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Instructions aux auteurs

ecologia mediterranea publie des articles de recherche originaux sur des sujets se rapportant à l'écologie fondamentale ou appliquée des régions méditerranéennes. La revue exclut les articles purement descriptifs ou de systématique. ***ecologia mediterranea*** privilégie les domaines scientifiques suivants : bioclimatologie, biogéographie, biologie de la conservation, biologie marine, biologie des populations, écologie des communautés, écologie forestière, écologie génétique, écologie marine, écologie microbienne, écologie du paysage, écologie de la restauration, écologie végétale et animale, écophysiologie, paléoclimatologie, paléoécologie. La revue accepte également des articles de synthèse, des notes/communications courtes, des comptes rendus d'ouvrages, des résumés de thèses, ainsi que des commentaires sur les articles récemment parus dans ***ecologia mediterranea***. La revue publie aussi des actes de colloques faisant l'objet d'un numéro spécial. Dans ce cas, prendre contact avec les éditrices.

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À préciser sur la première page lors de la soumission d'un manuscrit.

Article de recherche : contribution inédite découlant d'une étude complète. Ce type d'article fait typiquement une vingtaine de pages et environ 6 000 à 8 000 mots.

Note/communication courte : observation nouvelle ou rapport d'expérience dans un contexte pertinent avec les sujets visés par la revue. Ce type d'article fait typiquement une dizaine de pages et environ 3 000 à 4 000 mots.

Article de synthèse : revue critique et originale de sujets spécifiques d'actualité ou d'un champ de recherche de pointe dans le domaine de l'écologie méditerranéenne. Ce type d'article fait typiquement une vingtaine de pages et environ 6 000 à 8 000 mots.

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TEXTE

Les articles (dactylographiés en Times 12, double interligne, format A4) doivent être rédigés en anglais ou en français. Si l'article soumis n'est pas rédigé en anglais, il est demandé (en plus des résumés) une version anglaise abrégée ainsi qu'une traduction en anglais des titres des figures et tableaux. L'article doit être complet : type de manuscrit, titres anglais et français, auteur(s) et adresse(s), résumés en anglais et en français (au minimum), version anglaise abrégée (si le texte n'est pas en anglais), mots clés anglais et français, texte, puis remerciements, bibliographie, liste des titres des figures et tableaux puis les figures et tableaux (un(e)/page). Ainsi, pour la soumission du manuscrit, les illustrations seront intégrées au document et non envoyées séparément. Le texte des articles de recherche doit comporter quatre parties non numérotées : introduction, méthodes, résultats, discussion. Les sous-titres ne sont pas numérotés. Par exemple :

Introduction
Méthodes
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Résultats
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L'emploi de mots soulignés est à proscrire. Les noms d'auteurs cités figureront en minuscules dans le texte comme dans la bibliographie. En français, n'utilisez les majuscules que pour les noms propres, sauf exception justifiée. Les ponctuations doubles (: ; ? !) sont précédées d'un espace, contrairement aux ponctuations simples (, .). En revanche, toutes les ponctuations sont suivies d'un espace. La mise en forme définitive du texte sera assurée par la revue.

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La première page contient :

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Les résumés doivent comporter 300 mots au maximum et la version abrégée (français si le manuscrit est en anglais et anglais si le manuscrit est en français) 1 000 mots (environ une page). Le nombre de mots clés est limité à six, dans la langue des résumés ; ils ne doivent généralement pas figurer dans le titre.

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Ouvrage

Harper J.L., 1977. *Population biology of plants*. Academic Press, London, 300 p.

Chapitre d'ouvrage

May R.M., 1989. Levels of organisation in ecology. *In*: Cherret J.M. (ed.), *Ecological concepts*. Blackwell Scientific Public, Oxford: 339-363.

Acte de conférence

Grootaert P., 1984. Biodiversity in insects, speciation and behaviour in Diptera. *In*: Hoffmann M. & Van der Veken P. (eds.), *Proceedings of the symposium on* "*Biodiversity: study, exploration, conservation*". Ghent, 18 November 1992: 121-141.

Rapport et thèse

Jaouadi W., 2011. *Écologie et dynamique de régénération de l'*Acacia tortilis *(Forsk.) Hayne subsp.* raddiana *(Savi) Brenan var.* raddiana *dans le parc national de Bouhedma (Tunisie).* Thèse de doctorat de l'Institut national agronomique de Tunisie, 180 p.

CITATIONS ET RENVOIS APPELÉS DANS LE TEXTE

Les mots « figures » et « tableaux » annoncés dans le texte sont écrits en toutes lettres et en minuscules. Indiquer le nom d'auteur et l'année de publication (mais indiquer tous les auteurs dans la bibliographie). Exemples : "Since Dupont (1962) has shown that...", or "This is in agreement with previous results (Durand *et al.* 1990; Dupond & Dupont 1997) ...". Le numéro de page de la citation n'est mentionné que dans le cas où elle est entre guillemets. Si la publication est écrite par plus de deux auteurs, le nom du premier doit être suivi par *et al.*

ABRÉVIATIONS, NOMENCLATURE ET MOTS LATINS

L'usage d'un acronyme ou d'une abréviation technique doit être précédé de sa signification lors de sa première apparition. Les codes de nomenclature doivent être respectés selon les conventions internationales. Les mots latins doivent être mis en italiques (*et al., a priori,* etc.), et en particulier les noms de plantes ou d'animaux. Lors de la première apparition du nom d'une espèce, il est demandé d'y faire figurer le nom d'auteur (exemple : *Olea europaea* L.).

FIGURES ET TABLEAUX

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The editorial committee thanks the associate editors and reviewers who have participated in this volume for their advices, corrections and opinions.

