet and dry arid, respectively, see Appendix 2 of ESM). Thus, the climate treatment applied during our experiment was representative of average differences in aridity occurring in Tunisia between these two sub-climates. In contrast, differences in humidity between the wet and dry seasons during the course of our experiment were higher the year of our experiment than average in both the wet and dry arid.

All sebkhas, whose size ranges between 10 and 300 km^2, had similar lentil-like shapes and habitat organization. The most important central part, with no vegetation, can be inundated during the wetter winter season during very wet years. The central part is surrounded at the edge of the sebkhas by several circular belts of shrubby halophytic vegetation. Chaieb and others (2019) distinguished four habitats in relation to elevation and salinity stress, from the central part to the edge of the sebkhas at the ecotone with crop fields. Soil texture is highly

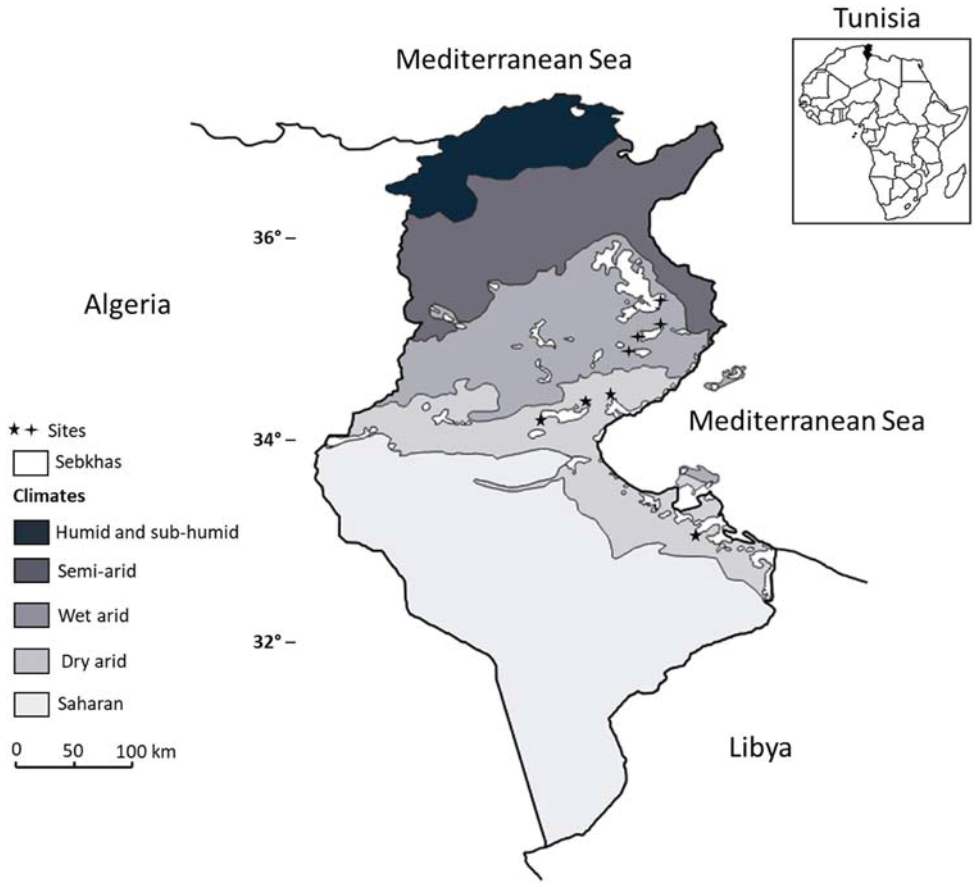

Figure 1. Geographical distribution of the eight sebkhas in the arid climate of Tunisia.

influenced by the presence of sand throughout the sebkhas, although there is a slight but significant increase in clay from the upper most habitat (H4) to the lowest one (H1) (from 6.25 ± 0.8% of clay, 12.25 ± 0.7% of silt and 81.5 ± 1.2% of sand in H4, that is, loamy sand texture, to 18 ± 1.5, 14.5 ± 0.5 and 67.5 ± 1.2 in H1, respectively, that is, sandy loam texture, $n = 8$). Habitat 1, the most saline and lowest habitat, has very low vegetation cover (< 20%) and is occupied by only one species, *Halocnemum strobilaceum* (Amaranthaceae), a C_3 shrub present from the Mediterranean area to western Asia (Liu 1985) and known as a highly salinity-tolerant species (Redondo-Gómez and others 2010). Habitat 2, also only occupied by *H. strobilaceum,* has higher cover (20–50%) and biomass. Habitat 3 is dominated by *Arthrocnemum macrostachyum* (Amaranthaceae), a C_3 shrub, known as a salt-accumulator (Redondo-Gómez and others 2010). Other shrub species associated with *A. macrostachyum* are *Suaeda mollis, Limoniastrum monopetalum* and *Atriplex halimus*. Habitat 4 is co-dominated by several shrub species (*Salsola tetrandra, Zygophyllum album*, *Reaumuria vermiculata* and *Nitraria retusa*) and *Lygeum spartum* (Poaceae), a widespread rhizomatous perennial grass native of the Mediterranean region and known to be tolerant to salinity. Human disturbance due to agriculture is very low in sebkhas because of the very low soil fertility and palatability of halophytic shrubs, which make them an excellent natural system for studying the effects of stress in arid climates, in particular in developing countries like Tunisia where disturbance is overall very high. Only low grazing by sheep can be observed at the upper edge of habitat 4 (Chaieb and others 2019), but we disregarded those grazed areas.

Experimental Design

Late August 2016, we selected for the climate treatment four sebkhas (blocks) in the wet arid climate and four sebkhas in the dry arid climate (Figure 1). Each block was separated from each other by at least 50 km, as shown in Figure 1. Each block was split into four main plots for the habitat treatment, with four levels of salinity along an increasing gradient of salinity stress from H4 to H1.

Each plot had a size of approximately 500 m^2, and plots were separated from each other by 10–20 metres in average, since the whole topographic gradient was in general not longer than 200 metres (Chaieb and others 2019). Thus, there was a total of 32 main plots (2 climates × 4 blocks × 4 habitats). We applied a target and a neighbour treatment within each main plot, with three individuals of each target species planted with and without neighbours. For the target treatment, we selected three dominant species of the four habitats for transplantation in the whole experimental design. The three target species have increasing tolerances to salinity stress from *L. spartum* to *A. macrostachyum* and *H. strobilaceum* (Chaieb and others 2019). In each of the 32 main plots, we randomly selected nine subplots in open areas without vegetation (with at least 1 m distance from the centre of the open plot to the nearest shrub) and nine subplots covered by a dominant shrub individual. Subplots were separated from each other by a minimum distance of two metres. Thus, in each main plot, there were three replicates of each target species, transplanted with and without neighbours in 18 subplots. The selected neighbour species were *H. strobilaceum* in H1 and H2, *A. macrostachyum* in H3 and *S. tetrandra* in H4. Transplanted individuals were grown from rooted cuttings of the three species, collected in early September 2016 from their own habitats in at least two sebkhas of each climate condition. Collected individuals had an average above-ground height of 15 cm and were harvested in mesh bags 20 cm deep and 10 cm diameter filled with the soil of each corresponding habitat. Individuals in mesh bags were first transplanted in the common garden of the Tunisian Ministry of Environment at Sfax, the main town at the vicinity of our sites. Transplants were grown there until mid-November 2016 with irrigation every 15 days with 20 mm of tap water per transplant. Mid-November 2016, all species had formed roots in the nursery. Thus, they were transplanted at this date in all treatments, after removing the mesh bags but not the soil surrounding roots, and the experiment lasted until late September 2017. Transplants with neighbours were transplanted beneath northern edge of the shrub canopy, and each transplant was watered after transplantation with 1 l of tap water. The results of Appendix 3 of ESM show that salinity level around the roots of the transplants of the three target species was similar at time of transplantation in the plots, since salinity strongly decreased in the common garden due to watering of the transplants with tap water during 2.5 months.

Data Collection and Interaction Index Calculation

We recorded survival of all target individuals early April 2017, at the end of the wet season and late September 2017, after the dry season (Appendix 2 of ESM). Although transplants were measured at the beginning of the experiment, we did not record biomass nor measured them at the end of the experiment, since survival was too low, in particular in the most saline habitats of the dry arid climate. Survival rates were calculated in each subplot, in terms of per cent of the three individuals transplanted per treatment combination and per block.

Soil water content and soil salinity were measured at 5 cm distance from each transplant individual, early April and late September 2017, using a Wet Sensor HH2 moisture meter (Delta-T Devices, Cambridge, England). Only soil salinity data in the spring and soil water content in the summer are shown here since soil salinity was too high in the most saline plots in the summer for our probe and soil water content similarly high in all plots in the spring.

We used the relative interaction index (RII) (Armas and others 2004) to assess the effect of the dominant shrubs on the target species in all treatments. This index is based on the comparison of target performance with and without neighbours: $RII = (A - B)/(A + B)$.

A is the per cent survival with neighbours in a main plot and B the per cent survival without neighbours in the same plot. Values of RII vary between − 1 and 1, with negative values indicating competition and positive ones facilitation.

Statistical Analyses

We used a generalized linear mixed-effects model (GLMM) to test the effects of the climate, salinity, target, neighbour treatments and their interactions on spring survival. Salinity, the continuous variable, was log-transformed before analyses to meet parametric model assumptions and to homogenize the gradient to avoiding aggregated point patterns. We used two forms of salinity in this analysis (log (salinity) and $(\log \text{salinity})^2$) to eventually detect nonlinear relationships (Maalouf and others 2012). Since only linear effects were significant in the GLMM, nonlinear ones are not shown in Table 1.

To test the effects of the climate, habitat, target treatments and their interactions on RII survival calculated at the two seasons, we used a split–split-plot mixed ANOVA model with blocks as a random

Table 1. Results of the Split–Split-Plot ANOVAs on the Effects of the Climate, Habitat, Neighbour Treatments and Their Interactions on Soil Salinity in Spring and Soil Moisture in Summer.

Effects	*df*	Salinity in spring		Soil moisture in summer	
		F	*p*	*F*	*p*
Climate	1	17.3	< **0.001**	80.4	< **0.001**
Error (block)	7				
Habitat	3	268.1	< **0.001**	458.7	< **0.001**
Climate × habitat	3	4.8	**0.006**		
Error (block/subplot)	21				
Target	2	747	< **0.001**	105.6	< **0.001**
Climate × target	2	9.5	**0.003**	0.3	**0.020**
Habitat × target	6	54.9	< **0.001**	5.5	< **0.001**
Climate × habitat × target	6	10.2	< **0.001**	1.1	**0.003**
Residual error	448				

Significant ($p < 0.05$) effects are indicated in bold.

effect, climate as main treatment, habitat as sub-treatment and target as sub-sub-treatment. We also used a split–split-plot mixed analysis of variance (ANOVA) to test the effect of the climate, habitat, neighbour treatments and their interactions on salinity in spring season and soil moisture in summer season, with blocks as a random effect, climate as main treatment, habitat as sub-treatment and neighbour as sub-sub-treatment. Soil moisture and salinity variables were log-transformed to meet normality before ANOVAs.

Data analysis was done in Rversion 3.3.3 (R Core Team 2017). The GLMM model used for survival was performed with the function glmer and the package ime4. The split–split-plot mixed ANOVAs used for RIIs, salinity and soil moisture variables were performed with the function AOV and the package agricolae (De Mendiburu 2017) for linear mixed effect models. We used Tukey HSD tests after ANOVAs when necessary. In addition, sample *t* tests were used to test if RII values were different from zero.

Results

Climate, habitat and neighbour treatments all had highly significant effects on spring salinity, with higher values in dry arid climate, towards the centre of the sebkhas and in the open subplots than in wet arid climate, at the edge of the sebkhas and in the shrub subplots, respectively (Figure 2 and Table 1). However, there was a highly significant habitat by neighbour interaction, because in both climates the neighbour effect was not significant in H4 only (see Tukey tests, Figure 2). Additionally, the neighbour effect was stronger towards the centre of the sebkhas in the dry arid climate (highly significant climate by habitat by neighbour interaction, Figure 2 and Table 1). Overall, these results show that effects on salinity did not collapse in the most severe environmental conditions (centre of the sebkhas in dry arid climate).

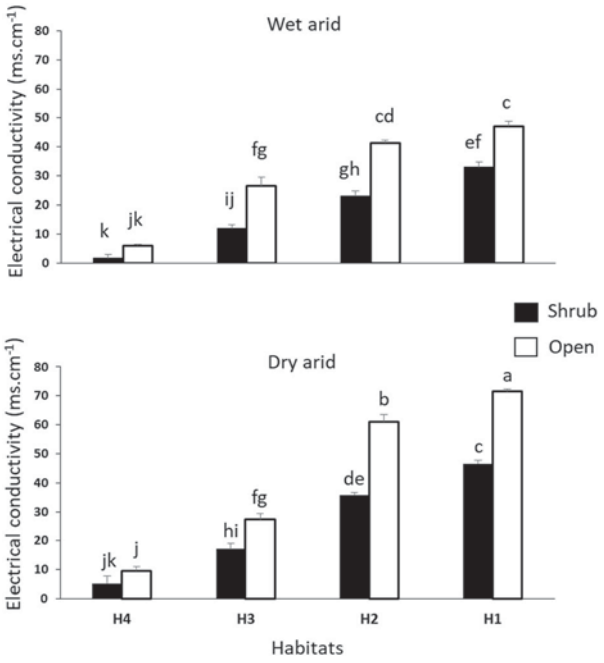

Figure 2. Means ($n = 4$, ± SE) of spring soil salinity (electrical conductivity) with and without neighbour in the four habitats of the two climate conditions. Letters show the results of the HSD Tukey test for the climate × habitat × neighbour interaction ($p < 0.001$, Table 3) in the split–split-plot ANOVA.

Climate, habitat and neighbour treatments had all highly significant effects on summer soil mois-

ture, with higher values in wet arid climate, towards the centre of the sebkhas and in the shrub subplots, than in dry arid climate, at the edge of the sebkhas and in open subplots, respectively (Figure 3 and Table 1). However, there was a weakly significant climate by habitat interaction, because the climate effect was not significant in H3 (see Tukey test). There was also a significant habitat by neighbour interaction, because differences in soil moisture between shrub and open subplots increased from the edge towards the centre of the sebkhas (results of Tukey test not shown).

In spring, salinity strongly decreased survival in all treatments (highly significant salinity effect in Table 2 and Figure 4 and see Appendix 4 of ESM for results for each species). There was a highly significant climate effect due to overall higher survival in wet arid than dry arid climate. There was a highly significant climate by neighbour interaction, with over all targets, lower survival with neighbours than in the open in wet arid climate, but higher survival with neighbours than in the open in dry arid climate (Figure 4). However, there was a weakly significant climate by neighbour by salinity interaction, because the negative effect of neighbours on survival in wet arid climate occurred only in low saline conditions and switched to positive in high-saline conditions, while the positive effect of neighbours in dry conditions tends to vanish with increasing salinity (Figure 4). There was also a highly significant salinity by target interaction because the decrease in survival with increasing salinity was stronger for *L. spartum* than for the two shrubs, with almost no survivors for the grass at the highest salinity level (Appendix 4 of ESM). Finally, there was a significant climate by salinity by neighbour by target interaction because the positive effect of neighbours on survival in dry arid climate was only observed for the two shrub species, while there was no effect of neighbours in dry arid climate for the grass species whose survival was only affected by salinity (Appendix 4 of ESM).

In spring, habitat had a significant effect on RII survival, for the three targets and in both climates, with higher RII values at mid positions along the topography gradient than in the two extreme habitats (Table 3, Figure 5 and results of the Tukey test for the habitat effect). However, there was a highly significant climate by habitat interaction because the highest RII value was observed in H2 in wet arid climate but in H3 in dry arid climate (see the results of the Tukey test in Figure 5). In addition, the results of sample *t* tests show that facilitation was only significant in H2 in the wet arid climate and in H3 in the dry arid one. Overall, these results show evidence that facilitation peaked at a

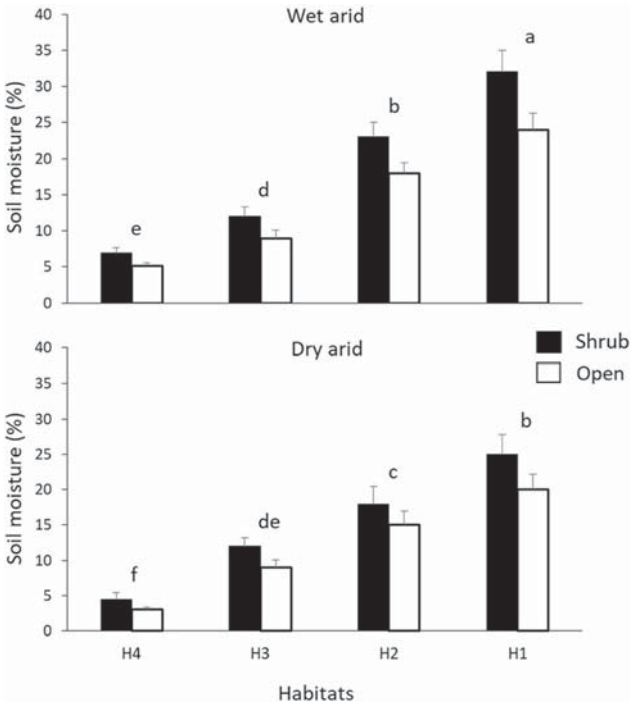

Figure 3. Means (n = 4, ± SE) of summer soil moisture with and without neighbours in the four habitats of the two climate conditions. Letters show the results of the HSD Tukey test for the climate × habitat interaction (p = 0.012, Table 3) in the split–split-plot ANOVA.

Table 2. Results of Generalized Linear Mixed-Effects Models (GLMM) on the Effects of the Climate, Salinity, Neighbour and Target Treatments and Their Interactions on Survival in Spring.

Effects	Survival		
	df	Chisq	*P*
Climate	1	34	< **0.001**
Salinity	1	174.8	< **0.001**
Neighbour	1	0.3	0.551
Target	2	0.4	0.807
Climate × salinity	1	1.4	0.422
Climate × neighbour	1	26.5	< **0.001**
Salinity × neighbour	1	9.0	0.678
Climate × target	2	13.2	0.967
Salinity × target	2	5.2	< **0.001**
Neighbour × target	2	9.8	**0.007**
Climate × salinity × neighbour	1	5.5	**0.021**
Climate × salinity × target	2	4.1	0.289
Climate × neighbour × target	2	1.8	0.472
Salinity × neighbour × target	2	3.23	0.235
Climate × salinity × neighbour × target	2	8.1	**0.008**

Significant ($p < 0.05$) effects are indicated in bold.

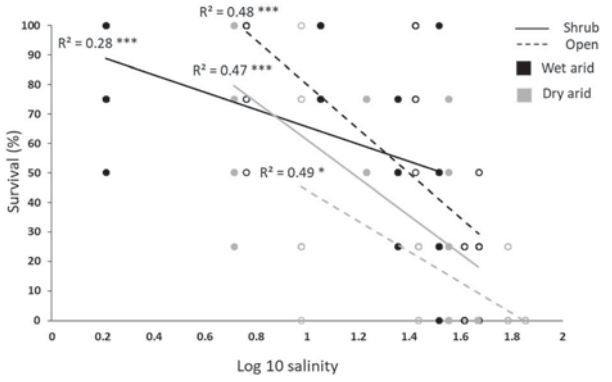

Figure 4. Spring survival of the three target species (*H. strobilaceum*, *A. macrostachyum* and *L. spartum*) along the soil salinity gradient in the two climate conditions and with and without neighbours. Linear curves show variation in survival for the three pooled target species along the salinity gradient in the two climate and neighbour conditions, with R^2 and p values of regressions close to curves (significant salinity × climate × neighbour interaction in the GLMM, Table 1: $p < 0.01$). See ''Appendix 4 of ESM'' for species curves.

medium position along the topography gradient and collapsed towards the centre of the sebkhas, and in particular in the dry arid climate, consistent with results of Figure 5. The absence of a significant three-way interaction suggests that this interaction between the climate and habitat treatments was valid over all species at that date.

In late summer, only the target treatment had a (weakly) significant single effect on RII survival, with higher RII values for *L. spartum* than for the two shrub species (Table 3, Figure 6 and result of the Tukey test not shown). There was a highly significant habitat by target interaction because over all climate conditions, RII decreased from the edge to the centre of the sebkhas for *L. spartum*, but rather peaked at intermediate position for the two shrub species. However, this effect was particularly strong only in H4 of the wet arid climate, with significant facilitation for the grass and significant competition for the two shrub species (significant climate by habitat by target interaction, Table 3 and results of Tukey and *t* tests in Figure 6). Overall, these results highlight that the collapse of facilitation increased and became more species-specific from the spring to the summer seasons.

Discussion

In response to our first question, we found that the relationship between plant–plant interactions and salinity was unimodal with maximum facilitation at intermediate salinity levels and a collapse of facilitation at extreme salinity levels. In response to our second question, this collapse was not due to a decrease in the facilitative effect of the shrubs, but rather occurs because salinity stress exceeded the threshold tolerance of the target species even below shrubs. Increasing aridity did not change the shape of the curve of plant–plant interaction along the

Table 3. Results of the Split–Split-Plot ANOVAs on the Effects of the Climate, Habitat, Target Treatments and Their Interactions on RII Survival Calculated in Spring and Summer.

Effects	*df*	RII in spring		RII in summer	
		F	*p*	*F*	*p*
Climate	1	1.3	0.2	0.3	0.5
Error (block)	7	7			
Habitat	3	4.5	**0.005**	1.9	0.1
Climate × habitat	3	6.8	< **0.001**	4.9	**0.031**
Error (block/subplot)	21				
Target	2	1.3	0.2	3.6	**0.030**
Climate × target	2	0.4	0.6	3.9	**0.020**
Habitat × target	6	0.7	0.6	5.4	< **0.001**
Climate × habitat × target	6	0.2	0.9	3.5	**0.003**
Residual error	448				

Significant ($p < 0.05$) effects are indicated in bold.

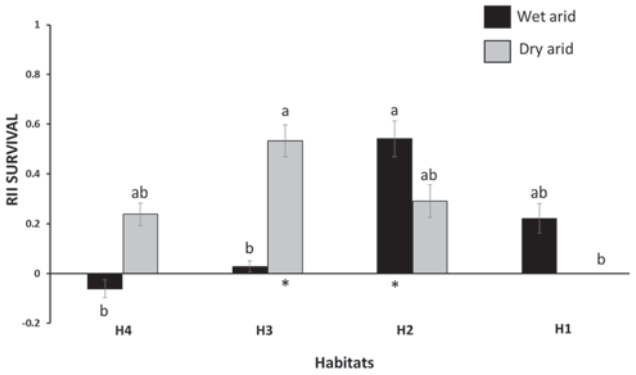

Figure 5. Means ± SE ($n = 4$) of relative interaction index (RII survival) calculated in spring for the three pooled target species in the four habitats of the two climate conditions. Letters show results of the HSD Tukey test for the climate × habitat interaction ($p < 0.001$, Table 2) in the split–split-plot ANOVA. Results of one-sample *t* tests are shown below bars: *, $p < 0.05$.

salinity gradient, but it does induce an earlier collapse of facilitation along the gradient. Finally, the three target species had contrasting responses to neighbours, in particular after the summer drought and in the least saline habitat. Separating direct non-resource and resource gradients and controlling for species effects, as in our study, may certainly help unifying facilitation theories, which is crucial for understanding the role of facilitation for diversity, ecosystem functioning and restoring degraded ecosystems in water-stressed countries in a global change context.

The Collapse of Facilitation Along the Salinity Gradient

In our study, we attempt separating the effects of direct non-resource from direct resource stresses on plant–plant interactions, by assessing changes in plant–plant interactions along a salinity gradient in similar climatic conditions. Separating drought from salinity stress for plants is not easy, since it is known that a major consequence of NaCl stress is the loss of intra-cellular water and both stresses have in common to induce an osmotic stress (Mahajan and Tuteja 2005). Thus, when salinity stress is increasing in constant climatic conditions, drought stress may increase as well for plants. Additionally, we are aware that drought stress also varied within each climate condition since the salinity gradient was set up along a complex gradient of topography. Thus, an experiment conducted in controlled conditions of salinity and moisture availability might certainly be useful to really separating both stresses. However, increasing drought stress along the topography gradient within each climate cannot explain the negative effect of increasing salinity on plant survival since

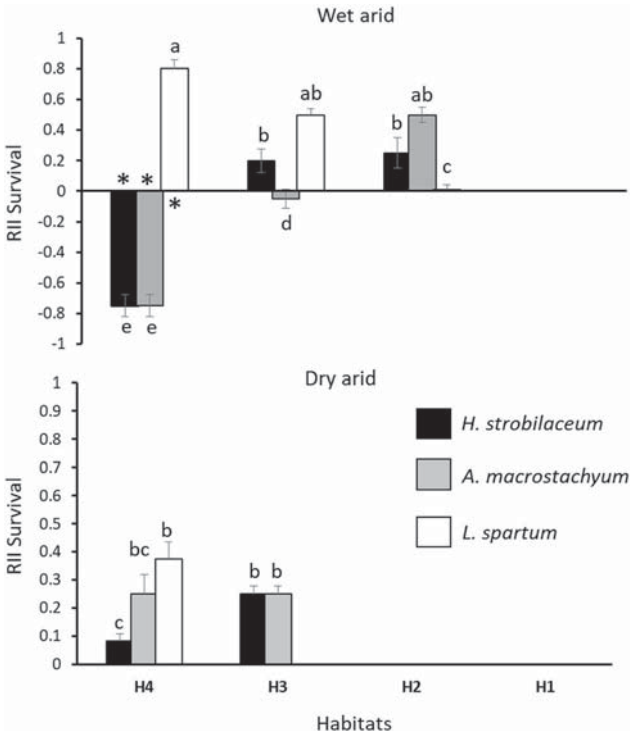

Figure 6. Means ± SE (n = 4) of relative interaction index (RII survival) calculated in summer for the three target species in the four habitats of the two climate conditions. Letters show results of the HSD Tukey test for the climate × habitat × target interaction (p = 0.003, Table 2) in the split–split-plot ANOVA. Results of one-sample t tests are shown above or below bars: *, $p < 0.05$.

the most saline habitat where survival was the lowest was also the wettest.

We did not find a switchback to competition in the most saline habitats likely because salinity is not a direct resource gradient, consistent with refined facilitation theory (Michalet 2007; Maestre and others 2009; Michalet and others 2014a). Facilitation vanished in the most saline habitat, at both seasons, in both climatic conditions and for the three target species, consistent with the collapse of facilitation theory (Michalet and others 2006). However, facilitation did not collapse because of a decrease in the facilitative effects of shrubs on abiotic conditions, as predicted by Michalet and others (2006, 2014a). Our measurements of soil electrical conductivity showed that shrubs still strongly decreased salinity stress in the most saline habitats. Additionally, results on survival rates showed that all target plants (even below shrubs) died in the spring above a threshold of salinity that was observed in the most saline habitat of both climatic conditions. Thus, our study highlights that the collapse of facilitation along a direct non-resource gradient can occur even when nurses still ameliorate the environment, as shown by Qi and others (2018) for two target species along an intertidal salinity gradient.

He and Bertness (2014) argued that SGH exceptions occur when weak stress gradients or stresses outside of species' niches are examined, multiple stresses co-occur cancelling out their effects, temporally dependent effects are involved, or results are improperly analysed. Indeed, Qi and others (2018) showed with modelling and field results that weak gradients are unlikely to support the SGH and Leong and others (2019) that isolating resource gradients provide SGH support in pitcher plants. As argued above, our gradient was not complex since we could separate salinity from drought stresses. Additionally, our salinity gradient was not weak, with electrical conductivity varying from less than 5 ms cm^{-1}, where target spring survival was close to 100%, to close to 80 ms cm^{-1}, where most plants died. Third, we did not examine the effect of salinity outside species' niches, since our most saline habitat was naturally colonized by the most stress-tolerant target species, *H. strobilaceum*, whose facilitative response also vanished at this stressful end of its niche. Fourth, life-history stage of our target species did not shift across our salinity gradient since we used transplants of sim-

ilar stages in all habitats. Thus, the collapse of facilitation found in our study could not be explained by any of these four reasonable exceptions. It is likely that alternatively supports of the SGH might result from assessing gradients that exclude the most extreme portions of the stress gradient or complex gradients involving stress factors that may cancel each other (Pugnaire and others 2015). Finally, studies assessing intraspecific interactions along gradients with abrupt end, as often occurring in intertidal systems (for example, mussel beds or chord grass communities, Figure 1B, C in He and Bertness 2014) and some terrestrial ones (for example, tree lines, Fajardo and McIntire 2011), cannot detect a collapse of facilitation since the nurse and target die at the stressful end of their niche in close association.

One can also argue that the important mortality that occurred early in the experiment might have impeded to straightforwardly test the collapse of facilitation. It is true that a higher number of replicates of transplants or an early replacement of dead individuals would have strengthened our conclusions. However, it should be noted that mortality was only high for *Lygeum spartum*, the species least tolerant to salinity, in particular in the most saline habitats. In contrast, the two halophitic shrubs, and in particular *Halocnemum strobilaceum*, survived well in the early spring in the wet arid climates even in the most saline habitats, due to the facilitation of the shrub (see Appendix 4 of ESM). This was likely due the high winter rainfall that occurred right after transplantation (see Appendix 2 of ESM). In addition, most facilitative experiments have shown that increasing facilitation in stressful environments is due to the high mortality of target plants in no-neighbours plots, a process called environmental severity effect (Michalet and others 2014b). Thus, a high mortality in open plots is not a condition impeding the test of facilitation models. Finally, an increasing mortality occurring with neighbours at extreme of environmental gradients is specifically the evidence of a collapse of facilitation, as early found in Argentina by Kitzberger and others (2000) for natural seedlings of an austral conifer.

Other soil properties than salinity might have influenced the survival of transplants in interaction with the effect of neighbours. There were in particular significant differences in soil texture across the topography gradient due to erosion, with slight increase in clay content from the upper most habitat (H4) to the lowest one (H1, see methods). However, soil texture is overall sandy in Tunisian sebkhas (from loamy sand in H4 to sandy loam in H1, Chaieb and others 2019). In addition, *L. spartum*, the species which survived the least in the lowest habitats, could not have been negatively influenced by an excess of clay since it is known to occur on soils of contrasting soil textures (including clay soils) throughout the Mediterranean Basin (Spampinato and others 2018).

The Effect of Increasing Aridity

Our design was not set up in order to straightforwardly assess the effect of increasing water stress since we had only two points along the drought gradient in similar conditions of low salinity, the H4 position from the two climate conditions. Additionally, the increase in aridity from wet to dry arid climate was likely too low to test facilitation models as argued above. However, it is interesting to notice that the increase in water stress from wet to dry arid climate at the H4 position did not induce an increase in competition, but a decrease in competition or an increase in facilitation, depending on the season and the target species. Since the dry arid climate in central Tunisia is very dry (less than 200 mm per year) as compared to other facilitation studies, we can consider that this habitat is close to the stressful end of the water stress gradient. Thus, this increase in RII from wet to dry arid climate at the H4 position does not support the switchback to competition model (Michalet 2007; Maestre and others 2009; Malkinson and Tielbörger 2010) and the results of many experiments conducted in dry environments (Tielbörger and Kadmon 2000; Maestre and Cortina 2004; Armas and Pugnaire 2005; Noumi and others 2016). We argue that this might be explained by two main reasons. First, we did not measure growth due to low survival in most treatments and several studies have shown that competition for water is more likely to be observed for growth than for survival (Liancourt and others 2005b; Forey and others 2010). Second, we assessed plant–plant interactions only with the observational method, comparing the performance of a target with neighbours to that of a target transplanted in naturally open areas. Several authors have shown that using the observational method rather than the removal method in the same system exacerbates facilitative interactions, due to including long-term positive effects of neighbours in the former only (Maestre and others 2003, 2005; Michalet 2006; Michalet and others 2015; Noumi and others 2016). Indeed, our soil water measurements showed that in all treatments there was more available water below shrubs than in open areas. This might also suggest that shrubs

from arid saline depressions are not good competitors for water, in contrast to grass neighbours (Maestre and others 2003; Maestre and Cortina 2004).

However, our system allows us to assess the interactive effects of increasing aridity and salinity, comparing the curve of interactions along the salinity gradient, either spatially in the two climates or temporally before and after the summer drought. Both of these comparisons showed that increasing aridity induced an earlier collapse of facilitation along the salinity gradient, with no more facilitation in H1 and H2 for all target species after the summer drought in the dry arid climate, whereas in the wet arid climate, facilitation was still present in H1 before the summer drought and in H2 after the summer drought. Several experiments have shown that the interaction between drought stress and disturbance induced collapses of plant–plant interactions (Forey and others 2010; Soliveres and others 2011; Maalouf and others 2012; Le Bagousse-Pinguet and others 2014; Verwijmeren and others 2019), consistent with models (Kéfi and others 2007). We showed that the interaction between two stresses also induced a collapse of facilitation.

Plant–plant interactions in arid systems are known to be also highly dependent on the climate of the year of the experiment (Kitzberger and others 2000; Gómez-Aparicio and others 2004). Thus, one limitation of our study is certainly its short duration and further experiments conducted in the same system during years with contrasting climates would certainly allow a better understanding of changes in interactions along salinity gradients. The year of our experiment was extremely wet during winter (that is, the beginning of our experiment) but drier than average during spring and summer seasons (Appendix 2 of ESM). We may expect less contrasts between interactions measured in early spring and late summer in years with drier winter and wetter spring and summer seasons. Thus, as observed by Kitzberger and others (2000) in the Andes of Argentina, a drier winter would have certainly induced in spring an earlier collapse of facilitation along the salinity gradient than the year of our experiment.

The Effect of Species Tolerances to Salinity Stress

There were weak target species effects on RII before the dry season but contrasting responses to neighbours after the dry season, in particular in the wet arid climate. The strongest target species effect was observed in the least saline habitat, where the two shrubs dominating the most saline habitats had negative responses to neighbours and the grass naturally occurring in the least saline habitat a positive response to neighbours. Thus, there was a trade-off between species tolerance to salinity and competitive responses, consistent with experiments showing that stress-tolerant species are more negatively affected by neighbours than stress-intolerant species, which are generally facilitated in the same environmental conditions (Liancourt and others 2005a, 2017; Forey and others 2010; Qi and others 2018). Thus, this effect has been taken into account in most refined facilitation theories (Michalet and others 2006; Maestre and others 2009). However, this species effect did not change the fundamental shape of collapse of facilitation, but just induced an earlier collapse along the salinity gradient for *L. spartum*, the grass target least tolerant to salinity stress than for the two most tolerant shrubs.

Conclusions

Assessing the impact on plant–plant interactions of salinity along topographic gradients in two conditions of aridity allowed us to disentangle effects of direct non-resource and resource stresses on variation in facilitation along complex environmental gradients, a highly debated issue in ecology. Consistent with refined facilitation theories, we found a strong collapse of facilitation along the salinity gradient. However, this decrease in facilitation was not due to a collapse of the mitigating effects of shrub nurses on salinity stress, but to exceeding the threshold of salinity tolerance of target species even in the presence of neighbours. Increasing aridity through space or time induced an earlier collapse of facilitation, as rather observed when disturbance and stress interact along complex environmental gradients. Although we could assess with our design the direct effect of water stress in absence of salinity stress only at two positions along the drought gradient, we did not observe a switchback to competition at the extreme end of this resource stress gradient as predicted by refined facilitation theories. This is likely due to the observational method exacerbating long-term facilitation and/or the low negative effect of halophytic shrubs on soil water availability. Finally, we found contrasting target species responses to neighbours, mostly after the summer drought in the wet arid climate, consistent with refined facilitation theories. Our results are consistent with studies showing that the collapse of facilitation at extremes of drought and

disturbance gradients threatens diversity and ecosystem functioning and stability (Kéfi and others 2007; Verwijmeren and others 2013, 2019; Berdugo and others 2019, 2020).

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REFERENCES

Armas C, Pugnaire FI. 2005. Plant interactions govern population dynamics in a semi-arid plant community. J Ecol 93:978–89.

Armas C, Ordiales R, Pugnaire FI. 2004. Measuring plant interactions: a new comparative index. Ecology 85:2682–6.

Austin MP, Smith TM. 1989. A new model for the continuum concept. Vegetatio 83:35–47.

Berdugo M, Maestre FT, Kéfi S, Gross N, Le Bagousse-Pinguet Y, Soliveres S. 2019. Aridity preferences alter the relative importance of abiotic and biotic drivers on plant species abundance in global drylands. J Ecol 107:190–202.

Berdugo M, Delgado-Baquerizo M, Soliveres S, Herńandez-Clemente R, Zhao Y, Gaitán JJ, Gross N, Saiz H, Maire V, Lehmann A, Rillig MC, Solé RV, Maestre FT. 2020. Global ecosystem thresholds driven by aridity. Science 367:787–90.

Bertness MD, Callaway RM. 1994. Positive interactions in communities. Trends Ecol Evol 9:191–3.

Bruno JF, Stachowicz JJ, Bertness MD. 2003. Inclusion of facilitation into ecological theory. Trends Ecol Evol 18:119–25.