Éditorial – *Editorial*

Élise BUISSON
et Brigitte TALON

Éditrices en chef
Editor-in-Chief

Comme annoncé dans le précédent éditorial, *ecologia mediterranea* s'est dotée de deux co-éditrices en chef, D^r^ Élise Buisson et D^r^ Brigitte Talon, rattachées à l'Institut Méditerranéen de Biodiversité et d'Écologie marine et continentale. Le comité éditorial est en cours de remaniement et est ouvert à toutes nouvelles propositions de votre part. Il compte désormais un spécialiste en écologie marine et nous espérons que cela incitera nos lecteurs à proposer des articles dans ce domaine.

La revue prévoit pour cette année 2014 de nouvelles formes de contenus, comme la publication de notes ou communications courtes, qui permettent soit de traiter de sujets d'actualités peu explorés dans la littérature, soit d'avancer de nouvelles idées, soit de rapporter de manière concise les résultats d'une étude originale ou pionnière dans les domaines abordés par *ecologia mediterranea*.

Le présent numéro se caractérise par une grande diversité des nationalités des auteurs (Algérie, Espagne, France, Portugal, Royaume-Uni, Slovénie, Tunisie), diversité qui reflète bien l'ancrage de la revue dans la communauté scientifique méditerranéenne. Trois articles concernent l'ensemble ou une grande partie du bassin méditerranéen (Hannane *et al.*, Rego & Rocha et Muminović *et al.*), deux plus spécifiquement la péninsule Ibérique (López-Villalta et Simonson & Allen), et enfin deux les montagnes de l'ouest de la Méditerranée (Garraud & Abdulhak) ou les pépinières de Tunisie (Bouali *et al.*).

Ce numéro illustre bien le dynamisme de la revue que nous espérons maintenir et enrichir : des financements de la Région PACA ont été obtenus et assureront la publication 2014 et, ce mois-ci, nous avons fait la demande d'évaluation auprès de Thomson Reuters (pour indexation). Nous avons cependant toujours besoin de nouvelles bonnes volontés pour poursuivre le travail. N'hésitez pas à contacter le comité éditorial pour vous investir.

As announced in the previous editorial, ecologia mediterranea *has two new co-editors-in-chief, Dr. Elise Buisson and Dr. Brigitte Talon, attached to the Mediterranean Institute of Biodiversity and Ecology. The editorial board is being reorganized and is open to new proposal. A marine ecologist now belongs to the board and we hope this will encourage our readers to submit articles in this field.*

Additionally to publishing research papers and reviews, the journal now publishes short communications, which allow either to address hot topics under-explored in the literature, or to report new ideas or recent advances, or to report concise results of an original or pioneer study in the areas covered by ecologia mediterranea.

This issue is characterized by a great diversity in author nationalities (Algeria, France, Portugal, Slovenia, Spain, Tunisia, United Kingdom), which shows the integration of the journal anchor in the Mediterranean scientific community. Three articles concern the whole or a large part of the Mediterranean basin (Hannane et al.*, Rego & Rocha et Muminović* et al.*), two specifically the Iberian Peninsula (López-Villalta et Simonson & Allen), and finally two western Mediterranean mountains (Garraud & Abdulhak) or tree nurseries in Tunisia (Bouali* et al.*).*

This issue illustrates the dynamism of the journal which we hope to maintain and enrich: we received funds from the PACA region and this ensures the 2014 publication. This month, we thus submitted ecologia mediterranea *to Thomson Reuters for evaluation. We still however need new good will to continue the work. Do not hesitate to contact the editorial board to get involved.*

Retama-rhizobia symbiosis studies in some countries of the Mediterranean Basin

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Abstract

The bacteria called rhizobia are nitrogen-fixing bacteria which establish symbioses with plant species in the legume family. They induce positive interaction between soil microorganisms and the plant and are essential for plant growth in semiarid Mediterranean ecosystems that usually present severe water stress, scarcity of plants, low available nutrients and microbiological activity. Considered as one of the endemic legume shrubs of the Mediterranean basin, Retama *plays an important role in nitrogen cycling, and thus, can be used to restore heavily disturbed and degraded soils. These species are adapted to harsh environmental conditions and their establishment and growth are enhanced by their ability to enter into effective symbiosis with multiple rhizobia species. In this article, we review the cumulative evidence of the* Retama*-rhizobia symbiosis in the Mediterranean basin and its ecological impact on revegetation and soil fertilization.*

Keywords: leguminous, rhizobia, biofertilizers, revegetation, semiarid areas, ecosystem.

Introduction

The genus *Retama* belongs to the Fabaceae (subfamily Faboideae, tribe Genisteae) (Käss & Wink 1997; Pardo *et al.* 2004), which occurs in Africa, Canary Islands, Southern Europe and Western Asia (Zohary 1959). *Retama* species are 3 to 4 m shrubs (Figure 1), which usually have a positive effect on soil fertility, plant establishment and growth, under its canopy (Pugnaire *et al.* 1996b). It has a remarkable capacity to withstand drought and the associated Mediterranean summer stresses due to its crown architecture and its deep root system (Haase *et al.* 1996, 1999; Valladares & Pugnaire *et al.* 1999). *Retama* species are considered as being of great importance in nitrogen cycling, and consequently can be used as biofertilizers to restore, improve, and increase the quality of degraded soils (Requena *et al.* 2001; Rodríguez-Echeverría & Pérez-Fernandez, 2005). Fruits from *Retama raetam* are traditionally used in some places to treat diabetes (Gushash 2006). Also, *Retama* extracts present anti-ulcerogenic and anti-inflammatory properties (Bremner *et al.* 2009; El-Toumy *et al.* 2011; Benbacer *et al.* 2012; González-Mauraza *et al.* 2013).

Based on previous studies on the association between rhizobia and *Retama* from different Mediterranean areas (Spain, Algeria and Morocco), it has been noticed that *Bradyrhizobium* is the dominant genus of symbiotic nitrogen-fixing bacteria associated with *Retama* species (Rodríguez-Echeverría *et al.* 2003; Boulila *et al.* 2009; Guerrouj *et al.* 2013).