Bulleri F, Eriksson BK, Queirós A, Airoldi L, Arenas F, Arvanitidis C, Bouma TJ, Crowe TP, Davoult D, Guizien K, Ivesa L, Jenkins SR, Michalet R, Olabarria C, Procaccini G, Serrao EA, Wahl M, Benedetti-Cecchi L. 2018. Harnessing positive species interactions as a tool against climate-driven loss of coastal biodiversity. PLOS Biol 16:1–19.

Butterfield BJ, Bradford JB, Armas C, Prieto I, Pugnaire FI. 2016. Does the stress-gradient hypothesis hold water? Disentangling spatial and temporal variation in plant effects on soil moisture in dryland systems. Funct Ecol 30:10–19.

Callaway RM. 2007. Positive interactions and interdependence in plant communities. Dordrecht: Springer.

Cavieres LA, Brooker RW, Butterfield BJ, Cook BJ, Kikvidze Z, Lortie CJ, Michalet R, Pugnaire FI, Schob C, Xiao S, Anthelme A, Aschehoug ET, Björk RG, Dickinson K, Gavilán R, Kanka R, Maalouf JP, Mark A, Noroozi J, Parajuli R, Phoenix GK, Reid A, Ridenour WM, Rixen C, Wipf S, Zhao L, Escudero A, Zaitchik BF, Lingua E, Aschehoug ET, Callaway RM. 2014. Facilitative plant interactions and climate simultaneously drive alpine plant diversity. Ecol Lett 17:193–202.

Chaieb G, Abdelly C, Michalet R. 2019. Interactive effects of climate and topography on soil salinity and vegetation zonation in North-African continental saline depressions. J Veg Sci 30:312–21.

De Mendiburu F. 2017. Agricolae: Statistical Procedures for Agricultural Research.—R package version 1.2-8. https://CRAN.R-project.org/package=agricolae.

Emberger L. 1958. Afrique du nord et Australie méditerranéenne. Climatology and Microclimatology: Proceedings of the Canberra Symposium. UNESCO Arid Zone Res 11:141–147.

Fajardo A, McIntire EJB. 2011. Under strong niche overlap conspecifics do not compete but help each other to survive: facilitation at the intraspecific level. J Ecol 99:642–50.

Fariña JM, He Q, Silliman BR, Bertness MD. 2017. Biogeography of salt marsh plant zonation on the Pacific coast of South America. J Biog 45:238–47.

Forey E, Touzard B, Michalet R. 2010. Does disturbance drive the collapse of biotic interactions at the severe end of a diversity–biomass gradient? Plant Ecol 206:287–95.

Gómez-Aparicio L, Zamora R, Gómez JM, Hódar JA, Castro J, Baraza E. 2004. Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. Ecol Appl 14:1128–38.

He Q, Bertness MD. 2014. Extreme stresses, niches, and positive species interactions along stress gradients. Ecology 95:1437–43.

He Q, Bertness MD, Altieri AH. 2013. Global shifts towards positive species interactions with increasing environmental stress. Ecol Lett 16:695–706.

Holmgren M, Scheffer M. 2010. Strong facilitation in mild environments: the stress gradient hypothesis revisited. J Ecol 98:1269–75.

Kéfi S, Rietkerk M, Alados CL, Pueyo Y, Papanastasis VP, ElAich A, De Ruiter PC. 2007. Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. Nature 449:213–17.

Kitzberger T, Steinaker DF, Veblen TT. 2000. Effects of climatic variability on facilitation of tree establishment in Northern Patagonia. Ecology 81:1914–24.

Le Bagousse-Pinguet Y, Maalouf JP, Touzard B, Michalet R. 2014. Importance, but not intensity of plant interactions relates to species diversity under the interplay of stress and disturbance. Oikos 123:777–85.

Leong FWS, Lam WN, Tan HTW. 2019. Digestive mutualism in a pitcher plant supports the monotonic rather than hump-shaped stress-gradient hypothesis model. Oecologia 190:523–34.

Liancourt P, Callaway RM, Michalet R. 2005a. Stress tolerance and competitive-response ability determine the outcome of biotic interactions. Ecology 86:1611–18.

Liancourt P, Corcket E, Michalet R. 2005b. Stress tolerance abilities and competitive responses in a watering and fertilization field experiment. J Veg Sci 16:713–22.

Liancourt P, Le Bagousse-Pinguet Y, Rixen C, Dolezal J. 2017. SGH: stress or strain gradient hypothesis? Insights from an elevation gradient on the roof of the world. Ann Bot 120:29–38.

Liu YX. 1985. Flora in desertis republicae populorum sinarum. Tomus I. Science Press (ed), Beijing (in Chinese).

Lortie CJ, Filazzola A, Sotomayor DA. 2016. Functional assessment of animal interactions with shrub-facilitation complexes: a formal synthesis and conceptual framework. Funct Ecol 30:41–51.

Maalouf JP, Le Bagousse-Pinguet Y, Marchand L, Touzard B, Michalet R. 2012. The interplay of stress and mowing disturbance for the intensity and importance of plant interactions in dry calcareous grasslands. Ann Bot 11:821–8.

Maestre FT, Cortina J. 2004. Do positive interactions increase with abiotic stress? A test from a semi-arid steppe. Proc R Soc B 271:331–3.

Maestre FT, Bautista S, Cortina J. 2003. Positive, negative, and net effects in grass-shrub interactions in mediterranean semiarid Grasslands. Ecology 84:3186–97.

Maestre FT, Valladares F, Reynolds JF. 2005. Is the change of plant–plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments. J Ecol 93:748–57.

Maestre FT, Callaway RM, Valladares F, Lortie CJ. 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. J Ecol 97:199–205.

Mahajan S, Tuteja N. 2005. Cold, salinity and drought stresses: An overview. Arch Biochem 444:139–58.

Malkinson D, Tielbörger K. 2010. What does the stress-gradient hypothesis predict? Resolving the discrepancies. Oikos 119:1546–52.

McArthur RH, Wilson EO 1967. The theory of Island Biogeography. Princeton Univ Press.

Michalet R. 2006. Is facilitation in arid environments the result of direct or complex interactions? New Phytol 169:3–6.

Michalet R. 2007. Highlighting the multiple drivers of change in interactions along stress gradients. New Phytol 173:3–6.

Michalet R, Pugnaire FI. 2016. Facilitation in communities: underlying mechanisms, community and ecosystem implications. Funct Ecol 30:3–9.

Michalet R, Brooker RW, Cavieres LA, Kikvidze Z, Lortie CJ, Pugnaire FI, Valiente-Banuet A, Callaway RM. 2006. Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? Ecol Lett 9:767–73.

Michalet R, Le Bagousse-Pinguet Y, Maalouf JP, Lortie CJ. 2014a. Two alternatives to the stress-gradient hypothesis at the edge of life: the collapse of facilitation and the switch from facilitation to competition. J Veg Sci 25:609–13.

Michalet R, Schöb C, Lortie CJ, Brooker RW, Callaway RM. 2014b. Partitioning net interactions among plants along altitudinal gradients to study community responses to climate change. Funct Ecol 28:75–86.

Michalet R, Brooker RW, Lortie CJ, Maalouf JP, Pugnaire FI. 2015. Disentangling direct and indirect effects of a legume shrub on its understorey community. Oikos 124:1251–62.

Muhamed H, Touzard B, Le Bagousse-Pinguet Y, Michalet R. 2013. The role of biotic interactions for the early establishment of oak seedlings in coastal dune forest communities. Forest Ecol Manag 297:67–74.

Noumi Z, Chaieb M, Le Bagousse-Pinguet Y, Michalet R. 2016. The relative contribution of short-term versus long-term effects in shrub-understory species interactions under arid conditions. Oecologia 180:529–42.

O'Brien MJ, Pugnaire FI, Armas C, Rodríguez-Echeverría S, Schöb C. 2017. The shift from plant–plant facilitation to competition under severe water deficit is spatially explicit. Ecol Evol 7:2441–8.

Padilla FM, Pugnaire FI. 2006. The role of nurse plants in the restoration of degraded environments. Front Ecol Environ 4:196–202.

Pugnaire FI, Zhang L, Li R, Luo T. 2015. No evidence of facilitation collapse in the Tibetan plateau. J Veg Sci 26:233–42.

Qi M, Sun T, Xue S, Yang W, Shao D, Martínez-López J. 2018. Competitive ability, stress tolerance and plant interactions along stress gradients. Ecology 99:848–57.

R Core Team. 2017. R: a language and environment for statistical computing.—R Project for Statistical Computing, Vienna, Austria. http://www.r-project.org/.

Redondo-Gómez S, Mateos-Naranjo E, Figueroa ME, Davy AJ. 2010. Salt stimulation of growth and photosynthesis in an extreme halophyte, *Arthrocnemum macrostachyum*. Plant Biol 12:79–87.

Soliveres S, Maestre FT. 2014. Plant–plant interactions, environmental gradients and plant diversity: a global synthesis of community-level studies. Perspect Plant Ecol Evol Syst 16:154–63.

Soliveres S, García-Palacios P, Castillo-Monroy AP, Maestre FT, Escudero A, Valladares F. 2011. Temporal dynamics of herbivory and water availability interactively modulate the outcome of a grass–shrub interaction in a semi-arid ecosystem. Oikos 120:710–19.

Soliveres S, Smit C, Maestre FT. 2015. Moving forward on facilitation research: response to changing environments and effects on the diversity, functioning and evolution of plant communities. Biol Rev 90:297–313.

Spampinato G, Musarella CM, Cano-Ortiz A, Signorino G. 2018. Habitat, occurrence and conservation status of the Saharo-Macaronesian and Southern-Mediterranean element *Fagonia cretica* L. (Zygophyllaceae) in Italy. J Arid Land 10:140–51.

Sthultz CM, Gehring CA, Whitham TG. 2007. Shifts from competition to facilitation between a foundation tree and a pioneer shrub across spatial and temporal scales in a semiarid woodland. New Phytol 173:135–45.

Tielbörger K, Kadmon R. 2000. Temporal environmental variation tips the balance between facilitation and interference in desert plants. Ecology 81:1544–53.

Verwijmeren M, Rietkerk M, Wassen MJ, Smit C. 2013. Interspecific facilitation and critical transitions in arid ecosystems. Oikos 122:341–7.

Verwijmeren M, Smit C, Bautista S, Wassen MJ, Rietkerk M. 2019. Combined grazing and drought stress alter the outcome of nurse: beneficiary interactions in a semi-arid ecosystem. Ecosystems 22:1295–307.

Wright AJ, Wardle DA, Callaway R, Glaxiola A. 2017. The overlooked role of facilitation in biodiversity experiments. Trends Ecol Evol 32:383–90.

Zhang G, Zhao W, Zhou H, Yang Q, Wang X. 2018. Extreme drought stress shifts net facilitation to neutral interactions between shrubs and sub-canopy plants in an arid desert. Oikos 127:381–91.

2. SÉPARATION DES EFFETS DES VOISINS DE COURT ET LONG TERME ET DES DÉTERMINANTS ENVIRONNEMENTAUX ET BIOTIQUES DE CES INTERACTIONS

Cette partie du travail a fait l'objet d'un article publié dans la revue *Oikos*, sous la référence suivante :

G Chaieb, X Wang, C Abdelly and R Michalet: Shift from short-term competition to facilitation with drought stress is due to a decrease in long-term facilitation. *Oikos* (2020). https://doi.org/10.1111/oik.07528.

Introduction

Dans cette étude, nous avons fait l'hypothèse que l'augmentation avec le stress hydrique des effets négatifs de court terme devrait être due à des effets de traits des voisins alors qu'une augmentation ou un collapse des effets positifs de long terme avec le stress salin devrait être dû à des effets de sévérité environnementale.

Pour répondre à ces hypothèses, nous avons étudié les changements dans les effets à court et à long terme des arbustes dominants sur trois graminées d'espèces cibles avec des stress croissants de sécheresse et de salinité. L'effet du stress dû à la sécheresse a été évalué dans le temps, du printemps humide à l'été sec, tandis que l'effet du stress salin croissant a été évalué dans l'espace, en comparant les effets des voisins dans les habitats 3 et 4. Plus précisément nous avons voulu répondre à trois questions. 1) Quelles sont les directions des effets à court et à long terme des arbustes dominants? 2) Comment varient les effets à court et à long terme avec l'augmentation du stress dû à la sécheresse dans le temps et le stress de la salinité dans l'espace? 3) Est-ce que les variations des effets à court et à long termes avec les stress croissants de sécheresse et de salinité sont dues aux effets de voisinage ou de l'environnement?

Résultats principaux

Avant la saison sèche estivale et dans les deux habitats sélectionnés, conformément à la littérature, nos résultats montrent que les effets à court-terme sont négatifs et les effets de long-terme positifs. Cependant, après la saison sèche, les effets à court-terme sont passés de négatifs à positifs, tandis que les effets de long-terme ont disparu. Les changements des interactions de court-terme se sont révélés être de nature environnementale alors que ceux de long-terme de nature biotique.

La disparition des effets positifs de long terme pendant la saison sèche a été clairement due à la perte de la réserve en eau des microhabitats où les voisins ont été éliminés, effet entraînant la baisse dramatique de la survie des cibles. Ainsi on peut conclure qu'une augmentation de la facilitation de court-terme avec augmentation de la sécheresse temporelle (du printemps à l'été), conforme au SGH, est en fait dû à un collapse de la facilitation de long-terme. Ces résultats questionnent donc les conclusions des études expérimentales qui proposent que l'augmentation avec le stress hydrique de la facilitation mesurée par la seule méthode expérimentale confirment le SGH. L'utilisation des deux méthodes, observationnelle et expérimentale en parallèle permet ainsi de mieux comprendre les mécanismes de changements d'interactions le long des gradients environnementaux.

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Research

Shift from short-term competition to facilitation with drought stress is due to a decrease in long-term facilitation

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Disentangling short- and long-term neighbour effects, using both removal and observational methods within a single experiment, has strongly improved our understanding of the driving mechanisms of plant–plant interactions. However, there has been no attempt to assess two important underlying processes of their changes along gradients, either environmental-severity (changes in target performance without neighbours) or neighbour-traits (changes in performance with neighbours) effects, the former previously shown in alpine communities to be involved in competition and the latter in facilitation. We addressed this goal in an experiment conducted in continental saline depressions (sebkhas) from the Mediterranean arid climate of central Tunisia. We quantified short- and long-term effects of dominant shrubs, transplanting three target grass species in open, nurse and removed-nurse microhabitats of two habitats of different salinity levels in height sebkhas. The design extended geographically from central Tunisia to the Libyan border, 500 km southeastward. We used the relative interaction index to calculate short- and long-term effects before and after the dry summer seasons and environmental-severity and neighbour-trait effects. Short-term effects were slightly negative and long-term effects strongly positive before the dry summer season in the two habitats. Short-term effects switched to positive with increasing drought stress, due to an environmental-severity effect, whereas long-term effects decreased due to a neighbour-trait effect. Salinity did not affect neither short- nor long-term shrub effects. Soil moisture measurements showed that both changes were due to vanishing shrub soil engineering-effects during the summer drought. We conclude that an increase in short-term facilitation with increasing drought stress through time, apparently supporting the stress gradient hypothesis, might be due to a decrease in long-term facilitation. Thus, we recommend using, as much as possible, both the removal and observational methods in experiments assessing changes in plant–plant interactions along stress gradients to avoid wrong conclusions.

Keywords: competition, drought, environmental-severity effects, facilitation, long-term effects, Mediterranean climate, neighbour-trait effects, salinity, short-term effects

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Introduction

Facilitation, the positive effect of an organism on another one within a trophic level (Callaway 2007), is now widely recognized as an important biotic interaction occurring more frequently in stressful or disturbed environmental conditions (Bruno et al. 2003, Brooker et al. 2008, He et al. 2013, Soliveres and Maestre 2014, Bulleri et al. 2018). Facilitation is crucial in severe environments since it allows species untolerant to stress or disturbance to persist in extreme habitats, thus increasing diversity (Hacker and Gaines 1997, Liancourt et al. 2005, Michalet et al. 2006, Xiao et al. 2009, Le Bagousse-Pinguet et al. 2014a, Cavieres et al. 2014). In addition, facilitation within plant communities can scale-up to interactions at other trophic levels, such as pollinators or soil microbes, ultimately shaping ecological networks, the diversity of dependent communities and ecosystem functioning (Losapio and Schöb 2017, Lozano et al. 2017, Losapio et al. 2019, Wang et al. 2020). Another key property of facilitation in water-limited systems is its potential use as engineering tool for restoring degraded habitats (Padilla and Pugnaire 2006, Ibáñez and Rodríguez 2020). However, variation in facilitation and competition at the stressful end of drought gradients is a highly debated issue in plant community ecology (Maestre et al. 2005, 2009, Michalet 2007, He and Bertness 2014, Michalet et al. 2014a, Soliveres et al. 2015). Understanding under which biotic and environmental conditions facilitation is more likely to prevail in extremely stressed conditions is crucial for predicting the mediating role of facilitation in species responses to climate change and using facilitation for ecological restoration of degraded arid systems (Michalet and Pugnaire 2016).

The stress gradient hypothesis pioneer theory proposed that facilitation should increase monotonically with increasing either stress or disturbance (Bertness and Callaway 1994, Brooker and Callaghan 1998) and that competition should dominate in undisturbed and not stressed conditions, following Grime's model (1973). In cold terrestrial environments and coastal systems, the SGH theory has been supported by several experiments (Callaway et al. 2002, reviewed by Michalet et al. 2014b, Bulleri et al. 2018). In contrast, in dry systems contrasting results have been found, either supporting the SGH (Gómez-Aparicio et al. 2004, Sthultz et al. 2007, Muhamed et al. 2013) or finding a switchback to competition (Tielbörger and Kadmon 2000, Maestre and Cortina 2004, O'Brien et al. 2017) or collapse of facilitation (Kitzberger et al. 2000, Le Bagousse-Pinguet et al. 2014b, Zhang et al. 2018, Berdugo et al. 2019) at the stressed end of environmental gradients. Thus, facilitation theory has been refined by several authors (Michalet et al. 2006, Michalet 2007, Maestre et al. 2009, Holmgren and Scheffer 2010, Malkinson and Tielbörger 2010, Verwijmeren et al. 2013) and there is almost a consensus to consider that different relationships between biotic interactions and environmental severity may exist depending on species strategies, stress factors and methods (reviewed by Michalet et al. 2014a, but see He and Bertness 2014).