Despite the wide geographical distribution of *Retama* species in different regions of the Mediterranean countries, and regarding its important ecological role, limited information are available on the genetic diversity, host specificity, symbiotic performance and efficiency of the rhizobia spontaneously associated with *Retama* shrubs. The aim of this paper is to present a review of the information related to the *Retama*-rhizobia symbiosis in order to plan further research.

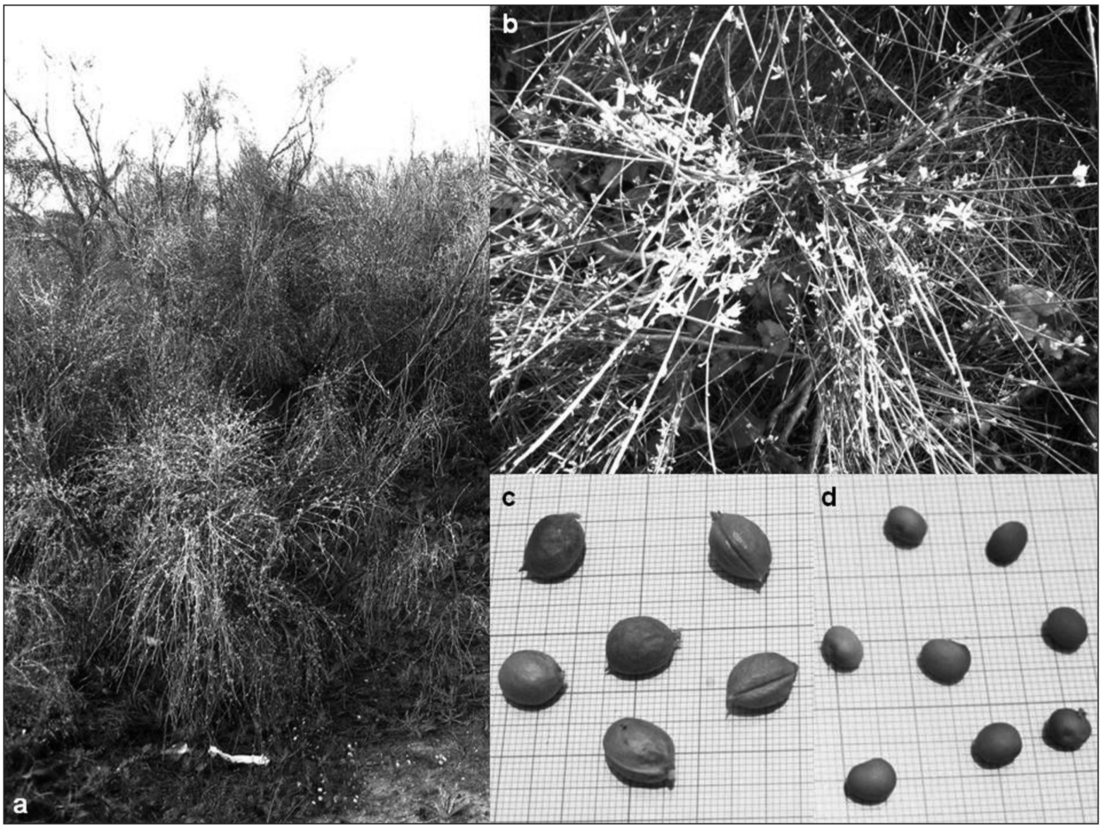

Figure 1 – **Retama monosperma** *(L.) Boiss subsp.* **bovei** *Webb. a: shrubby plant; b: flowers; c: legumes; d: seeds (Pictures taken in Cape falcon site Oran Algeria, April 2011).*

Effects of *Retama* species on soil, microclimate and vegetation

Throughout many microbiological researches undertaken by several authors, it has been shown that *Retama* species have positive effects on their environment and vegetation in various inland environments of the central and southern Iberian Peninsula (*R. sphaerocarpa* L. Boiss) (Espigares *et al.* 2004; López Pintor *et al.* 2003, 2006; Moro *et al.* 1997; Pugnaire *et al.* 1996a; Rodríguez-Echeverría & Pérez-Fernandez 2005), and the Mediterranean coast of the Sinai Peninsula (*R. raetam* Forssk) (Elbanna *et al.* 2002). In Tunisia, the shrub legume is widely used in dune stabilization and soil fixation (Ferchichi 1996).

Retama formation which generates semi-natural savanna-like systems of remarkable productivity have been intensively exploited (Gómez Sal *et al.* 1999). The facilitative effects of *R. sphaerocarpa* may increase system's forage productivity, especially by increasing pasture yield (Rivest *et al.* 2011). Pugnaire *et al.* (1996b) have described the facilitative effect of *Retama* on herbaceous plants growing in its understory, constituting "islands of fertility", which are points of high biological activity scattered in a heterogeneous landscape where facilitation among plants is the dominant interaction (Went 1942; García-Moya & McKell 1970; Garner & Steinberger 1989; Callaway & Walker 1997). The microhabitat surrounding the *R. monosperma* canopy, created by structures such as the roots, and by higher litter and organic matter content confers a greater stability to the soil structure (Dellafiore *et al.* 2008) and reduces the free drainage capacity typical of sand; thereby, retaining more moisture in the soil and reducing leaching losses (Ehrenfeld 1990; Elbanna *et al.* 2002; Flores & Jurado 2003; Moro *et al.* 1997; Pugnaire *et al.* 2004; Ranwell 1972). Its canopy ameliorates the micro-environmental conditions by reducing temperature and insulation extremes. It also provides nutrients to the under storey *via* litter fall (Olson 1958; Connell & Slatyer 1977; Muñoz Vallés *et al.* 2011). The vegetation growing under the canopy benefits from all these processes, increasing its productivity (López Pintor *et al.* 2003).

At the regeneration stage of the shrub, the interaction between the herbaceous vegetation and the shrub is negative for the shrub itself and positive for the herbs (Espigares *et al.* 2004). This suggests a shift from competition to facilitation with age of *Retama*, as reciprocal positive interactions have been described between herbaceous plants and adult individuals of the shrub (Espigares *et al.* 2004). The negative effects of grasses on the photochemical efficiency of *Retama* juveniles decreased with higher water availabilities or heavier irrigation pulses, depending on the studied plant community, because the increase in water availability might compensate for competition for water and light between annuals and *Retama* juveniles (Soliveres *et al.* 2013).

The improvements which occur in the physical, chemical and biological properties of the rhizosphere soil of *R. sphaerocarpa* could facilitate the establishment and growth of new plants in the surrounding areas (Caravaca *et al.* 2003). *Retama*, a deep-rooted, N_2-fixing shrub (Figure 2), increases top-soil water content as well as nitrogen and magnesium availability, but diminishes phosphorous availability (Rolo *et al.* 2012). It contributes only 1.7% of the standing biomass in the inter dune, and the highest density can be found at the dune base (9.5%) (Russow *et al*. 2008).

The biological nitrogen fixation (BNF) of *R. raetam* only leads to local nitrogen input which creates fertile islands surrounding these shrubs. Calculated on a hectare scale, this nitrogen input is very low, up to 0.11 kg nitrogen ha^{-1} $year^{-1}$ (Russow *et al.* 2008). In Tunisia, *R. raetam* legume improved at great scale chemical and physical properties of the soil compared to *Genisteae saharae*. Mishra *et al*. (1997) reported that the clay content was greater in soils under *R. raetam* legume (7%), which may be attributed to reduced soil erosion due to the presence of litter on the surface and also to the stabilization of aggregates due to the presence of more organic matter in the surface layers. This result indicates that *G. saharae* and *R. raetam* can be considered as candidate legumes for soil fertility improvement (Rejili *et al.* 2012). *Retama* seedlings can be produced in nurseries and there is an increasing awareness of its value in revegetation projects (Valladares *et al.* 2002). High transplanting performance of *R. sphaerocarpa* seedlings is linked to a suite of attributes that promote fast seedling establishment during the wet season, which probably enhances drought avoidance during the dry season and helps to avoid photo-inhibition during the summer drought (Villar-Salvador *et al.* 2008).

Figure 2 – Roots nodules from de* R. monosperma *(L.) Boiss
(Pictures taken in Cape falcon site Oran Algeria, December 2011).

Therefore, revegetation projects including plant inoculation with mutualistic microorganisms should be more successful than those without inoculation (Herrera *et al.* 1993; Franco & Faria 1997; Requena *et al.* 2001). Some preliminary studies with sterilized soils suggested that the seeds of *Retama* contain viable rhizobia that can produce nodules under artificial conditions (Pérez-Fernández & Lamont 2000). Thus, the rhizosphere bacteria are considered as an alternative plant strategy for coping with environmental limitations. In this context Marulanda *et al.* (2006), showed that the combination of microbial groups may be used to increase plant growth stimulating effects and survival of *Retama* plants used in revegetation programs.

Symbiotic nitrogen fixation: interest in the agricultural and ecological fields

The symbiotic systems are a major source of nitrogen in most legumes with an average of 80% of nitrogen derived from BNF (Vance 2001; Graham & Vance 2003). Thus, most recent estimates of annual nitrogen fixation inputs by crop legumes, as given in a recent report (Herridge *et al.* 2008) were 21.45 Tg, and the inputs of pasture and fodder legumes 12 to 25 Tg.

BNF is an efficient source of fixed N_2, which plays an important role in land remediation (Rejili *et al*. 2012). Microorganisms are the main protagonists in the maintenance of soil quality and its structural stability (Caravaca *et al.* 2005; Bastida *et al.* 2007) because microbial activity plays a fundamental role in the biogeochemical cycle of elements (Rodríguez-Navarro *et al*. 1994). In fact, a different strategy for rehabilitation of degraded soils in semiarid Mediterranean regions is based on management of plant-microbe symbioses (Cardinale *et al.* 2010). Wild legume shrubs in particular have the additional benefits to establish symbiosis with nitrogen-fixing microorganisms, determining a net input of nitrogen into the ecosystem (Requena *et al.* 2001). Interest in biological nitrogen fixation has focused on the symbiotic systems of leguminous plants and rhizobia, because these associations have the greatest quantitative impact on the nitrogen cycle (Rejili *et al.* 2012). A study by Villar-Salvador *et al*. (2008) showed that the *Bradyrhizobium* strain used to inoculate *R. sphaerocarpa* seedlings survived at least two years in transplanted inoculated plants in spite of the presence of other native rhizobial strains in the field.

Apparently, the use of BNF in agriculture provides a renewable source of nitrogen to supplement or replace fertilizer (Peoples *et al.* 1995 a-b). Since inoculation is simple, environmentally friendly and cheap, nodulated plants are more likely to overcome transplant stress than non-nodulated ones (Valladares *et al.* 2002). The search for new inoculants strains is ongoing and driven by the need to: (1) provide rhizobia for new legume cultivars and species; (2) extend legume cultivation into new and/or hostile environments; and (3) optimize the productivity of currently-grown species (Herridge 2008). Valladares *et al.* (2002) suggested that inoculation and low background fertilization (instead of high fertilization) should be used when producing high quality seedlings of *R. sphaerocarpa*, an autochthonous Mediterranean shrub. Howieson *et al*. (2008) and Howieson & Ballard (2004) considered that legumes introduced to new environments often require parallel selection of appropriate rhizobial inoculants and then, the commercial manufacture of these inoculants.