In this paper, we focus on the importance of the method used to quantify neighbours effects and of the type of stress (resource versus non-resource). As originally shown by Maestre et al. (2003, 2005), results of experiments in dry systems provided contrasting results depending on the method used to quantify interactions, with dominant positive effects of neighbours, when using an observational method (comparison of target performances with neighbours and in naturally occurring open areas between neighbours) and dominant negative effects of neighbours, when using a removal method (comparison of target performances with neighbours and in removed-neighbours conditions). This apparent discrepancy has been explained by within-community differences in microhabitats between vegetated and open patches, due to ecosystem-engineering effects or conversely disturbance and erosion and the time-scale of the quantified interactions (Michalet 2006, Schöb et al. 2012, but see Steinbauer et al. 2016). Michalet et al. (2015) and Noumi et al. (2016) proposed two different indices for disentangling short- from long-term effects of neighbours in experiments associating both the observational and removal procedures in the same community. Short-term effects (canopy effects in Michalet et al. 2015) were quantified using the removal method (with neighbours versus removed-neighbours conditions) and long-term effects (soil effects in Michalet et al. 2015) comparing target responses in removed-neighbours versus open conditions (Noumi et al. 2016). Thus, the net neighbour effects (i.e. the sum of short- and long-term effects) were quantified in both studies with the observational method. Consistent to Maestre et al. (2005) and Michalet (2006), most field experiments found more negative short- than long-term effects. However, the direction of changes of both effects with increasing stress seems highly dependent on systems, species and stress type (Michalet et al. 2015, 2017, Noumi et al. 2016, Pistón et al. 2018).

In this study, we aim assessing the role of the type of stress in driving changes in direction of short- and long-term effects of neighbours along stress gradients in dry systems. Michalet (2007), Maestre et al. (2009) and Michalet et al. (2014a) have argued that stress gradients related to resource factors (e.g. water or nutrient) should rather show an increase in competition with increasing stress, consistent to the McArthur and Wilson (1967) theory and Taylor et al. (1990) strategy model, whereas stress gradients related to non-resource factors (e.g. cold or salinity) were more likely to show an increase or a collapse of facilitation with increasing stress depending on the level of stress. Specifically, we aim to disentangle the effects of water and salinity stresses in a dry system and to test the hypothesis that increasing drought stress should increase negative short-term effects, due to increase in competition for water, whereas increasing salinity stress should increase or induce a collapse of positive long-term effects, because of variation in soil-engineering effects.

Another important conceptual and methodological progress recently made in plant–plant interactions studies for understanding the driving mechanisms of changes in facilitation and competition along environmental gradients is

decomposing the net effect of neighbours in neighbour-trait and environmental-severity effects (Michalet et al. 2014b). Plant–plant interactions experiments generally use indices of interactions, such as the relative interaction index (RII, Armas et al. 2004), to quantify effects of neighbours on target species or understorey communities. As many indices based on relative differences or ratios of performances, they cannot disentangle changes in interactions along gradients that are due to changes in the performance of targets growing in with- or without-neighbours conditions, the former being induced by changes in the effects of the nurse (neighbour-trait effects), whereas the latter being induced by a simple direct effect of increasing stress on the isolated target species (environmental-severity effect). This distinction is crucial for understanding changes in plant–plant interactions along environmental gradients. For example, for temperate alpine communities, Michalet et al. (2014b) showed that increases in competition with decreasing cold stress towards lower subalpine elevations, were due to neighbour-trait effects, i.e. increase in neighbours competitive ability, consistent to Grime's model (1974), whereas increases in facilitation with increasing cold stress towards higher alpine elevations were due to environmental-severity effects, i.e. higher strain for the target species when growing in removed-neighbours conditions (Liancourt et al. 2017). Such differences are crucial for understanding the mediating role of competition and facilitation for species responses to climate change. Thus, we aim to apply these concepts and methods to dry systems, with the hypothesis that an increase in negative short-term effects with drought stress should be due to neighbour-trait effects, whereas an increase or collapse in positive long-term effects with salinity stress should be due to environmental-severity effects.

To address these hypotheses we assessed changes in short- and long-term effects of dominant shrubs on three target grass species with increasing drought and salinity stresses in continental saline depressions from the Mediterranean climate of central Tunisia. The effect of drought stress was assessed through time from the wet spring to the dry summer seasons, whereas the effect of salinity stress was assessed through space, comparing effects of neighbours in two habitats with low and high salinity levels across a topography gradient. We aim at answering three questions. 1) What are the directions of short- and long-term effects of dominant shrubs? 2) How vary short- and long-term effects with increasing drought stress through time and salinity stress through space? 3) Are variations in short- and long-term effects with increasing drought or salinity stresses due to neighbour-trait or environmental-severity effects?

Material and methods

Study sites and target species

The study was conducted in continental saline depressions (locally called sebkhas) from central Tunisia, at the northern edge of the Sahara desert (Supplementary material Appendix 1). In central and southern Tunisia the climate is Mediterranean arid, with mean annual precipitation included between 100 and 300 mm. Mean of annual temperatures is 19°C, with 4.6°C in winter and 37.0°C in summer. In the Mediterranean arid climate, summer is the driest season but precipitation is also very low during other seasons and unpredictable among years, due to high rainshadow effects (Michalet 1991).

Sebkhas are widely developed in central and southern Tunisia due to the occurrence of low-elevation depressions in an arid climate with important potential evaporation and low rainfall. All sebkhas have a lentil-like shape with sizes varying between 10 and 300 km^2. The overall habitat distribution of these sebkhas is similar, with an important central part with no vegetation inundated from early December to late February during the wet season and several surrounding belts of halophytic plant communities. Four main habitats and corresponding plant communities can be distinguished with increasing elevation and decreasing salinity from the central part with no vegetation to the edge of the sebkhas (Chaieb et al. 2019). In order to disentangle the role of salinity from drought stress on plant–plant interactions, we focused here on the two intermediate habitats of the transect, because the lowest habitat with very low vegetation cover and very high salinity can be inundated during the wet season and the highest one with very low salinity is highly disturbed by ploughing by local farmers.

The lower of these two intermediate habitats, hereafter called high saline habitat, is dominated by the shrub *Arthrocnemum macrostachyum* and has an electrical conductivity varying between 20 and 30 ms cm^{-1}, depending on seasons and microhabitats (Chaieb et al. 2019). *Arthrocnemum macrostachyum* (Amaranthaceae) is a C_3 shrub present from the Mediterranean area to western Asia and known as a salt-accumulator (Winter et al. 1976, Redondo-Gómez et al. 2010). Other species are mostly shrubs, such as *Suaeda mollis*, *Limoniastrum monopetalum* and *Atriplex halimus*. The upper habitat, hereafter called low saline habitat, is co-dominated by various shrub species (*Salsola tetrandra*, *Zygophyllum album*, *Reaumuria vermiculata* and *Nitraria retusa*) and *Lygeum spartum* (Poaceae), a widespread rhizomatous perennial grass native of the Mediterranean region. *S. tetrandra* (Amaranthaceae) is a C3 shrub present in dry regions of Africa and Asia, which was used as nurse in our experiment. Electrical conductivity varies between 5 and 15 ms cm^{-1}, depending on seasons and microhabitats (Chaieb et al. 2019).

Experimental design

In order to assess changes in short- and long-term effects of dominant shrubs with increasing drought and salinity stresses, late September 2018, we first selected height sebkhas (blocks) in the arid climate of central Tunisia. The eight sebkhas were distributed from Mahdia in north-central Tunisia to the Libyan border, 500 km away in southeast direction, thus, representing a large range of climatic conditions within the Mediterranean arid climate (Supplementary material

Appendix 1). In each sebkha, we selected for the salinity treatment two main plots, one in the high and one in the low saline habitat, as explained above. Thus, there was a total of 16 mains plots (two habitats × eight blocks). Within each of the 16 main plots we applied a neighbour and a target treatment to assess short- and long-term effects of shrubs on target species. Following Michalet et al. (2015), the neighbour treatment had three modalities, nurse, removed and open. In the nurse subplots target species were planted on the northern edge of the shrub patches, while in the removed subplots target were planted in a similar microhabitat where the shrub was cut at ground level with scissors. Open subplots were chosen in naturally non-vegetated areas, at least at 50 cm-distance from any shrub. The nurse shrub were different species in the two habitats, *A. macrostachyum* in the high-saline habitat and *S. tetrandra* in the low-saline habitat. The size of the individuals of the former species chosen as nurses was included between 1 and 2 m for canopy diameter and approximatively 1 m for height, whereas the other species was taller (approximately 2 m tall) and had a lower canopy diameter (approximately 1 m). Three grass species were chosen as targets for the species treatment, *Aristida adscensionis*, *Lygeum spartum* and *Hyparrhenia hirta*. Since our main goal was not to assess the species-specificity of responses to the effect of neighbours, the three chosen species had close tolerances to salinity stress, although *L. spartum* can occur more frequently in the high-saline habitat than the other two species more restricted to the low-saline habitat (Chaieb et al. 2019).

Three individuals of each target species were transplanted in each of the three microhabitats of the neighbour treatment (nurse, removed and open) in each main plot, with one transplant individual per subplot. Thus, there was a total of 432 subplots (16 main plots × three species × three microhabitats × three transplant replicates). In early September 2018, target species individuals were harvested in their own habitats in three of the height sebkhas. Sampled target individuals had an average height of 15 cm and were grown from rooted cuttings of the three species. Cuttings were transplanted in meshed bags of 20 cm-deep and 10 cm-diameter filled with the soil of each corresponding habitat, that were placed in the common-garden of the Tunisian Ministery of Environment at Sfax, the main town at the vicinity of our sites. Transplants were grown there until mid-November 2018 with an irrigation of 20 mm of tap water per transplant every 15 days. Mid-November 2018 all individuals were transplanted in all subplots during three days. Each transplant was watered right after transplantation with one litter of tap water.

Data collection and calculation of indices

The experiment lasted until late September 2019 and we only recorded transplant survival in spring (early April) and at the end of the summer (late September) since there was too low survival at the the end of the experiment for analyzing biomass responses to treatments. Survival rate was calculated at the block level in all combinations of the habitat per species and neighbour treatments.

We used the relative interaction index (RII) (Armas et al. 2004) to quantify both the short- and long-term effects of the shrubs on target species. This index is based on the comparison of target performance with and without neighbours:

$$RII_{neighbour} = \left(X_{with\ neighbour} - X_{without\ neighbour}\right) / \left(X_{with\ neighbour} + X_{without\ neighbour}\right)$$

Values of RII vary between −1 and 1, with negative values for competition and positive ones for facilitation. In order to disentangle short- from long-term effects of the shrubs, following Michalet et al. (2015), we calculated two $RII_{neighbour}$, short-term $RII_{neighbour}$ and long-term $RII_{neighbour}$, respectively. Short-term $RII_{neighbour}$ quantifies the short-term effects of the shrub, calculating the relative difference in survival rate between targets from nurse and removed microhabitats

$$\text{Short-term } RII_{neighbour} = \left(X_{nurse} - X_{removed}\right) / \left(X_{nurse} + X_{removed}\right)$$

Long-term $RII_{neighbour}$ quantifies the long-term effects of the shrub, calculating the relative difference in target survival rate between targets from removed and open microhabitats.

$$\text{Long-term } RII_{neighbour} = \left(X_{removed} - X_{open}\right) / \left(X_{removed} + X_{open}\right)$$

Additionally, in order to depict neighbour-trait and environmental-severity effects during changes in both short- and long-term interactions with increasing drought stress from the spring to the summer seasons, we calculated a RII_{season} by quantifying the relative difference in target survival rate between the summer and spring seasons:

$$RII_{season} = \left(X_{summer} - X_{spring}\right) / \left(X_{summer} + X_{spring}\right)$$

Values of RII_{season} vary between −1 and 0, with significant negative values indicating that the performance of the target decreased with increasing drought stress from spring to summer seasons. There are two RII_{season}, one without neighbours and one with neighbours. When RII_{season}, without neighbours is significantly negative and RII_{season}, with neighbours is equal to 0, this means that the change in $RII_{neighbour}$ with increasing stress from spring to summer seasons is due to an environmental-severity effect (change in performance of the target without neighbours). In contrast, when the RII_{season}, with neighbours is significantly negative and the RII_{season}, without neighbours is equal to 0, this means that the change in $RII_{neighbour}$ with increasing stress from spring to summer seasons is due to a neighbour-trait effect (change in performance of the target with neighbours). Finally, when both RII_{season} are significantly negative, this means that the change in $RII_{neighbour}$ with increasing stress from spring to summer seasons is due to both an environmental-severity and a neighbour-trait effect. Note that RII_{season} can be calculated for both changes in short- and long-term $RII_{neighbour}$. The difference,

like for the two $RII_{neighbour}$, is that for short-term RII_{season} without neighbours the microhabitat without neighbours is the removed microhabitat, whereas for long-term RII_{season} without neighbours the microhabitat without neighbours is the open microhabitat. For short-term RII_{season} with neighbours the microhabitat with neighbours is the nurse microhabitat, whereas for long-term RII_{season} with neighbours the microhabitat with neighbours is the removed microhabitat.

In addition, soil salinity (electrical conductivity) and soil moisture were measured in all subplots in early April and late September 2018, using a Wet Sensor HH2 moisture meter.

Statistical analyses

We tested the effects of the habitat, neighbour and species treatments and their interactions on spring and summer survival, separately, using a generalized linear mixed-effects model (GLMM). A GLMM was also used to test the effects of soil moisture, habitat, neighbour and species treatments and their interactions on survival at the two season. We calculated nonparametric 95% confidence intervals (CI) of RIIs by bootstrap sampling with 999 iterations (Kirby and Gerlanc 2013). We tested two forms of soil moisture in this analysis, Log (soil moisture) and Log (soil moisture)^2, to eventually detect non-linear relationships (Maalouf et al. 2012). Since only linear effects were significant in the GLMM, non-linear ones were not shown in Table 2. To test the effects of the season, habitat and neighbour treatments and their interactions on salinity (electrical conductivity) and soil moisture, we used a split–split-plot mixed analysis of variance (ANOVA), with blocks (sebkhas) as random effect, season as main treatment, habitat as sub-treatment and neighbour as sub-sub-treatment. Soil moisture and salinity variables were log-transformed to meet normality before ANOVA.

All analyses were done using R ver. 3.3.3 (<www.r-project.org>). We used the function *glmer* for binomial family to perform generalized linear mixed-effects models (GLMM) on survival. The split–split-plot ANOVAs on salinity and soil moisture were performed with the package 'agricolae' (De Mendiburu 2017), using the function *ssp.plot*. Post hoc tests after GLMMs were performed with function lsmeans (Lenth, 2016). *LSD.test* (agricolae package) was used after split–split-plot ANOVAs when necessary. CIs were calculated with the *bootES* function ('bootES' package; Kirby and Gerlanc 2013).

Results

There were significant effects of the habitat, neighbour and species treatments on spring survival (Table 1), with lower survival in the high than low saline habitat, in the open than in the removed microhabitats (with intermediate values for the nurse microhabitat, see results of the Tukey test in Fig. 1A–C) and for *Hyparrhenia hirta* than for the other two species (Fig. 1 and results of Tukey tests for the species treatment not shown). However, there was a significant neighbour by species interaction, with a similar survival in the nurse than removed microhabitats for *Lygeum spartum* only. In summer, results were similar for the species treatment (Table 1, Fig. 1D–F). In contrast, the habitat effect was not significant and the highest survival was found in the nurse microhabitats, since survival strongly decreased from spring to summer seasons only in the removed microhabitats.

Table 1. Results of generalized linear mixed-effects models (GLMM) on the effects of the habitat, neighbour and species treatments and their interactions on survival rates in spring and summer seasons. Significant ($p < 0.05$) effects are indicated in bold.

		Spring		Summer	
Effects	df	χ^2	p	χ^2	p
habitat	1	7.3	**0.007**	2.6	0.104
neighbour	2	42.8	**<0.001**	41.2	**<0.001**
species	2	17	**<0.001**	27.3	**<0.001**
habitat × neighbour	2	0.7	0.704	0	0.992
habitat × species	2	1.6	0.460	3.3	0.186
neighbour × species	4	10.5	**0.033**	1.1	0.896
habitat × neighbour × species	4	1.4	0.838	0	1

In order to more clearly depict changes in shrub effects with increasing drought from spring to summer seasons and the underlying processes of these changes in interaction, we pooled survival for the two habitats and three species for calculating short-term and long-term $RII_{neighbour}$ at each season and RII_{season} with and without neighbours (Fig. 2). For short-term effects, $RII_{neighbour}$ was weakly negative in spring and significantly shifted to positive in summer (non-overlapping CIs), with confidence intervals indicating significant competition and facilitation, respectively. RII_{season} was strongly negative without neighbours and significantly shifted to neutral with neighbours (confidence interval overlapping 0 value). These results provide evidence that the shift from short-term competition to facilitation with increasing drought stress through time was due to an environmental-severity effect. In contrast, for long-term effects, $RII_{neighbour}$ was strongly positive in spring and significantly decreased to weakly positive in summer, while RII_{season} was weakly negative without neighbours and significantly decreased to highly negative with neighbours. These results provide evidence that the decrease in long-term facilitation with increasing drought stress through time was due to a neighbour-trait effect. All together, these results show that the shift from short-term competition to facilitation with increasing drought stress through time was due a decrease in long-term facilitation.

In order to depict the underlying environmental processes driving these changes in short- and long-term effects of shrubs with increasing drought stress, we analyzed the relationships existing between target survival and soil moisture in the three microhabitats (Fig. 3). There was a highly significant neighbour by soil moisture interaction in the GLMM (Table 2). Indeed, overall species and habitats, there was a highly significant decrease in survival with decreasing soil moisture in the removed microhabitats ($R^2 = 0.41$, Fig. 3), whereas there was no significant relationship for the nurse microhabitats and a weaker relationship for the open microhabitats ($R^2 = 0.11$).

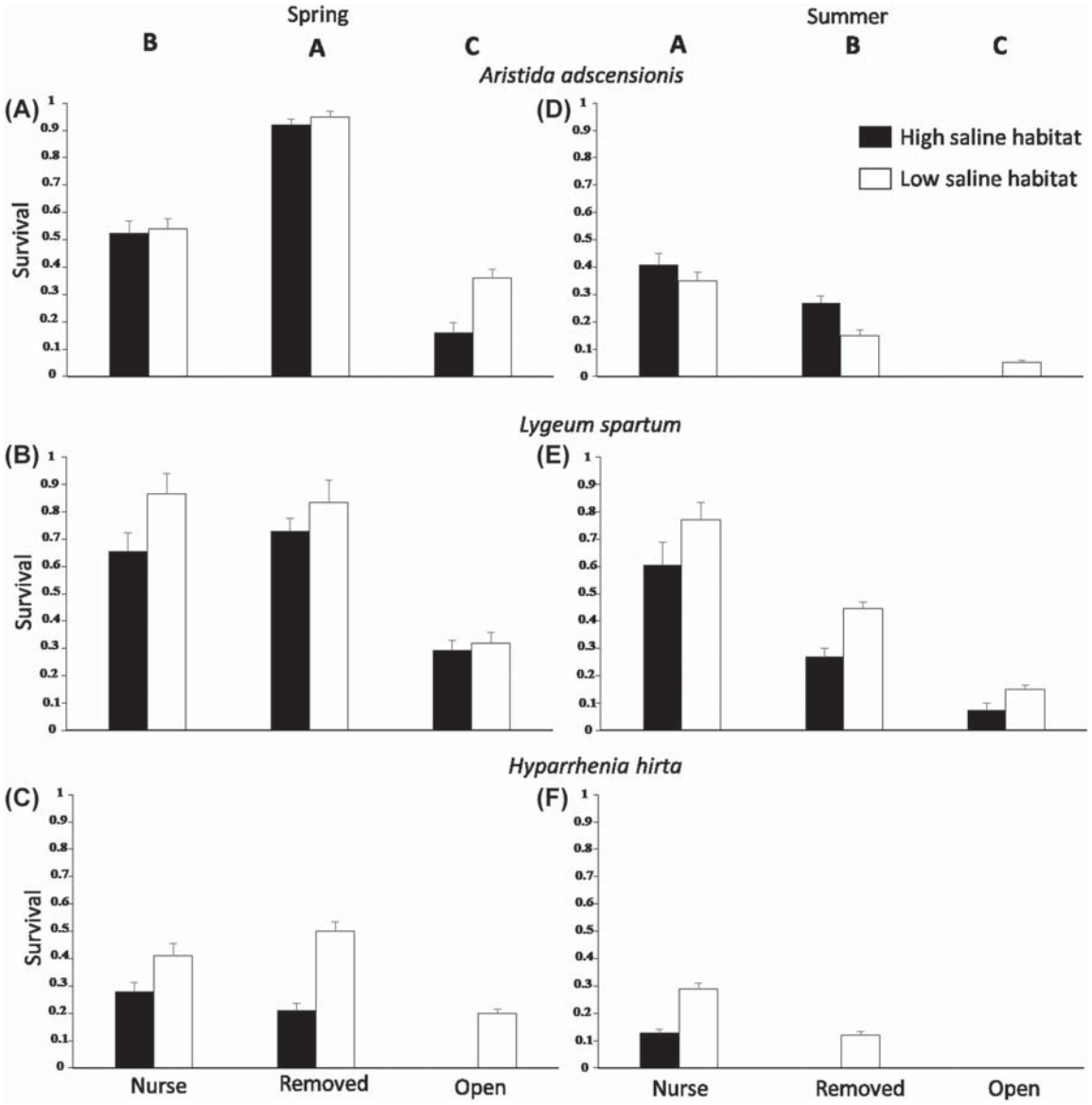

Figure 1. Means ± SE (n = 8) of survival rate of the three target species (*A. adscensionis*, *L. spartum* and *H. hirta*), in spring and summer seasons and in the nurse, removed and open microhabitats of the two habitats (high saline and low saline). Letters show results of the HSD Tukey tests for the neighbour effect in the two analyses, separately for spring and summer seasons ($p < 0.01$, Table 1).

This result strongly suggests that the decrease in long-term facilitation and resulting shift from short-term competition to facilitation observed with increasing drought stress through time was primarily due to water evaporation in removed microhabitats during the summer season.

This suggestion was supported by changes in soil water contents observed from spring to summer seasons in the three microhabitats. Indeed, for the two habitats, the strongest decrease in soil moisture during the dry summer season was observed in the removed microhabitats (highly significant season by neighbour interaction in Table 3 and see results of Tukey tests in Fig. 4A–B). The ANOVA on soil conductivity showed that there was a higher increase in salinity during summer in the removed microhabitat than in the other two microhabitats (highly significant season × neighbour interaction in Table 3 and see results of Tukey test in Fig. 4C–D).

Discussion

In response to our first question, in spring before the dry season and in both habitats, short-term interactions were negative and long-term interactions positive. In response to our second question, increasing salinity stress through space across the topography gradient did not affect neither short- nor long-term interactions. In contrast, increasing drought stress through time from spring to summer seasons shifted short-term competition to facilitation and decreased

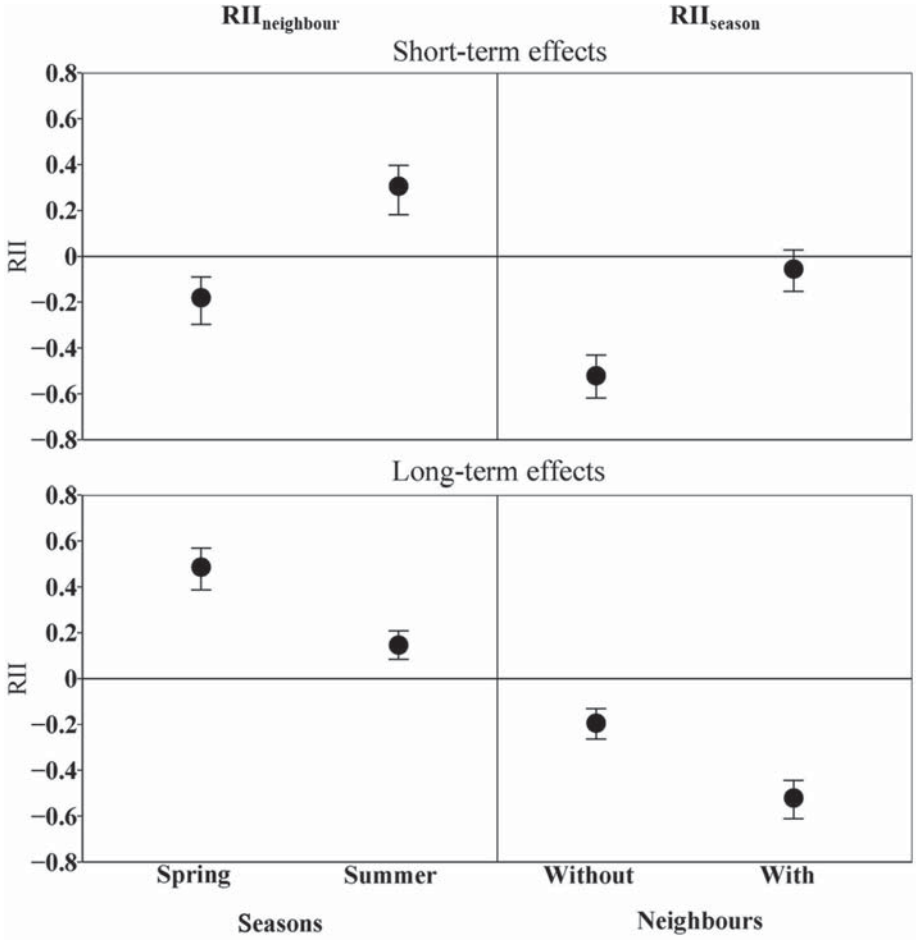

Figure 2. Means ± 95% confidence interval (CI) of $RII_{neighbour}$ at spring and summer seasons (left) and of RII_{season} without and with neighbours (right) for short- (upper panels) and long-term (lower panels) effects. An RII is statistically significant when the boot-strapped 95% CI does not overlap the solid line of zero, and is statistically distinct from other RIIs when 95% CIs do not overlap.

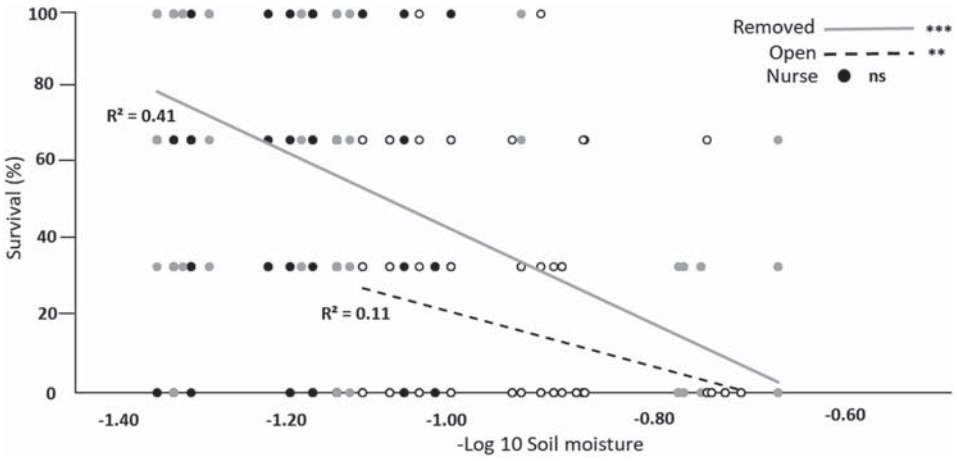

Figure 3. Survival rate of the three target species with increasing soil moisture (x-axis) in the three microhabitats of the two habitats and at the two seasons. Linear curves show variation in pooled survival for each microhabitat, with significances and R^2 of regressions near legend and curves when significant, respectively (highly significant neighbour × moisture interaction in the GLMM, Table 2).

Table 2. Results of the generalized linear mixed-effects model (GLMM) on the effects of the soil moisture, habitat, neighbour and species treatments and their interactions on survival. Significant ($p < 0.05$) effects are indicated in bold.

	Survival		
Effects	df	χ^2	p
moisture	1	14.3	**<0.001**
habitat	1	19.3	**<0.001**
neighbour	2	23.2	**<0.001**
species	2	37.4	**<0.001**
moisture × habitat	1	1.4	0.229
moisture × neighbour	2	26.5	**<0.001**
habitat × neighbour	2	9.0	**0.011**
moisture × species	2	13.2	**0.001**
habitat × species	2	5.2	0.075
neighbour × species	4	16	**0.003**
moisture × habitat × neighbour	2	1.2	0.539
moisture × habitat × species	2	1.1	0.573
moisture × neighbour × species	4	7	0.136
habitat × neighbour × species	4	1.2	0.885
moisture × habitat × neighbour × species	4	1.3	0.869

long-term facilitation. In response to our third question, these shifts were due to environmental severity and neighbour-trait effects, respectively. Together these results show that a shift from competition to facilitation along a temporal stress gradient, predicted by the SGH theory and evidenced with the removal method, might be induced by a decrease in long-term facilitation due to neighgour-trait effects. Separating short- from long-term neighbour effects and neighbour-trait from environmental-severity effects in plant–plant interactions experiments certainly improves our understanding of the driving mechanisms of changes in competition and facilitation along stress gradients.

The direction of short- and long-term interactions before the dry season

Early April before the dry summer season and in the two habitats of this arid system, short-term interactions were negative and long-term interactions positive. This result is consistent with the prediction of Michalet (2006), the results of the pioneer meta-analysis of Maestre et al. (2005) and those of several experiments using both the observational and removal methods in the same community (Maestre et al. 2003, Michalet et al. 2015, Tirado et al. 2015, Noumi et al. 2016). The effects of the neighbour treatment on soil moisture and soil salinity were both highly significant, with, before the dry summer season and in the two habitats, approximately 30% lower soil moisture in the open than in the other two microhabitats, and approximately 15% lower salinity in the latter two than in the former. This suggests that positive long-term effects were positive at that date, due to both higher water availability and less salinity for the target species in the soils of the removed than open microhabitats. Similar results for soil moisture were found by Maestre et al. (2003) in semi-arid Spain and explained by long-term soil-engineering effects of nurse species (Michalet 2006). Alternatively, in studies where long-term effects were negative, soils were drier in removed than open microhabitats, due to interference effects induced by thick slow-decomposing shrub litter (Kane et al. 2011, Michalet et al. 2017, Pistón et al. 2018) or deep water infiltration in galleries of facilitated burrowing animals (Noumi et al. 2015). On the other hand, negative short-term effects were negative in spring in our study likely because of light competition for the target species, since soil moisture was not significantly lower in the nurse than removed microhabitats and there were no differences in salinity. Maestre et al. (2003) showed that the nurse grass *Stipa tenacissima* outcompeted the shrub *Pistacia lentiscus* in semi-arid Spain due to short-term water competition (in addition of light competition), but this effect was not observed in our study.

Table 3. Results of the split–split-plot ANOVAs on the effects of the season, habitat and neighbour treatments and their interactions on soil salinity and soil moisture. Significant ($p < 0.001$) effects are indicated in bold.

		Soil moisture		Salinity	
Effects	df	F	p	F	p
season	1	123	**<0.001**	13.6	**0.001**
error (block)	7				
habitat	1	99.4	**<0.001**	151	**<0.001**
season × habitat	1	3.4	0.070	0.7	0.395
error (block/subplot)	21				
neighbour	2	69.8	**<0.001**	10.5	**<0.001**
season × neighbour	2	15.2	**<0.001**	3.9	**0.028**
habitat × neighbour	2	2.7	0.087	0	0.936
habitat × season × neighbour	2	0	0.983	0.3	0.714
Residuals	36				

Changes in interactions with increasing salinity and drought stresses

Although increasing salinity stress along the topography gradient, from the upper low saline to the lower high saline habitat, significantly decreased target survival, at least in spring, there were no effects of salinity stress on both short- and long-term interactions (no significant habitat by neighbour interactions in Table 1). The three species had weak differences in distribution along the salinity gradient and, thus, likely close tolerances to salinity, which may explain why they did not differ in their responses to the salinity stress (no significant habitat by species interactions in Table 1). However, we expected either an increase or a collapse of long-term facilitation with increasing salinity since several studies, at least from intertidal systems, have shown that facilitation is highly sensitive to this non-resource direct stress factor (Bertness and Ewanchuk 2002, Pennings et al. 2003, Qi et al. 2018). The likeable explanations are that, in our study, the difference in salinity between the two habitats was too weak to significantly affect neighbour effects or that salinity level was below the threshold of tolerance of the target species (Qi et al. 2018).

In opposition to our hypothesis and the prediction of Michalet (2006), short-term negative effects did not increase

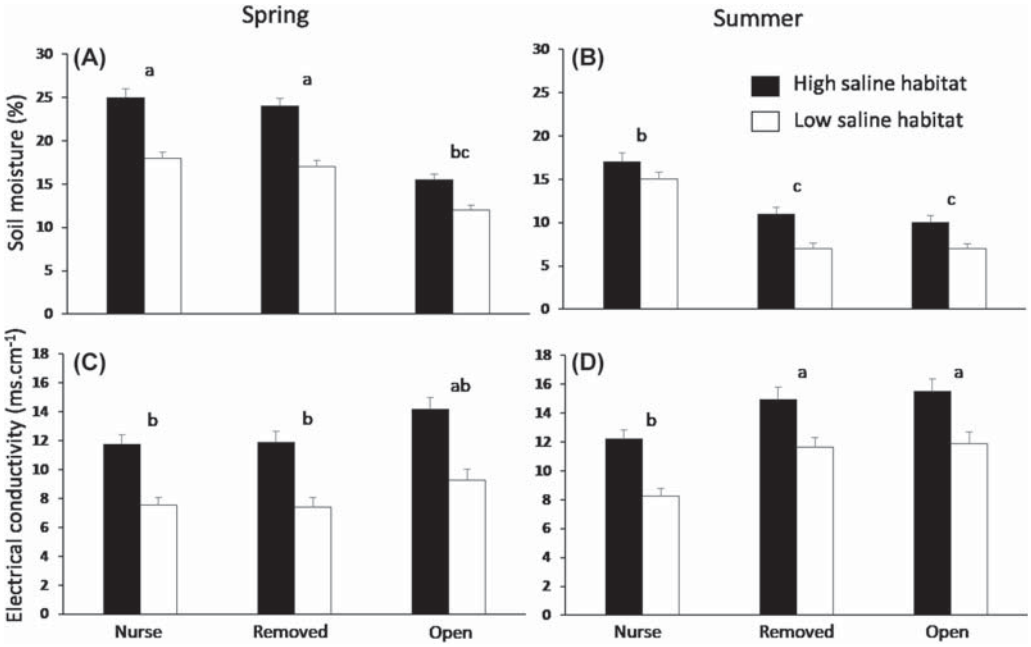

Figure 4. Means ± SE (n = 8) of soil moisture (A and B) and soil salinity (electrical conductivity, C and D) in the three microhabitats of the two habitats at spring (A and C) and summer (B and D) seasons. Letters show the results of the HSD Tukey tests for the season × neighbour interaction for soil moisture and salinity, respectively ($p < 0.001$ and $p < 0.05$, Table 3).

with increasing drought stress during the summer because of presumed increased competition for water. Indeed, our GLMM analysis on the effect of soil moisture on survival clearly showed that target survival in nurse microhabitats was not significantly affected by the decreased in soil moisture that occurred mostly during the dry season. Michalet et al. (2014b) have shown for alpine communities that increases in competition are generally due to neighbour-trait effects, consistent to competition theories that predict that competition increases along environmental gradients due to changes in traits of the competitors (Grime 1974, Tilman 1982). In contrast, in our study RII_{season} was not significantly negative in the removed microhabitats, which is evidence that changes in short-term interactions with increasing drought stress were not due to neighbour-trait effects. These results suggest that a switchback of facilitation to competition in very dry conditions is more likely to occur, when nurses are grasses and targets ligneous species, as in the studies of Davis et al. (1998), Maestre et al. (2003) and Maestre and Cortina (2004). In contrast, when nurses are shrubs, like in the study of Sthultz et al. (2007) or ours, short-term effects are very unlikely to become more negative with increasing drought stress (Michalet 2007), likely because the increase in water competition does not outweighs the benefit of shading for microclimate stress mitigation (Holmgren et al. 1997, Gómez-Aparicio et al. 2005, Muhamed et al. 2013).

Thus, in our study short-term interactions shifted from negative to positive with increasing drought stress from spring to summer seasons, as found by other authors assessing the effects of drought stress on plant–plant interactions along temporal gradients (Greenlee and Callaway 1996, Sthultz et al. 2007, Delerue et al. 2015). This increase in short-term facilitation with increasing stress, supporting the SGH theory (Bertness and Callaway 1994), was due to an environmental-severity effect. This result is consistent with Michalet et al. (2014b) who found for alpine communities that increases in facilitation with increasing stress are generally due to a decrease in performance of the target without neighbours, but not to an increase in performance of the target with neighbours (i.e. neighbour-trait effect). Indeed, our GLMM analysis on the effect of soil moisture on survival showed that there was a highly significant decrease in survival with decreasing soil moisture in the removed microhabitats. However, at the same time long-term positive effects strongly decreased and became weakly significant and this change was only due to a neighbour-trait effect. Indeed, the same GLMM analysis showed that the decreased survival with decreasing soil moisture was much stronger and more significant in removed than open microhabitats and the ANOVA on soil moisture data that the strongest decrease in soil moisture from spring to summer season occurred in the removed plots. Thus, these results are evidence that in our study the shift from short-term competition to facilitation with increasing stress was due to a decrease in long-term facilitation. In other words, our results show that the soil-engineering effects of the shrubs on soil moisture are the driving factors of the long-term facilitation observed before the summer drought and that their collapse during the summer due to intense evaporation has driven the increase in short-term facilitation.