The inoculation of a legume plant by a compatible rhizobia strain induces physical and chemical changes in the plant that facilitate carbon and nutrient transfer between the host roots and the rhizobia (Dean *et al*. 2009). Rejili *et al.* (2012) showed that legume-rhizobia symbiosis improves enzyme activities, microbial biomass and respiration of field soils, regenerates microbiological properties and the microflora activity involved in the decomposition of organic matter. Also, Dean *et al*. (2009) demonstrated that plant-rhizobia interactions influence plant resistance to insect herbivores and that some rhizobia strains confer greater resistance to their mutualist partners than others do.

Improvement in nutrient use efficiency and in nitrogen fertilizer are important, due in part to the increasing costs of fertilizers, environmental pollution, and the need for higher crop yields on a sustainable basis (Bohlool *et al*. 1992). Indeed, the mechanisms of drought stress tolerance may involve an increase in root development, promotion of mineral nutrition, and water uptake (Ruíz-Lozano *et al.*

1995). *R. sphaerocarpa* could be used in the revegetation of moderately arsenic contaminated sites (Moreno-Jimenez *et al.* 2008); it could improve soil quality by acting as a phyto-stabilizer species (Fitz & Wenzel 2002). Thus, a survey of symbiotic bacteria from *R. sphaerocarpa* shrubs grown in high mercury-contaminated soils in Spain was performed to produce a collection of rhizobia which could be well-adapted to the environmental conditions of this region and be used for restoration practices (Ruíz-Díez *et al.* 2012). However, rhizobial strains which are tolerant to other heavy metals, have been isolated from a variety of herbaceous (Carrasco *et al.* 2005; Pajuelo *et al.* 2008) and shrubby legumes (Ruíz-Díez *et al.* 2009).

Legume-Rhizobia Root-Nodule (LRRN) Symbiosis: Root Nodulating Bacteria (RNB)

The microorganisms able to fix N_2 were first isolated in 1888 by Beijerinck, a Dutch microbiologist, who named them *Bacillus radicicola*. Subsequently, they were called *Rhizobium leguminosarum* by Frank (1889). Previously, the term bacteroids coined for the bacteria-like bodies found in root nodules and by the end of the 19th century, the first pure cultures of rhizobia were on sale to farmers in Europe under the trade name “Nitragin” (Fred *et al.* 1932). Most recent taxonomic studies have made use of a polyphasic approach (Graham *et al.* 1991; Vandamme *et al.* 1996), with genetic, phenotypic, chemotaxonomic, phylogenetic data combined to establish a comprehensive picture of the relationships between bacteria, and to propose a suitable classification. In 1982, fast-growing rhizobial strains were also isolated from soybean nodules and from soil of the People’s Republic of China, within the center of origin and diversity of this legume (Keyser *et al.* 1982). Later, fast growing strains were isolated from other primary and secondary centers of soybean origin (Xu & Ge 1984; Dowdle & Bohlool 1985; Young *et al.* 1988; Rodríguez-Navarro 1996). These fast growers were classified as the new species *R. fredii* (Scholla & Elkan 1984), later reclassified as *Sinorhizobium fredii* and *S. xinjiangensis* (Chen *et al.* 1988), and newly proposed to change to the genus *Ensifer* (Young 2003).