Implications for experiments assessing changes in neighbour effects along stress gradients

Our results have important implications for studies assessing changes in competition and facilitation along stress gradients. First, they clearly show that a shift from short-term

competition to facilitation along a temporal stress gradient may provide a wrong support of the SGH model, as it can be induced as in our study by a decrease in long-term facilitation. Thus, we recommend using both the removal and observational procedures when possible to avoid such wrong demonstration. Interestingly, the observational method has been recently strongly criticized because results can be confounded by the occurrence of within-community habitat heterogeneities independent on soil-engineering effects that are likely to overestimate facilitation (Steinbauer et al. 2016). Our results highlighted the reversal of the coin of rigorous experimental methods, such as the removal procedure, providing support of a theory despite hidden processes supporting an opposite theory. As argued by Körner (2003) for plant–plant interactions experiments in alpine communities, we have to be aware that creating unrealistic experimental conditions, such as the removed microhabitats of the removal procedure, might lead to wrong biological and ecological conclusions. Thus, this is crucial when possible to also base on natural patterns occurring in communities to complement a statistically rigorous method with a more natural observational method.

Data availability statement

Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.cnp5hqc2v> (Chaieb et al. 2020).

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Author contributions – RM and CA designed the experiment, GC and RM conducted the field work, GC and XW analysed the data and GC and RM wrote the draft of the text, and the four authors corrected the manuscript and gave final approval.

References

Armas, C. et al. 2004. Measuring plant interactions: a new comparative index. – Ecology 85: 2682–2686.
Berdugo, M. et al. 2019. Aridity preferences alter the relative importance of abiotic and biotic drivers on plant species abundance in global drylands. – J. Ecol. 107: 90–202.
Bertness, M. D. and Callaway, R. M. 1994. Positive interactions in communities. – Trends Ecol. Evol. 9: 191–193.
Bertness, M. D. and Ewanchuk, P. J. 2002. Latitudinal and climate-driven variation in the strength and nature of biological interactions in new england salt marshes. – Oecologia 132: 392–401.
Brooker, R. W. and Callaghan, T. V. 1998. The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. – Oikos 81: 196–207.
Brooker, R. W. et al. 2008. Facilitation in plant communities: the past, the present and the future. – J. Ecol. 96: 18–34.
Bruno, J. F. et al. 2003. Inclusion of facilitation into ecological theory. – Trends Ecol. Evol. 18: 119–125.
Bulleri, F. et al. 2018. Harnessing positive species interactions as a tool against climate-driven loss of coastal biodiversity. – PLoS Biol. 16: 1–19.
Callaway, R. M. 2007. Positive interactions and interdependence in plant communities. – Springer.
Callaway, R. M. et al. 2002. Positive interactions among alpine plants increase with stress. – Nature 417: 844–848.
Cavieres, L. A. et al. 2014. Facilitative plant interactions and climate simultaneously drive alpine plant diversity. – Ecol. Lett. 17: 193–202.
Chaieb, G. et al. 2019. Interactive effects of climate and topography on soil salinity and vegetation zonation in North-African continental saline depressions. – J. Veg. Sci. 30: 312–321.
Chaieb, G. et al. 2020. Data from: Shift from short-term competition to facilitation with drought stress is due to a decrease in long-term facilitation. – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.cnp5hqc2v>.
Davis, M. A. et al. 1998. Competition between tree seedlings and herbaceous vegetation: support for a theory of resource supply and demand. – J. Ecol. 86: 652–661.
De Mendiburu, F. 2017. Agricolae: statistical procedures for agricultural research. – R package ver. 1.2-8. <https://CRAN.R-project.org/package=agricolae>.
Delerue, F. et al. 2015. Weak evidence of regeneration habitat but strong evidence of regeneration niche for a leguminous shrub. – PLoS One 10: e0130886.
Gómez-Aparicio, L. et al. 2004. Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. – Ecol. Appl. 14: 1128–1138.
Gómez-Aparicio, L. et al. 2005. Canopy vs. soil effects of shrubs facilitating tree seedlings in Mediterranean montane ecosystems. – J. Veg. Sci. 16: 191–198.
Greenlee, J. T. and Callaway, R. M. 1996. Abiotic stress and the relative importance of interference and facilitation in montane bunchgrass communities in western Montana. – Am. Nat. 148: 386–396.
Grime, J. P. 1973. Competitive exclusion in herbaceous vegetation. – Nature 242: 344–347.
Grime, J. P. 1974. Vegetation classification by reference to strategies. – Nature 250: 26–31.
Hacker, S. D. and Gaines, S. D. 1997. Some implications of direct positive interactions for community species diversity. – Ecology 78: 1990–2003.
He, Q. and Bertness, M. D. 2014. Extreme stresses, niches and positive species interactions along stress gradients. – Ecology 95: 1437–1443.
He, Q. et al. 2013. Global shifts towards positive species interactions with increasing environmental stress. – Ecol. Lett. 16: 695–706.
Holmgren, M. and Scheffer, M. 2010. Strong facilitation in mild environments: the stress gradient hypothesis revisited. – J. Ecol. 98: 1269–1275.
Holmgren, M. et al. 1997. The interplay of facilitation and competition in plant communities. – Ecology 78: 1966–1975.
Ibáñez, I. and Rodríguez, A. 2020. Understanding neighborhood effects to increase restoration success of woody plant communities. – Ecol. Appl. 30: e02098.
Kane, J. M. et al. 2011. Drought-induced mortality of a foundation species (*Juniperus monosperma*) promotes positive afterlife effects in understory vegetation. – Plant Ecol. 212: 733–741.
Kirby, K. N. and Gerlanc, D. 2013. BootES: an R package for bootstrap confidence intervals on effect sizes. – Behav. Res. 45: 905–927.
Kitzberger, T. et al. 2000. Effects of climatic variability on facilitation of tree establishment in northern patagonia. – Ecology 81: 1914–1924.
Körner, C. 2003. Limitation and stress – always or never? – J. Veg. Sci. 14: 141–143.

Le Bagousse-Pinguet, Y. et al. 2014a. Facilitation displaces hotspots of diversity and allows communities to persist in heavily stressed and disturbed environments. – J. Veg. Sci. 25: 66–76.
Le Bagousse-Pinguet, Y. et al. 2014b. Importance, but not intensity of plant interactions relates to species diversity under the interplay of stress and disturbance. – Oikos 123: 777–785.
Lenth, R. V. 2016. Least-squares means: the R package lsmeans. – J. Stat. Softw. 69: 1–33.
Liancourt, P. et al. 2005. Stress tolerance and competitive-response ability determine the outcome of biotic interactions. – Ecology 86: 1611–1618.
Liancourt, P. et al. 2017. SGH: stress or strain gradient hypothesis? Insights from an elevation gradient on the roof of the world. – Ann. Bot. 120: 29–38.
Losapio, G. and Schöb, C. 2017. Resistance of plant–plant networks to biodiversity loss and secondary extinctions following simulated environmental changes. – Funct. Ecol. 31: 1145–1152.
Losapio, G. et al. 2019. Facilitation between plants shapes pollination networks. – Ecology 100: e02619.
Lozano, Y. M. et al. 2017. Disentangling above- and below-ground facilitation drivers in arid environments: the role of soil microorganisms, soil properties and microhabitat. – New Phytol. 216: 1236–1246.
Maalouf, J. P. et al. 2012. The interplay of stress and mowing disturbance for the intensity and importance of plant interactions in dry calcareous grasslands. – Ann. Bot. 11: 821–828.
Maestre, F. T. and Cortina, J. 2004. Do positive interactions increase with abiotic stress? A test from a semi-arid steppe. – Proc. R. Soc. B 271: 331–333.
Maestre, F. T. et al. 2003. Positive, negative and net effects in grass–shrub interactions in mediterranean semiarid grasslands. – Ecology 84: 3186–3197.
Maestre, F. T. et al. 2005. Is the change of plant–plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments. – J. Ecol. 93: 748–757.
Maestre, F. T. et al. 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. – J. Ecol. 97: 199–205.
Malkinson, D. and Tielbörger, K. 2010. What does the stress-gradient hypothesis predict? Resolving the discrepancies. – Oikos 119: 1546–1552.
McArthur, R. H. and Wilson, E. O. 1967. The theory of Island biogeography. – Princeton Univ. Press.
Michalet, R. 1991. Nouvelle synthèse bioclimatique des milieux méditerranéens. Application au Maroc septentrional. – Rev. Ecol. Alp. 1: 59–80.
Michalet, R. 2006. Is facilitation in arid environments the result of direct or complex interactions? – New Phytol. 169: 3–6.
Michalet, R. 2007. Highlighting the multiple drivers of change in interactions along stress gradients. – New Phytol. 173: 3–6.
Michalet, R. and Pugnaire, F. I. 2016. Facilitation in communities: underlying mechanisms, community and ecosystem implications. – Funct. Ecol. 30: 3–9.
Michalet, R. et al. 2006. Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? – Ecol. Lett. 9: 767–773.
Michalet, R. et al. 2014a. Two alternatives to the stress-gradient hypothesis at the edge of life: the collapse of facilitation and the switch from facilitation to competition. – J. Veg. Sci. 25: 609–613.
Michalet, R. et al. 2014b. Partitioning net interactions among plants along altitudinal gradients to study community responses to climate change. – Funct. Ecol. 28: 75–86.
Michalet, R. et al. 2015. Disentangling direct and indirect effects of a legume shrub on its understorey community. – Oikos 124: 1251–1262.
Michalet, R. et al. 2017. Direct litter interference and indirect soil competitive effects of two contrasting phenotypes of a spiny legume shrub drive the forb composition of an oromediterranean community. – Oikos 126: 1090–1100.
Muhamed, H. et al. 2013. The role of biotic interactions for the early establishment of oak seedlings in coastal dune forest communities. – For. Ecol. Manage. 297: 67–74.
Noumi, Z. et al. 2015. Limitations to the use of facilitation as a restoration tool in arid grazed savanna: a case study. – Appl. Veg. Sci. 18: 391–401.
Noumi, Z. et al. 2016. The relative contribution of short-term versus long-term effects in shrub-understory species interactions under arid conditions. – Oecologia 180: 529–542.
O'Brien, M. J. et al. 2017. The shift from plant–plant facilitation to competition under severe water deficit is spatially explicit. – Ecol. Evol. 7: 2441–2448.
Padilla, F. M. and Pugnaire, F. I. 2006. The role of nurse plants in the restoration of degraded environments. – Front. Ecol. Environ. 4: 196–202.
Pennings, S. C. et al. 2003. Geographic variation in positive and negative interactions among salt marsh plants. – Ecology 84: 1527–1538.
Pistón, N. et al. 2018. The balance of canopy and soil effects determines intraspecific differences in foundation species' effects on associated plants. – Funct. Ecol. 32: 2253–2263.
Qi, M. et al. 2018. Competitive ability, stress tolerance and plant interactions along stress gradients. – Ecology 99: 848–857.
Redondo-Gómez, S. et al. 2010. Salt stimulation of growth and photosynthesis in an extreme halophyte, *Arthrocnemum macrostachyum*. – Plant Biol. 12: 79–87.
Schöb, C. et al. 2012. Combining observational and experimental methods in plant-plant interaction research. – Plant Ecol. Divers. 5: 27–36.
Soliveres, S. and Maestre, F. T. 2014. Plant–plant interactions, environmental gradients and plant diversity: a global synthesis of community-level studies. – Perspect. Plant Ecol. Evol. Syst. 16: 154–163.
Soliveres, S. et al. 2015. Moving forward on facilitation research: response to changing environments and effects on the diversity, functioning and evolution of plant communities. – Biol. Rev. 90: 297–313.
Steinbauer, M. J. et al. 2016. How to differentiate facilitation and environmentally driven co-existence. – J. Veg. Sci. 27: 1071–1079.
Sthultz, C. M. et al. 2007. Shifts from competition to facilitation between a foundation tree and a pioneer shrub across spatial and temporal scales in a semiarid woodland. – New Phytol. 173: 135–145.
Taylor, D. R. et al. 1990. On the relationship between r/k selection and environmental carrying capacity: a new habitat templet for plant life-history strategies. – Oikos 58: 239–250.
Tielbörger, K. and Kadmon, R. 2000. Temporal environmental variation tips the balance between facilitation and interference in desert plants. – Ecology 81: 1544–1553.
Tilman, D. 1982. Resource competition and community structure. – Princeton Univ. Press.
Tirado, R. et al. 2015. Mutual positive effects between shrubs in an arid ecosystem. – Sci. Rep. 5: 1–8.
Verwijmeren, M. et al. 2013. Interspecific facilitation and critical transitions in arid ecosystems. – Oikos 122: 341–347.

Wang, C. et al. 2020. Disentangling large- and small-scale abiotic and biotic factors shaping soil microbial communities in an alpine cushion plant system. – Front. Microbiol. 11: 925.
Winter, K. et al. 1976. Mineral ion composition and occurrence of CAM-like diurnal malate fluctuations in plants of coastal and desert habitats of Israel and the Sinai. – Oecologia 25: 125–143.
Xiao, S. et al. 2009. The interplay between species' positive and negative interactions shapes the community biomass–species richness relationship. – Oikos 118: 1343–1348.
Zhang, G. et al. 2018. Extreme drought stress shifts net facilitation to neutral interactions between shrubs and sub-canopy plants in an arid desert. – Oikos 127: 381–391.

Supplementary material (available online as Appendix oik-07528 at <www.oikosjournal.org/appendix/oik-07528>). Appendix 1.

CHAPITRE IV : DISCUSSIONS

A l'issue de cette étude, qui s'est étalée sur plusieurs années d'observations et d'expérimentations, la pertinence des résultats obtenus, et leurs apports au niveau de l'écologie des communautés en milieux salins (notamment sous climat aride), contribuent à enrichir le débat, encore présent sur les changements d'interactions biotiques le long des gradients de stress.

1. SÉPARATRION DES STRESS, SALIN ET HYDRIQUE

Dans les environnements stressés hydriquement, la salinité affecte la structure, la diversité, la composition des communautés végétales et les traits fonctionnels desespèces (Gross et al., 2013; Coyle et al., 2014; Kraft et al., 2015 ;Swenson et al., 2007; Vamosi et al., 2009). Au cours de notre étude, nous avons constaté que la salinité intervient dans la distribution des types biologiques (sensu Raunkiaer 1934), le long des gradients topographiques. Les Chaméphytes se situent ainsi à des niveaux élevés de salinité au centre de la Sebkha et les thérophytes s'observent à des faibles niveaux de salinité à la périphérie de ces dépressions salines. Nous avons constaté aussi que la salinité modifie le couvert végétal et la richesse spécifique le long de la topographie, où ces paramètres augmentent avec la diminution de la salinité. En outre, le stress salin agit sur le fonctionnement de l'écosystème, et plus précisément sur la productivité et la décomposition de la matière organique, qui se révèlent plus importants au sein des habitats les moins salés (H4 & H5).

L'effet de l'aridité climatique sur la végétation est nettement moins prononcé que celui de la salinité. Le faible effet de l'aridité sur la végétation, est lié à la modification du gradient de salinité aux extrémités du gradient topographique. Par exemple, nous avons constaté que la salinité des habitats inférieurs (H1, H2 et H3) augmentait avec l'aridité spatiale (de l'aride supérieur à l'aride inférieur). A l'inverse, la salinité des habitats H4 et H5 est plus importante dans l'aride supérieur que dans l'aride inférieur. Cette différence de salinité entre les habitats les plus bas et les habitats les plus hauts du gradient topographique en situation d'aridité spatiale, s'explique d'une part par la forte demande évaporative dans l'aride inférieur (Duchaufour, 1997) et le débordement des eaux salés durant les précipitations dans l'aride supérieur. Néanmoins,

cette différence de salinité aux deux extrémités du gradient topographique d Sebkhas, induite par l'aridité du climat, n'engendre pas de changements significatifs de la richesse spécifique, ni de la composition de la végétation (Farina et al., 2017). Toutefois, l'aridité joue un rôle important dans la structure de la végétation au sein de ces écosystèmes (Floret & Pontanier,1982). En effet, au niveau des habitats les plus élevés de la Sebkha, nos résultats révèlent une abondance relative plus impotante des thérophytes, dans l'aride supérieur que dans l'aride inférieur. Cette dominance n'est pas due réellement à la salinité, mais plus tôt à l'effet du climat. En effet, les précipitations sont plus importantes dans l'aride supérieur que dans l'aride inférieur. Par conséquent, il s'en suit des pratiques agricoles plus fréquentes dans l'aride supérieur, où les conditions édapho-climatiques sont plus favorables à la pratique de la culture de l'orge et de l'olivier. Ceci engendre une perturbation majeure dans les habitas H4 et H5, sous climat aride supérieur, où la fertilité du sol favorise de ce fait la dominance des thérophytes.

Au cours de notre étude, nous n'avons pas pu tester efficacement l'effet de l'aridité indépendamment de la salinité pour les deux raisons fondamentalement suivantes :

i) On ne peut tester l'effet de l'aridité sur la végétation, que dans l'habitat 4, de par l'effet dominant de la salinité dans les habitats inférieurs, H1, H2 et H3. L'habitat 5 est quant à lui beaucoup trop perturbé par l'agriculture. Notre étude est uniquement effectuée en zone aride, où les contrastes climatiques sont insuffisants. Il serait donc sans doute nécessaire d'inclure des sebkhas des climat semi-aride et désertique.

Néanmoins, au cours de nos deux années d'expérimentation, nous avons pu tester l'effet de l'aridité sur les changements des interactions biotiques entre saisons. Cet effet d'aridité temporelle s'est révélé significatif sur les interactions biotiques au sein des écosystèmes salins.

2. EFFET DE LA SALINITÉ

Au cours de notre première expérimentation, nous avons constaté que la salinité entrainait un collapse de la facilitation dans les habitats les plus salés (H1 et H2), conformément à notre hypothèse initiale. Toutefois, ce collapse n'est pas dû à la disparition de l'effet facilitant du voisinage tel qu'il fut prédit par Michalet et al. (2006 & 2014), mais plutôt au seuil de tolérance

de la salinité, franchi par les espèces cibles à la fois avec et sans voisinage. Notre étude met donc en évidence que le collapse de la facilitation le long d'un gradient direct de non-ressources (salinité), peut avoir lieu même lorsque les espèces voisines améliorent l'environnement. Ce constat est donc conforme aux résultats de Qi et al. (2018). En outre, nos résultats ont montré que l'accroissement de l'aridité spatiale entraine une augmentation du collapse de la facilitation (Kizberger et al., 2000 ; Michalet et al., 2014). En revanche, dans notre deuxième expérimentation, effectuée uniquement au niveau des habitas H3 et H4, nous n'avons pas constaté un collapse de la facilitation, avec la salinité, étant donnée que l'étude fut effectuée uniquement dans des habitats de faible niveau de salinité. De plus, nous n'avons pas constaté de retour à la compétition dans les habitats les plus salins, du fait que la salinité n'est pas un gradient direct de ressources, ce qui est d'ailleurs conforme à la théorie de la facilitation affinée (Michalet 2007; Maestre et al. 2009; Michalet et al. 2014).