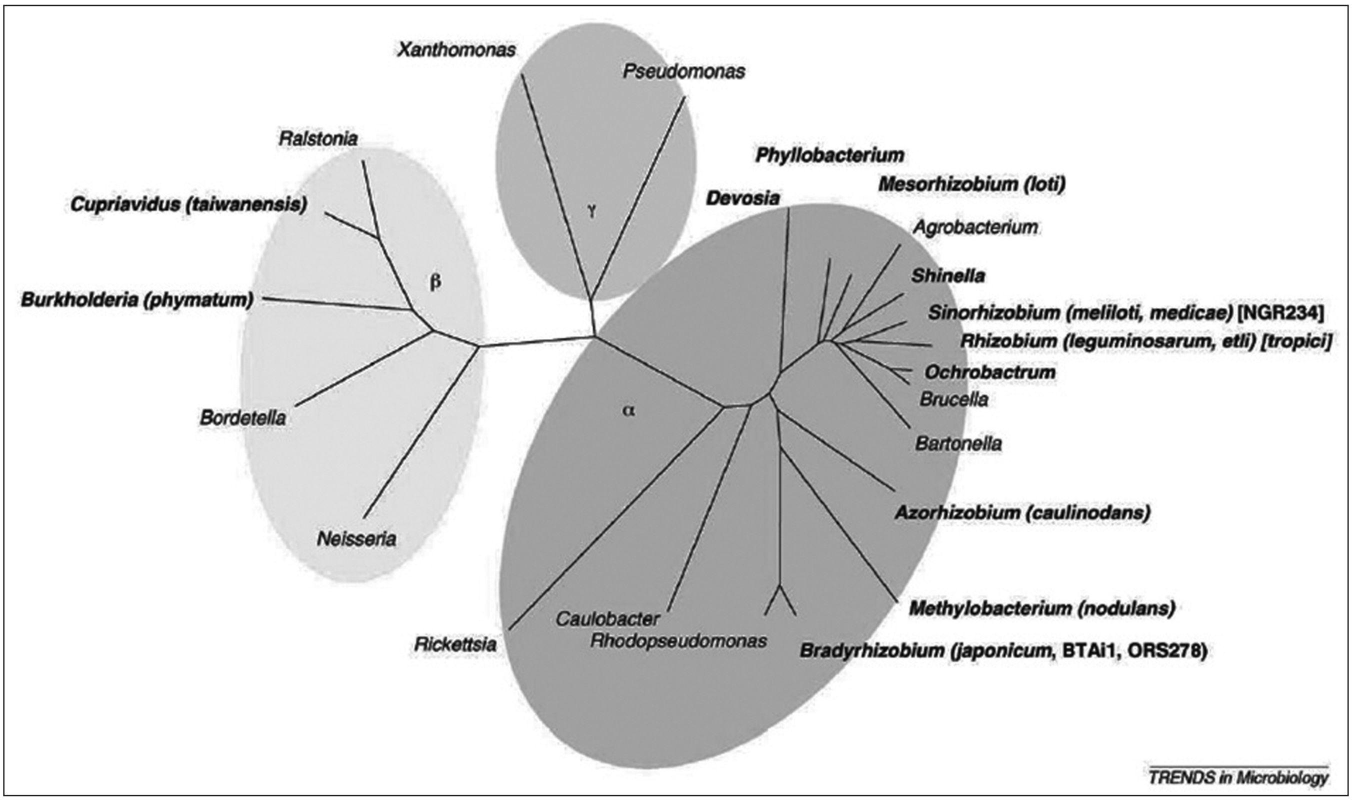

Figure 3 – Unrooted phylogenetic tree of 16S rRNA gene sequences from selected Alpha-, Beta- and Gammaproteobacteria. Genera in bold font contain rhizobia. Figure taken from Masson-Boivin **et al.** ***(2009).***

Until recently, all known legume-nodulating bacteria (LNB) belonged to genera within *Proteobacteria*, namely, *Rhizobium, Mesorhizobium, Bradyrhizobium, Allorhizobium, Sinorhizobium* and *Azorhizobium* (Figure 3) (Zakhia & de Lajudie 2001; Weir 2004). During the past years, the investigation of new nodule isolates led to the discovery of LNB in unexpected genera in *Proteobacteria: Methylobacterium* (Sy *et al.* 2001), *Devosia* (Rivas *et al.* 2002), *Blastobacter* (van Berkum & Eardly 2002) and recently, *Ochrobactrum* (Ngom *et al.* 2004). Moreover, strains belonging to genera in the *Proteobacteria*: *Burkholderia* (Garau *et al.* 2009; Moulin *et al.* 2001; Bontemps *et al.* 2010; Howieson *et al.* 2013) and *Ralstonia* (Chen *et al.* 2001) were shown to be LNB. More recently, Benhizia *et al.* (2004) reported the association between legume root nodules and strains belonging to γ *Proteobacteria*. Eardly & van Berkum (2004) and Vinuesa & Silva (2004) suggested a population-genetic approach to rhizobial speciation. Recent reports confirm that it is quite likely that more such bacteria, capable of effective nodulation will be discovered outside the traditional rhizobia (Barret & Parker 2006; Rasolomampianina *et al.* 2005; Zakhia *et al.* 2006).

Diversity and distribution of bacteria that nodulate *Retama* species

Rhizobia live in a mutualistic symbiotic relationship with legumes, a relationship that has existed and co-evolved for tens of millions of years (Sprent 1994). Leguminous shrubs belonging to the genera *Spartium, Cytisus, Genista* and *Retama* (Genisteae) were found nodulated in southern Italy and in western Spain by slow growing *Bradyrhizobium* (Requena *et al.* 1997; Quatrini *et al.* 2002; Rodríguez-Echeverría *et al.* 2003; Kalita *et al.* 2006). Most of them were grouped either with *B. canariense* or its sister species *B. japonicum* and *B. betae.* However, previous studies (Fernando & Jesus 1998; Kalita & Malek 2004) proved that other *Genista* species from Spain were nodulated by only *Bradyrhizobium* spp. This genus is known for its ability to nodulate a broad range of legumes (Table 1), and thus it could be the predominant group among the natural rhizobial populations in central-western Spain, where soils are acidic or with near-neutral pH (Rodríguez-Echeverría *et al.* 2003).

R. sphaerocarpa isolates from Spain (Rodríguez-Echeverría *et al.* 2003; Ruíz-Díez *et al.* 2009) (Table 2) showed a close relationship with *B. canariense* or *Phylobacterium myrsinacearum*. This study suggested that the native rhizobia could be suitable candidates as biofertilizers and/or inoculants of leguminous shrubs for use, in the restoration or revegetation of arid Mediterranean areas. In terms of symbiosis formation, the rhizobia from leguminous shrubs are generally promiscuous (Gonzalez-Andrés *et al*. 2005), but sometimes specific (Zahran 2001; Valladares *et al*. 2002). Promiscuous strains of *B. canariense* from *R. sphaerocarpa* established effective symbioses with the four plants tested (Table 2). In contrast, *P. myrsinacearum* bacteria from the same plant was only able to nodulate its own host plants (Ruíz-Díez 2009).

Phylogenetic analyses of bacteria within the genus *Bradyrhizobium* have been performed by sequencing of housekeeping genes, such as *dnaK, recA, glnII, atpD* and the internal transcribed spacer region (ITS) (Kalita & Malek 2010; Ramírez-Bahena 2009; Vinuesa *et al.* 2005b). However, it has been reported that phylogenetic analysis of symbiotic genes (*nif* and *nod*) is also essential for a better understanding of rhizobial evolution (Laguerre *et al.* 2001; Lloret & Martínez-Romero 2005; Rivas *et al.* 2009). Recently, Boulila et *al.* (2009) analyzed the genetic diversity of rhizobia nodulating *R. sphaerocarpa* and *R. reteam* in seven ecological-climatic areas of Northeastern Algeria (Figure 4), and classified all of them in the *Bradyrhizobium* genus within the group I defined by Menna *et al.* (2009). The phylogenetic analyses of *nifH* and *nodC* yielded the same conclusion as the analyses of the intergenic spacer (IGS) and the housekeeping genes, with the *Retama* nodule isolates forming single evolutionary *nifH* and *nodC* lineages within a monophyletic cluster including several other bradyrhizobial clades (Boulila *et al.* 2009). Comparison of 16S rRNA gene sequences suggests a close relationship between the Algerian *Retama* isolates and some *Genisteae* bradyrhizobia from Australia (Lafay & Burdon 2006) and Sicily (Cardinale *et al.* 2008). However, the phylogenetic inferences based on the IGS and the housekeeping

***Table 1 – Different species of* Bradyrhizobium.**

Genera/species	Principal and other reported hosts	Type of strain	Reference
Bradyrhizobium japonicum *(Rhizobium japonicum)*	Leguminous plants *Glycine, Vigna* and *Macroptilium*	strain ATCC 10324 = CCUG 27876 = CIP 106093 = DSM 30131 = HAMBI 2314 = IFO (now NBRC) 14783 = JCM 20679 = LMG 6138 = NRRL B-4507 = NRRL L-214 = USDA 6 = VKM B-1967	Jordan 1982
Bradyrhizobium elkanii *(Bradyrhizobium japonicum)*	*Glycine max*	USDA 76 = ATCC 49852 = DSM 11554 = IFO (now NBRC) 14791 = LMG 6134	Kuykendall *et al.* 1992
Bradyrhizobium diazoefficiens *(Bradyrhizobium japonicum)*	Soybean	USDA 110 = IAM 13628 = CCRC 13528 = NRRL B-4361 = NRRL B-4450 = TAL 102 = BCRC 13528 = JCM 10833 = TISTR 339 = SEMIA 5032 = 3I1B110 = ACCC 15034 = CCT 4249 = NBRC 14792 = R-12974 = CNPSo 46	Delamuta *et al.* 2013
Bradyrhizobium oligotrophicum *(Agromonas oligotrophica)*	Isolated from soil	strain ATCC 43045 = JCM 1494 = LMG 10732	Ramírez-Bahena *et al.* 2013
Bradyrhizobium betae	*Beta vulgaris*	strain PL7HG1 = CECT 5829 = LMG 21987 = NBRC 103048	Rivas *et al.* 2004
Bradyrhizobium canariense	*Chamaecytisus, Lupinus*	strain BTA-1 = ATCC BAA-1002 = CFNE 1008 = LMG 22265 = NBRC 103049	Vinuesa *et al.* 2005 a-b Stepkowski *et al.* 2005
Bradyrhizobium cytisi	*Cytisus villosus*	strain CTAW11 = CECT 7749 = LMG 25866	Chahboune *et al.* 2011
Bradyrhizobium daqingense	Soybean	strain CCBAU 15774 = CGMCC 1.10947 = HAMBI 3184 = LMG 26137	Wang *et al.* 2012
Bradyrhizobium denitrificans *(Blastobacter denitrificans)*	*Aeschynomene indica*	strain ATCC 43295 = DSM 1113 = HAMBI 2266 = LMG 8443 = VKM B-2062	Van Berkum *et al.* 2006
Bradyrhizobium huanghuaihaiense	Soybean	strain CCBAU 23303 = CGMCC 1.10948 = HAMBI 3180 = LMG 26136	Zhang *et al.* 2012
Bradyrhizobium iriomotense	*Entada koshunensis*	strain EK05 = LMG 24129 = NBRC 102520	Islam *et al.* 2008
Bradyrhizobium jicamae *Bradyrhizobium pachyrhizi*	*Pachyrhizus erosus*	strain PAC68 = CECT 7395 = LMG 24556 strain PAC48 = CECT 7396 = LMG 24246	Ramírez-Bahena *et al.* 2009
Bradyrhizobium lablabi	*Lablab purpureus* and *Arachis hypogaea*	strain CCBAU 23086 = HAMBI 3052 = LMG 25572	Chang *et al.* 2011
Bradyrhizobium liaoningense	*Glycine soja* *Glycine max*	strain 2281 = ATCC 700350 = CIP 104858 = NBRC 100396 = LMG 18230	Xu *et al.* 1995
Bradyrhizobium yuanmingense	*Lespedeza, Medicago, Melilotus*	strain CCBAU 10071 = CFNEB 101 = CIP 108027 = NBRC 100594	Yao *et al.* 2002
Bradyrhizobium retamae	*Retama sphaerocarpa* and *R. monosperma*	Ro19 = LMG 27393T = CECT 8261	Guerrouj *et al.* 2013

genes *dnaK*, *glnII*, and *recA* show that the *Retama* nodule isolates from the northeast of Algeria form a single evolutionary lineage with a specific clade of bradyrhizobia (Boulila *et al*. 2009).

The low genetic diversity of the symbiotic genes among the *Retama* isolates also suggests their recent acquisition, and supports the possibility that the symbiotic genes arose after bacterial divergence in rhizobia (Turner & Young 2000). Phylogenies of rhizobial populations based on symbiotic genes are more related with the host plant or with the geographic region from where bacteria were isolated than to their taxonomic affiliation based on core genes (Mahdhi *et al.* 2008). As mentioned above, the results were very different to those obtained for *R. raetam* growing in arid zones of Tunisia by Mahdhi *et al.* (2008). The *R. sphaerocarpa* rhizobial population showed higher haplotypic diversity than the *R. raetam* population, but this might be linked to the larger number of sites at which *R. sphaerocarpa* plants were found and the diversity of their ecological-climatic characteristics (Boulila *et al*. 2009).

A polyphasic approach (Vandamme *et al.* 1996) including phenotypic analysis and sequencing of the 16S rRNA gene (Mahdhi *et al.* 2008) showed that the majority of *R. raetam*