3. EFFET DE L'ARIDITÉ

Comme que précédemment évoqué, nous n'avons pas pu tester l'effet de l'aridité spatiale sur la variation des interactions biotiques. Toutefois, nos résultats de la première expérimentation (effectuée seulement avec la méthode observationnelle), suggèrent que l'aridité temporelle, en allant de la saison humide du printemps à la saison sèche de l'été, entraîne un accroissement du collapse de la facilitation, qui est plus précoce le long du gradient de salinité.

En outre, au cours de notre seconde expérimentation (conjointement effectuée par la méthode observationnelle et expérimentale), nous avons constaté que les effets de long terme varient de positifs à neutres, en allant de la saison humide vers la saison sèche. Il s'agit donc de l'effet de l'aridité temporelle, qui engendre un collapse des effets de long terme, par disparition de l'effet positif du voisinage sur l'eau du sol. On récapitule donc que le collapse des interactions biotiques peut avoir lieu aussi bien le long des gradients non ressource comme la salinité et la perturbation (Forey et al., 2010), que le long des gradients de ressource comme l'eau (Le Bagousse-Pinguet et al., 2014). Ce collapse peut donc être le résultat de la disparition de l'effet positif du voisinage sur les ressources (Saccone et al., 2009), ou alors au franchissement du seuil de tolérance de la salinité par les espèces cibles (Qi & al., 2018).

Par ailleurs, avec l'aridité croissante, nous n'avons pas constaté un retour à la compétition au cours de nos expérimentations. C'est uniquement au cours de notre seconde expérimentation, que nous avons constaté que les effets à court terme ont été négatifs durant le printemps, où les conditions sont favorables (Maestre et al. 2003, Michalet et al. 2015, Tirado et al. 2015, Noumi et al. 2016).

Notre système, nous donc a permis d'évaluer les effets interactifs de l'accroissement de l'aridité à l'échelle spatiale et à l'échelle temporelle et de la salinité, en comparant la variation des interactions biotiques le long du gradient topographique. Ceci montre que l'augmentation de l'aridité induisait un collapse plus précoce de la facilitation. Plusieurs travaux ont montré que l'interaction entre le stress dû hydrique et les perturbations, induisaitt un collapse des interactions biotiques (Forey et al., 2010; Soliveres et al., 2011; Maalouf et al., 2012; Le Bagousse Pinguet et al., 2014; Verwijmeren et al., 2019).

4. TYPES D'INTERACTIONS

Nous avons constaté durant la deuxième expérimentation réalisée, qu'avant la sécheresse, les interactions de court terme étaient négatives et les interactions de long terme étaient positives, ce qui confirme les résultats souvent rapportés par la littérature, que nos hypothèses préalables. Par contre, nous n'avons pas remarqué un accroissement de la compétition, de court terme au cours de la saison sèche, tel qu'il fut prédit par Michalet (2006). Ce constat d'absence de retour à la compétition est d'ailleurs bien signalé dans les parties précédentes de cette thèse. En outre, la disparition des effets négatifs à court terme peut être expliqué par deux phénomènes qui sont : (i) les déterminismes biotiques (sensu Michalet et al., 2014) et (ii) la stratégie fonctionnelle des espèces voisines, plus particulièrement en zone aride (Maestre & Cortina 2004; Noumi et al., 2015).

5. DÉTERMINISMES, BIOTIQUE ET ENVIRONNEMENTAL DES CHANGEMENTS DES INTERACTIONS

Au cours de notre travail de recherche, nous avons montré que le passage des interactions de court terme, de négatif à positif, était dus à des effets environnementaux, générés par le collapse des interactions de long terme, pour des raisons biotiques (effet des traits fonctionnels des voisins sensu Michalet et al., 2014b). Ce résultat est crucial, du fait qu'il pourrait remettre en cause les résultats d'autres études, montrant des changements de la compétition à la facilitation, avec le stress hydrique, mesuré uniquement par la méthode expérimentale, le long de gradients temporels de sécheresse (Greenlee & Callaway 1996 ; Delerue et al. 2015). En effet, nos résultats attestent d'un effet temporel, alors qu'il fallaint tester cela dans le cas d'un plus large gradient spatial de sécheresse.

Conformément aux observations de Michalet et al. (2014b) dans les écosystèmes alpins, nous avons par ailleurs montré que l'apparition de la facilitation (de court terme), avec le stress était due à un effet uniquement environnemental. Par contre, nous avons montré que l'accroissement de la facilitation de long terme, avec la diminution de l'aridité (de l'été au printemps) était dû à des effets plutôt biotiques. Ceci confirme le constat de l'augmentation de la compétition des milieux alpins, inférieurs aux milieux subalpins, thermiquement moins stressés (Michalet et al., 2014b). Ces résultats suggèrent que finalement, la facilitation qui croit des milieux non stressés aux milieux stressés, initialement proposée par le SGH, ne pourrait être qu'une réponse passive à l'effet de l'environnement. Cet effet du collapse de l'environnement s'explique simplement par la disparition de l'effet positif de long terme des voisins sur l'amélioration du sol. En revanche, l'augmentation de la compétition avec la diminution du stress (sensu Grime), et aussi de la facilitation (des milieux très stressés aux milieux moyennement stressés, sensu Michalet et al., 2006) semble être un effet dû aux changements de traits fonctionnels des espèces dominantes. Ce sont d'ailleurs ces changements, qui contribueraient le plus aux changements de diversité dans les communautés, et qui en auraient probablement le plus de conséquence évolutives (Michalet et al., 2011).

6. STARTEGIES FONCTIONELLES DES ESPECES.

Les résultats de la première expérimentation réalisée dans notre étude, montrent un faible effet des espèces cibles sur le RII, avant la saison sèche, ainsi que des réponses contrastées avec le voisinage, après la saison sèche, notamment dans l'aride supérieur. Le plus fort effet de ces espèces cibles, fut observé dans l'habitat le moins salin (H4), par les deux ligneuses dominantes dans les habitats les plus salins (H1 et H2), à savoir *Halocnemum strobilaceum* et *Arthrocnemum macrostachyum*. Ces deux espèces ont eu des réponses négatives au voisinage. Cependant, l'espèce cible, naturellement présente dans l'habitat 4 (*Lygeum spartum*) avait plutôt une réponse positive au voisinage. Ainsi, il en résulte un compromis entre la tolérance des espèces à la salinité, et leurs réponses compétitives. Ce constat est conforme à ceux d'autres travaux, montrant que les espèces tolérantes au stress sont négativement affectées par le voisinage, et les espèces intolérantes sont généralement facilitées dans les mêmes conditions environnementales (Liancourt et al. 2005a , 2017; Forey et al., 2010; Qi et al., 2018). Un tel résultat est rapporté dans la plupart des théories raffinées de la facilitation (Michalet et al. 2006; Maestre et al. 2009). Par ailleurs, cet effet des stratégies fonctionnelles des espèces n'a fondamentalement pas modifié le collapse de la facilitation. Il a tout simplement généré un collapse plus précoce, le long du gradient de salinité pour *L. spartum*, cible herbacée, moins tolérante au stress de salinité par rapport au deux chaméphytes *H. strobilaceum* et *A. macrostchyum* les plus tolérantes au sel.

CONCLUSION GÉNÉRALE & PERSPECTIVES

L'étude des interactions biotiques au sein des écosystèmes salins sous climat aride nous a permis de mieux comprendre la répartition de la végétation le long des gradients de stress. Nous avons à ce propos constaté que les gradients complexes interviennent d'une façon très significative sur la direction des gradients directes.

Nous avons montré que le collapse de la facilitation était le modèle le plus adapté pour comprendre les variations d'interactions biotiques aussi bien le long des gradients de salinité qu'avec les changements d'aridité. Le retour à la compétition en situation extrême d'aridité n'a

pas été vérifié dans notre étude. Nous avons en outre montré que les variation que l'augmentation de la facilitation prédite par le SGH lors d'une augmentation modérée de stress hydrique n'est qu'une réponse des plantes à l'effet négatif croissant de l'environnement abiotique, contrairement à l'augmentation de la compétition dans les environnements non stressés et celui de la facilitation dans les environnements très à moyennement stressés qui sont d'origine biotique.

La limitation principale de notre travail fut certainement le trop faible contraste d'aridité de notre gradient climatique. D'autres études explorant les variations d'interactions biotiques dans les dépressions salines des bioclimats semi-aride et saharien seraient cruciales pour confirmer nos résultats concernant les effets du stress hydrique.

RÉFÉRENCES BIBLIOGRAPHIQUES

- Armas C, Pugnaire FI. 2005. Plant interactions govern population dynamics in a semi-arid plant community. *J Ecol,* 93:978–989.
- Armas C, Ordiales R, Pugnaire FI. 2004. Measuring Plant Interactions: A New Comparative Index. *Ecology,* 85:2682–2686.
- Arunachalam AK, Maithani HN, Pandey H.N., & Tripathi RS, 1998. Leaf litter decomposition and nutrient mineralization patterns in regrowing stands of a humid subtropical forest after tree cutting. *For Ecol Managt*, 109: 151- 161.
- Austin MP, Smith TM. 1989. A new model for the continuum concept. *Vegetatio,* 83:35–47.
- Bagnouls F. & Gaussen H. 1953. Saison sèche et indice xérothermique. *Bull. Soc. Hist. Nat. de Toulouse*, 88: 193 – 240.
- Bamberg SA. & Major J. 1968. Ecology of the vegetation and soils associated with calcareous parent materials in three alpine regions of Montana. *Ecol Mono,* 38, 127–167.
- Belouadah A, Ati A. & Rokbi M. 2015. Characterization of new natural cellulosic fiber from *Lygeum spartum* L. *Carbo Poly*, 134: 429-437.
- Berdugo M, Maestre FT, Kéfi S, Gross N, Le Bagousse-Pinguet Y, Soliveres S. 2019. Aridity preferences alter the relative importance of abiotic and biotic drivers on plant species abundance in global drylands. *J Ecol,* 107:190–202.
- Berdugo M, Delgado-Baquerizo M, Soliveres S, Herńandez-Clemente R, Zhao Y, Gaitán JJ, Gross N, Saiz H, Maire V, Lehmann A, Rillig MC, Solé RV, Maestre FT. 2020. Global ecosystem thresholds driven by aridity. *Science,* 367:787–790.
- Bertness MD. 1991. Zonation of *Spartina patens* and *Spartina alterniflora* in New England salt marsh. *Ecology,* 72: 138–148.
- Bertness MD. & Pennings, S. C. 2000. Spatial variation in process and pattern in salt marsh plant communities in eastern North America. *In Concepts and controversies in tidal marsh ecology.* Springer (pp 39–57) USA.
- Bertness MD. & Ewanchuk PJ. 2002. Latitudinal and Climate-Driven Variation in the Strength and Nature of Biological Interactions in New England Salt Marshes. *Oecologia*

132: 392–401.

- Bertness MD. & Callaway RM. 1994. Positive interactions in communities. *Trends Ecol Evol,* 9:191–193.
- Brooker RW. & Callaghan TV. 1998. The Balance between Positive and Negative Plant Interactions and Its Relationship to Environmental Gradients: A Model. *Oikos* 81: 196–207.
- Brooker RW, Maestre FT, Callaway RM, Lortie CJ, Cavieres LA, Kunstler G, Liancourt P, Tielbörger K, Travis JMT, Anthelme F , Armas C, Coll L, Corcket E, Delzon S, Forey E, et al. 2008. Facilitation in plant communities: the past, the present, and the future. *J. Ecol*. 96: 18–34.
- Bruno JF, Stachowicz JJ, Bertness MD. 2003. Inclusion of facilitation into ecological theory. *Trends Ecol Evol,* 18:119–125.
- Bulleri F, Eriksson BK, Queirós A, Airoldi L, Arenas F, Arvanitidis C, Bouma TJ, Crowe TP, Davoult D, Guizien K, Ivesa L, Jenkins SR, Michalet R, Olabarria C, Procaccini G. et al. 2018. Harnessing positive species interactions as a tool against climate-driven loss of coastal biodiversity. *PLOS Biol*, 16:1–19.
- Butterfield BJ, Bradford JB, Armas C, Prieto I, Pugnaire FI. 2016. Does the stress-gradient hypothesis hold water? Disentangling spatial and temporal variation in plant effects on soil moisture in dryland systems. *Funct Ecol,* 30:10–19.
- Callaway RM. 1994. Facilitative and interfering effects of *Arthrocnemum subterminale* on winter annuals. *Ecology,* 75: 681–686.
- Callaway RM, Brooker RW, Choler P, Kikvidze Z, Lortie CJ, Michalet R, Paolini L, Pugnaire F, Newingham B, Aschehoug E, Armas C, Kikodze D. & Cook B. 2002. Positive interactions among alpine plants increase with stress. *Nature* 417: 844–848.
- Callaway RM. 2007. *Positive interactions and interdependence in plant communities*. Dordrecht: Springer. XII; 404p; ISBN 978-1-4020-6224-7.
- Castro H, Lehsten V, Lavorel S. & Freitas H. 2010. Functional response traits in relation to land use change in the Montado. *Agriculture, Ecosystems & Environment,* 137: 183–191.
- Cavieres LA, Badano EI, Sierra-Almeida A, Gómez-González S, & Molina-Montenegro MA.. 2006. Positive interactions between alpine plant species and the nurse

cushion plant *Laretia acaulis* do not increase with elevation in the Andes of central Chile. *New Phytol,* 169: 59–69.

- Cavieres LA, Brooker RW, Butterfield BJ, Cook BJ, Kikvidze Z, Lortie CJ, Michalet R, Pugnaire FI, Schôb C, Xiao S, Anthelme A, Aschehoug ET, Björk RG, Dickinson K, Gavilán R. et al. 2014. Facilitative plant interactions and climate simultaneously drive alpine plant diversity. *Ecol Lett,* 17:193–202.
- Chaieb G. 2015. *Relation Plante-sol en milieu salin sous bioclimat aride : Mise en évidence d'un modèle*. Mémoire de Mastère en Ecologie. Université d'Aix-Marseille, France.; 27p+ Annexes.
- Chaieb G, Abdelly C, Michalet R. 2019. Interactive effects of climate and topography on soil salinity and vegetation zonation in North-African continental saline depressions. *J Veg Sci,* 30:312–321.
- Chaieb G, Abdelly C. & Michalet, R. A Regional Assessment of Changes in Plant–Plant Interactions Along Topography Gradients in Tunisian Sebkhas. *Ecosystems* (2020).
- Chaieb G, Wang X, Abdelly C. & Michalet, R. 2020. Shift from short-term competition to facilitation with drought stress is due to a decrease in long-term facilitation. *Oikos*, 1-12.
- Chaves MM, Flexas J. & Pinheiro C. 2009. Photosynthesis under drought and salt stress: regulation mechanisms from whole plant to cell. *Ann Bot,* 103: 551–560.
- Daget P. & Poissonet J. 1971. Une méthode d'analyse phytosociologique des prairies. Critères d'application. *Ann Agro,* 22: 45–41.
- Dalanda Diallo M, Minda-Mahamat S, Ousmane N, Aliou D, Aliou G. 2015. Influence de la décomposition de la nécro-masse des espèces végétales tropicales sur le pH et la structure génétique des communautés bactériennes d'un sol ferrugineux tropical au Sénégal. *J. Appl. Biosci.* 91: 8547-8558
- Davis MA, Wrage KJ. & Reich P. 1998. Competition between tree seedlings and herbaceous vegetation: support for a theory of resource supply and demand. *J. Ecol*, 86: 652–661.
- De Martonne E. 1923. Aridité et indices d'aridité. *Comptes Rendus de l'Académie des Sciences,* 182: 1935–1938.
- De Mendiburu F. 2017. Agricolae: Statistical Procedures for Agricultural Research. – R

package version 1.2-8. https://CRAN.R-project.org/package=agricolae

- Delerue F, Gonzalez M, Michalet R, Pellerin S, Augusto L. 2015. Weak Evidence of Regeneration Habitat but Strong Evidence of Regeneration Niche for a Leguminous Shrub. *PLoS ONE,* 10: e0130886.
- Dobignard A. & Chatelain C. 2010-2013. *African Plant Database (version 3.4.0). Conservatoire et Jardin botaniques de la Ville de Genève and South African National Biodiversity Institute, Pretoria*, "accès [mois, année]", de < http://africanplantdatabase.ch>.
- Duchaufour P. 1997. *Abrégé de pédologie. Sol, végétation, environnement* ; Paris, Masson. Edit.. 291 p., ISBN : 2225828628.
- Emberger L. 1955. Une classification biogéographique des climats. *Travaux de l'Institut Botanique de Montpellier*, 7: 3–43.
- Emberger L. 1958. Afrique du nord et Australie méditerranéenne. Climatology and Microclimatology: *Proceedings of the Canberra Symposium*. *UNESCO Arid Zone Res* 11: 141–147.
- Fajardo A. & McIntire EJB. 2011. Under strong niche overlap conspecifics do not compete but help each other to survive: facilitation at the intraspecific level. *J Ecol,* 99: 642–650.
- Fariña JM, He Q, Silliman BR, Bertness MD. 2017. Biogeography of salt marsh plant zonation on the Pacific coast of South America. *J Biog,* 45: 238–247.
- Floret C. & PONTANIER R. 1982. L'aridité en Tunisie présaharienne : climat, sol, végétation et aménagement. Paris : *ORSTOM,* 150 : 552 p.
- Forey E, Touzard B, Michalet R. 2010. Does disturbance drive the collapse of biotic interactions at the severe end of a diversity–biomass gradient? *Plant Ecol,* 206: 287–295.
- Gibson N. & Kirkpatrick JB. 1985. Vegetation and flora associated with localised snow accumulation at Mount Field West Tasmania. *Austr J of Ecol,* 10, 91–99.
- Gómez-Aparicio L, Zamora R, Gómez JM, Hódar JA, Castro J, Baraza E. 2004. Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. *Ecol Appl,* 14: 1128–1138.

- Gómez-Aparicio L, Gómez JM, Zamora R. & Boettinger JL. 2005. Canopy vs. soil effects of shrubs facilitating tree seedlings in Mediterranean montane ecosystems. *J. Veg. Sci*, 16: 191–198.
- Greenlee JT. & Callaway RM. 1996. Abiotic Stress and the Relative Importance of Interference and Facilitation in Montane Bunchgrass Communities in Western Montana. *Am. Nat,* 148: 386–396.
- Greuter W, Burdet HM. & Long C. (Eds). 1984-1989. A critical inventory of vascular plants of the circum-Mediterranean countries. *Conservatoire Botanique de Genève*, 1: 3-4.
- Grime JP. 1973. Competitive exclusion in herbaceous vegetation. *Nature,* 242: 344–347.
- Grime JP. 1974. Vegetation classification by reference to strategies. *Nature,* 250: 26–31.
- Hachicha M. 2007. Les sols salés et leur mise en valeur en Tunisie. *Science et Changements Planétaires, Sécheresse,* 18 : 45–50.
- Hacker SD. & Gaines SD. 1997. Some Implications of Direct Positive Interactions for Community Species Diversity. *Ecology,* 78: 1990–2003.
- Hanafi A. & Jauffret S. 2008. Are long-term vegetation dynamics useful in monitoring and assessing desertification processes in the arid steppe, southern Tunisia. *J Arid Envi,* 72: 557–572.
- He Q. & Bertness MD. 2014. Extreme stresses, niches, and positive species interactions along stress gradients. *Ecology,* 95:1437–1443.
- He Q, Bertness MD, Altieri AH. 2013. Global shifts towards positive species interactions with increasing environmental stress. *Ecol Lett,* 16:695–706.
- Hu Y, & Schmidhalter U. 2005. Drought and salinity: a comparison of their effects on mineral nutrition of plants. *J. Soil Sci. Plant Nutr,* 168, 541–549.
- Holmgren M, Scheffer M. 2010. Strong facilitation in mild environments: the stress gradient hypothesis revisited. *J Ecol,* 98:1269–1275.
- Holmgren M, Scheffer M. & Huston MA. 1997. The interplay of facilitation and competition in plant communities. *Ecology,* 78: 1966–1975.
- Ibáñez I. & Rodríguez A. 2020. Understanding neighborhood effects to increase

restoration success of woody plant communities. *Ecol. Appl*. 0: 1–11.

- IPCC 2015. Climate change 2014. Mitigation of Climate Change. Summary for Policymakers and Technical Summary. Cambridge University Press. 1419 p.; ISBN 978-1-107-65481-5 paperback.
- Jauffret S. & Lavorel S. 2003. Are plant functional types relevant to describe degradation in arid, southern Tunisian steppes? *J Veg Sci,* 14 : 399–408.
- Jeddi K, Cortina J. & Chaieb M. 2009. *Acacia salicina*, *Pinus halepensis* and *Eucalyptus occidentalis* improve soil surface conditions in arid southern Tunisia. *J Arid Env,* 73: 1005–1013.
- Kane JM, Meinhardt KA, Chang T, Cardall BI, Michalet R, Witham TG. 2011. Drought-induced mortality of a foundation species (*Juniperus monosperma*) promotes positive afterlife effects in understory vegetation. *Plant Ecol*, 212: 733–741.
- Kéfi S, Rietkerk M, Alados CL, Pueyo Y, Papanastasis VP, ElAich A, De Ruiter PC. 2007. Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. *Nature,* 449:213–217.
- Körner C. (Eds). 2003. *Alpine Plant Life - Functional Plant Ecology of High Mountain Ecosystems* (2 nd ed.). Heidelberg: Springer. 349 p.
- Kirby KN. & Gerlanc D. 2013. BootES: An R package for bootstrap confidence intervals on effect sizes. *Behav Res*, 45: 905–927.
- Kitzberger T, Steinaker DF, Veblen TT. 2000. Effects of Climatic Variability on Facilitation of Tree Establishment in Northern Patagonia. *Ecology*, 81:1914–1924.
- Körner C. 2003. Limitation and stress– always or never? *J. Veg. Sci*. 14: 141–143.
- Le Bagousse-Pinguet Y, Xiao S, Brooker RW, Gross N, Liancourt P, Straile D. & Michalet R. 2014a. Facilitation displaces hotspots of diversity and allows communities to persist in heavily stressed and disturbed environments. *J. Veg. Sci*. 25: 66–76.
- Le Bagousse-Pinguet Y, Maalouf JP, Touzard B, Michalet R. 2014b. Importance, but not intensity of plant interactions relates to species diversity under the interplay of stress and disturbance. *Oikos,* 123:777–785
- Le Houérou HN. (Eds). 2008. *Bioclimatology and Biogeography of Africa*. Berlin Heidelberg: Springer-Verlag. 221p; ISBN 978-3-642-09893-2.

- Le Houérou HN. Bioclimatologie et biogéographie des steppes arides du Nord de l'Afrique : diversité biologique, développement durable et désertisation**.** In : Le Houérou H.-N. (ed.). Bioclimatologie et biogéographie des steppes arides du Nord de l'Afrique : diversité biologique, développement durable et désertisation. Montpellier : *CIHEAM*, 1995. p. 1-396. (Options Méditerranéennes : Série B. Études et Recherches; n. 10).
- Lenth RV. 2016. Least-Squares Means: The R Package lsmeans. *J. Stat. Softw*. 69: 1-33.
- Leong FWS, Lam WN, Tan HTW. 2019. Digestive mutualism in a pitcher plant supports the monotonic rather than hump-shaped stress-gradient hypothesis model. *Oecologia,* 190: 523–534.
- Liancourt P, Callaway RM, Michalet R. 2005a. Stress Tolerance and Competitive-Response Ability Determine the Outcome of Biotic Interactions. *Ecology,* 86:1611–1618.
- Liancourt P, Corcket E, Michalet R. 2005b. Stress tolerance abilities and competitive responses in a watering and fertilization field experiment. *J Veg Sci,* 16:713–722.
- Liancourt P, Le Bagousse-Pinguet Y, Rixen C, Dolezal J. 2017. SGH: stress or strain gradient hypothesis? Insights from an elevation gradient on the roof of the world. *Ann Bot* 120: 29–38.
- Liu YX, 1987. *Flora in desertis reipublicae populorum sinarum*, Tomus II (in Chinese). Scientific Publishing House, Beijing, pp. 110–116.
- Lortie CJ, Filazzola A, Sotomayor D.A. 2016. Functional assessment of animal interactions with shrub-facilitation complexes: a formal synthesis and conceptual framework. *Funct Ecol* 30:41–51.
- Losapio G. and Schöb, C. 2017. Resistance of plant–plant networks to biodiversity loss and secondary extinctions following simulated environmental changes. *Funct. Ecol*. 31: 1145–1152.
- Losapio G, Fortuna MA, Bascompte J, Schmid B, Michalet R, Neumeyer R, Cerretti, LC, Germann C, Haenni JP, Klopfstein S, Ortiz-Sanchez F, Pont AC, Rousse P, Schmid J, Sommaggio D, Schöb C. 2019. Plant interactions shape pollination networks via nonadditive effects. *Ecology,* 100: 1-9.
- Lozano YM, Armas C, Hortal S, Casanoves F. & Pugnaire FI. 2017. Disentangling

above- and below-ground facilitation drivers in arid environments: the role of soil microorganisms, soil properties and microhabitat. *New Phytol*, 216: 1236–1246.

- Maalouf JP, Le Bagousse-Pinguet Y, Marchand L, Touzard B, Michalet R. 2012. The interplay of stress and mowing disturbance for the intensity and importance of plant interactions in dry calcareous grasslands. *Ann Bot,* 11: 821–828
- Maestre FT, Cortina J. 2004. Do positive interactions increase with abiotic stress? A test from a semi-arid steppe. *Proc R Soc* B, 271: 331–333.
- Maestre FT, Bautista S, Cortina J. 2003. Positive, Negative, and Net Effects in Grass–Shrub Interactions in Mediterranean Semiarid Grasslands. *Ecology* 84:3186–3197.
- Maestre FT, Valladares F, Reynolds JF. 2005. Is the change of plant–plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments. *J Ecol,* 93: 748–757.
- Maestre FT, Callaway RM, Valladares F, Lortie CJ. 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *J Ecol,* 97:199–205.
- Maestre FT, Quero JL, Gotelli NJ, Escudero A, Ochoa V, Delgado-Baquerizo M, García-Gómez M, Bowker MA, Soliveres S. & Zaadi E. 2012. Plant species richness and ecosystem multifunctionality in global drylands. *Science,* 335, 214–218.
- Mahajan S, & Tuteja N. 2005. Cold, salinity and drought stresses: An overview. *Arch. Biochem,* 444:139–158.
- Malkinson D, Tielbörger K. 2010. What does the stress-gradient hypothesis predict? Resolving the discrepancies. *Oikos*, 119:1546–1552.
- McArthur RH. & Wilson EO. 1967. The theory of Island Biogeography. Princeton Univ Press.
- McIntyre S, Lavorel S. & Tremont RM. 1995. Plant life-history attributes: their relationship to disturbance response in herbaceous vegetation. *J of Ecol,* 83, 31–44.
- Michalet R. 1991. Nouvelle synthèse bioclimatique des milieux méditerranéens. Application au Maroc septentrional. *Rev. Ecol. Alp*. 1: 59–80.
- Michalet R, Gandoy C, Joud D, Pages JP. & Choler P. 2002. Plant community composition and biomass on calcareous and siliceous substrates in the northern French Alps: comparative effects of soil chemistry and water status. *Arctic, Antarctic, and Alpine Research,* 34, 102–113.

- Michalet R. 2006. Is facilitation in arid environments the result of direct or complex interactions? *New Phytol* 169: 3–6.
- Michalet R. 2007. Highlighting the multiple drivers of change in interactions along stress gradients. *New Phytol,* 173:3–6.
- Michalet R, Pugnaire FI. 2016. Facilitation in communities: underlying mechanisms, community and ecosystem implications. *Funct Ecol* 30: 3–9.
- Michalet R, Brooker RW, Cavieres LA, Kikvidze Z, Lortie CJ, Pugnaire FI, Valiente-Banuet A, Callaway RM. 2006. Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? *Ecol Lett* 9:767–773.
- Michalet R, Le Bagousse-Pinguet Y, Maalouf JP, Lortie CJ. 2014a. Two alternatives to the stress-gradient hypothesis at the edge of life: the collapse of facilitation and the switch from facilitation to competition. *J Veg Sci* 25:609–613.
- Michalet R, Schöb C, Lortie CJ, Brooker RW, Callaway RM. 2014b. Partitioning net interactions among plants along altitudinal gradients to study community responses to climate change. *Funct Ecol* 28:75–86.
- Michalet R, Brooker RW, Lortie CJ, Maalouf JP, Pugnaire FI. 2015. Disentangling direct and indirect effects of a legume shrub on its understorey community. *Oikos* 124:1251–1262.
- Michalet R, Maalouf JP. & Al Hayek, P. 2017. Direct litter interference and indirect soil competitive effects of two contrasting phenotypes of a spiny legume shrub drive the forb composition of an oromediterranean community. *Oikos* 126: 1090–1100.
- Miriti MN. 2006. Ontogenetic shift from facilitation to competition in a desert shrub. *J Ecol*, 94: 973–979.
- Muhamed H, Touzard B, Le Bagousse-Pinguet Y, Michalet R. 2013. The role of biotic interactions for the early establishment of oak seedlings in coastal dune forest communities. *Forest Ecol Manag,* 297:67–74.
- Naveh Z. & Whittaker RH. 1980. Structural and floristic diversity of shrublands and woodlands in northern Israel and other Mediterranean areas. *Vegetatio,* 41, 171–190.
- Noe GB. & Zedler JB. 2001. Spatio-temporal variation of salt marsh seedling establishment in relation to the abiotic and biotic environment. *J Veg Sci,* 12: 61–74.
- Noumi Z, Chaieb M, Michalet R, Touzard B. Limitations to the use of facilitation as a

restoration tool in arid grazed savanna: A case study. *App. Veg. Sci*, 18: 391–401.

- Noumi Z, Chaieb M, Le Bagousse-Pinguet Y, Michalet R. 2016. The relative contribution of short-term versus long-term effects in shrub-understory species interactions under arid conditions. *Oecologia,* 180:529–542.
- Ohsawa M. 1995. Latitudinal comparison of altitudinal changes in forest structure, leaf-type, and species richness in humid monsoon Asia. *Vegetatio,* 131: 3–10.
- Ozenda P. 1975. Sur les étages de végétation dans les montagnes du bassin méditerranéen. *Documents de cartographie écologique,* 16: 1–32.
- O'Brien MJ, Pugnaire FI, Armas C, Rodríguez-Echeverría S, Schöb C. 2017. The shift from plant–plant facilitation to competition under severe water deficit is spatially explicit. *Ecol Evol,* 7:2441–2448.
- Padilla FM, Pugnaire FI. 2006. The role of nurse plants in the restoration of degraded environments. *Front Ecol Environ,* 4:196–202.
- Pugnaire FI, Zhang L, Li R, Luo T. 2015. No evidence of facilitation collapse in the Tibetan plateau. *J Veg Sci,* 26:233–242.
- Pennings SC, & Callaway RM. 1992. Salt marsh plant zonation: the relative importance of competition and physical factors. *Ecology,* 73, 681–690.
- Pennings SC, Selig ER, Houser LT. & Bertness, M.D. 2003. Geographic Variation in Positive and Negative Interactions Among Salt Marsh Plants. *Ecology,* 84: 1527–1538.
- Pistón N, Michalet R, Schöb C, Macek P, Armas C. & Pugnaire FI. 2018. The balance of canopy and soil effects determines intraspecific differences in foundation species' effects on associated plants. *Funct. Ecol*, 32: 2253–2263.
- Qi M, Sun T, Xue S, Yang W, Shao D, Martínez-López J. 2018. Competitive ability, stress tolerance and plant interactions along stress gradients. *Ecology,* 99:848–857
- Raunkiær, C. (Eds) 1934. *The Life Forms of Plants and Statistical Plant Geography*. Oxford University Press; London.
- RCore Team. 2017. *R: a language and environment for statistical computing*. R Project for Statistical Computing, Vienna, Austria. http://www.r-project.org/
- Redondo-Gómez S, Mateos-Naranjo E, Figueroa ME, Davy AJ. 2010. Salt stimulation of growth and photosynthesis in an extreme halophyte, *Arthrocnemum macrostachyum*. *Plant Biol,* 12:79–87.

- Rengasamy P. 2006. World salinization with emphasis on Australia. *Journal of Experimental botany,* 57: 1017–1023.
- Slimani M., Cudennec C. & Feki, H.. 2007. Structure du gradient pluviométrique de la transition Méditerranée–Sahara en Tunisie: déterminants géographiques et saisonnalité. *Hydrol Sci J,* 52: 1088–1102.
- Soliveres S. & Maestre FT. 2014. Plant-plant interactions, environmental gradients and plant diversity: a global synthesis of community-level studies. *Perspect Plant Ecol Evol Syst* 16: 154–163.
- Soliveres S, García-Palacios P, Castillo-Monroy AP, Maestre FT, Escudero A, Valladares F. 2011. Temporal dynamics of herbivory and water availability interactively modulate the outcome of a grass–shrub interaction in a semi-arid ecosystem. *Oikos,* 120: 710–719.
- Soliveres S, Smit C, Maestre FT. 2015. Moving forward on facilitation research: response to changing environments and effects on the diversity, functioning and evolution of plant communities. *Biol Rev,* 90: 297–313.
- Spampinato G, Musarella CM, Cano-Ortiz A, Signorino G. 2018. Habitat, occurrence and conservation status of the Saharo-Macaronesian and Southern-Mediterranean element *Fagonia cretica* L. (Zygophyllaceae) in Italy. *J Arid Land,* 10: 140-151.
- Steinbauer MJ, Beierkuhnlein C, Arfin-Khan MA, Harter D, Irl S, Jentsch A, Schweige A, Svenning JC. & Dengler J. 2016. How to differentiate facilitation and environmentally driven co-existence. *J. Veg. Sci*, 27: 1071–1079.
- Sthultz CM, Gehring CA, Whitham TG. 2007. Shifts from competition to facilitation between a foundation tree and a pioneer shrub across spatial and temporal scales in a semiarid woodland. *New Phytol,* 173: 135–145.
- Taylor DR. Aarsen LW. & Loehlec C.1990. On the relationship between r/k selection and environmental carrying capacity: a new habitat templet for plant life-history strategies. *Oikos,* 58: 239–250.
- Tielbörger K, Kadmon R. 2000. Temporal environmental variation tips the balance between facilitation and interference in desert plants. *Ecology,* 81: 1544–1553.
- Tilman D. 1982. *Resource competition and community structure*. Monogr. Pop. Biol. 17. Princeton Univers. Press, Princeton, N.J. 296 p.

- Tirado R, Bråthen KA. & Pugnaire, FI. 2015. Mutual positive effects between shrubs in an arid ecosystem. *Scientific Reports,* 5: 1–8.
- Verwijmeren M, Rietkerk M, Wassen MJ, Smit C. 2013. Interspecific facilitation and critical transitions in arid ecosystems. *Oikos,* 122: 341–347
- Verwijmeren M, Smit C, Bautista S, Wassen MJ, Rietkerk M. 2019. Combined Grazing and Drought Stress Alter the Outcome of Nurse: Beneficiary Interactions in a Semi-arid Ecosystem. *Ecosystems,* 22: 1295–1307.
- Wang C, Michalet R, Liu Z, Jiang X, Wang X, Zhang G, An L, Chen S and Xiao S (2020) Disentangling Large- and Small-Scale Abiotic and Biotic Factors Shaping Soil Microbial Communities in an Alpine Cushion Plant System. *Front. Microbiol.* 11: 1–17.
- Whittaker, R. H. 1965. Dominance and Diversity in Land Plant Communities: Numerical relations of species express the importance of competition in community function and evolution. *Science,* 147: 250–260.
- Whittaker RH. (Eds). 1978. *Classification of Plant Communities* (Handbook of Vegetation Science), Kluwer Academic Publishers. 416 p. ISBN 978-94-009-9183
- Winter K, Winter, K., Troughton, JH, Evenari M, Läuchli A. & Lüttge, U.. 1976. Mineral ion composition and occurrence of CAM-like diurnal malate fluctuations in plants of coastal and desert habitats of Israel and the Sinai. *Oecologia,* 25: 125–143.
- Wright AJ, Wardle DA, Callaway R, Glaxiola A. 2017. The overlooked role of facilitation in biodiversity experiments. *Trends Ecol Evol,* 32: 383–390.
- Xiao S, Michalet R, Wang G. & Chen, S.Y. 2009. The interplay between species' positive and negative interactions shapes the community biomass–species richness relationship. *Oikos,* 118: 1343–1348.
- Zhang G, Zhao W, Zhou H, Yang Q, Wang X. 2018. Extreme drought stress shifts net facilitation to neutral interactions between shrubs and sub-canopy plants in an arid desert. *Oikos,* 127: 381–391.
- Zhu JK. 2001. Plant salt tolerance. *Trend Plan Sci,* 2: 66–71.