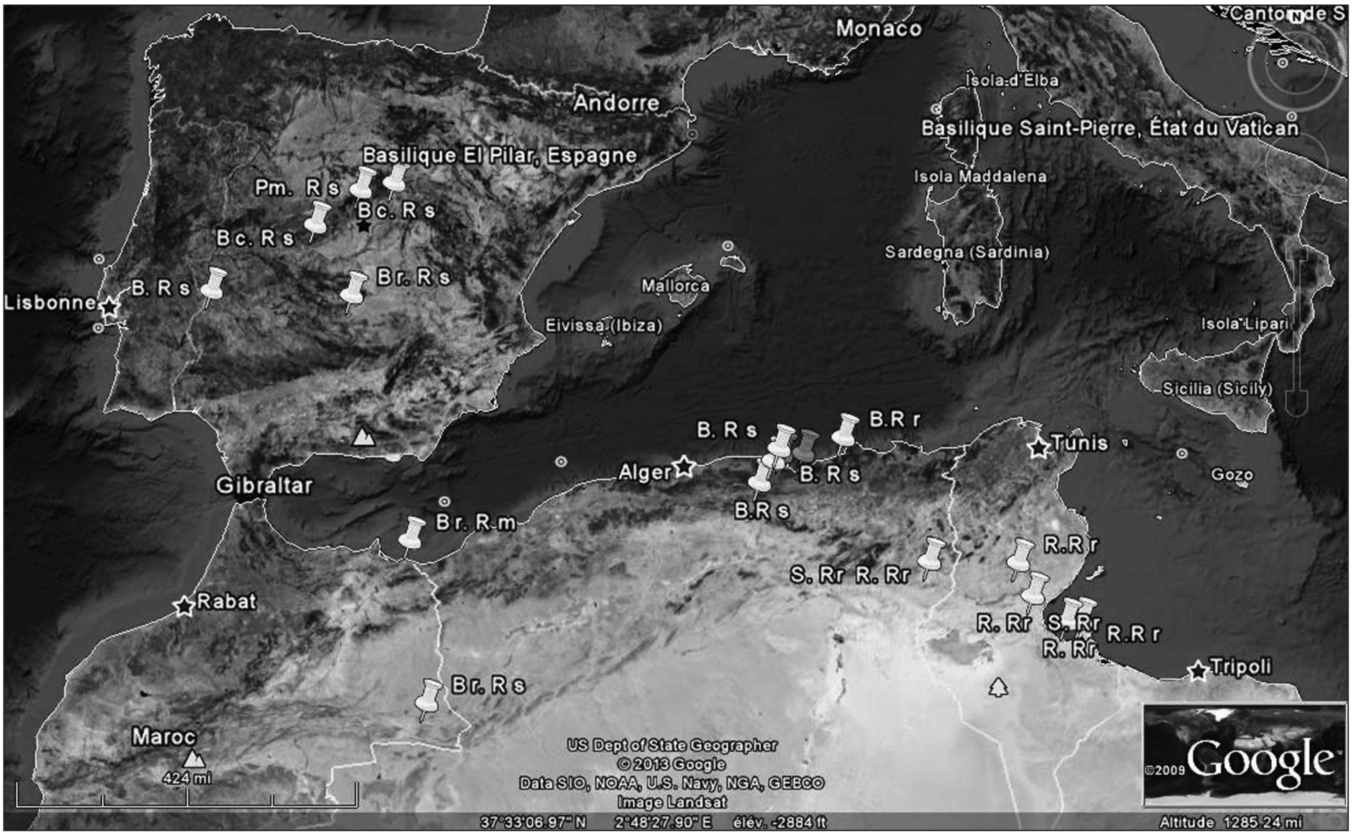

Figure 4 – Geographical distribution of bacteria nodulating* Retama *species

***B. R s:* Bradyrhizobium *from* Retama sphaerocarpa; *B. R r:* Bradyrhizobium *from* Retama raetam; *S. R r:* Sinorhizobium *from* Retama raetam; *B c. R s:* Bradyrhizobium canariense *from* Retama sphaerocarpa; *R. R s:* Rhizobium *from* Retama raetam; *B r. R s:* Bradyrhizobium retamae *from* Retama sphaerocarpa; *B r. R m:* Bradyrhizobium retamae *from* Retama monosperma; *P m. R s:* Phylobacterium myrsinacearum *from* Retama sphaerocarpa.**

Table 2 – Bacteria nodulating species of* Retama*:* Retama monosperma *(L.) Boiss.,* Retama raetam *(Forssk) Webb,* Retama sphaerocarpa *(L.) Boiss. (*R.: Retama; C.: Cytisus; S.: Spartium; Co.: Colutea*).

Hosts plants	Genera of the isolates	Reported hosts	Growth	Climate	Country	References
Retama monosperma (L.) Boiss.	*Bradyrhizobium retamae*	*R. monosperma* *R. sphaerocarpa*	Slow	Semi-arid	Morocco	Guerrouj *et al.* 2013
Retama raetam (Forsskal) Webb	*Sinorhizobium*	*R. raetam*	Fast	Arid	Tunisia	Mahdhi *et al.* 2008
	Rhizobium	*R. raetam*	Fast	Arid	Tunisia	Mahdhi *et al.* 2008
	Bradyrhizobium	*R. raetam* *R. sphaerocarpa*	Slow	Humid	Northeastern Algeria	Boulila *et al.* 2009
Retama sphaerocarpa (L.) Boiss.	*Bradyrhizobium*	*R. sphaerocarpa* *C. balansae* *C. multiflorus* *C. scoparius* *C. striatus*	Slow	Semi-arid	Spain	Rodríguez-Echeverría *et al.* 2003
	Bradyrhizobium canariense	*R. sphaerocarpa* *S. junceum* *Co. laburnuum* *Co. arborescens*	Slow	Semi-arid	Central Spain	Ruíz-Díez *et al.* 2009
	Phylobacterium myrsinacearum	*R. sphaerocarpa* *R. raetam*	Fast	Semi-arid	Central Spain	Ruíz-Díez *et al.* 2009
	Bradyrhizobium	*R. sphaerocarpa*	Slow	Semi-arid, sub-humid, humid	Northeastern Algeria	Boulila *et al.* 2009
	Bradyrhizobium retamae	*R. monosperma* *R. sphaerocarpa*	Slow	Arid	Spain and Morocco	Guerrouj *et al.* 2013

isolates are grouped in *Sinorhizobium* and *Rhizobium* branches (Table 2) as many indigenous legumes in Tunisia (Zakhia *et al.* 2004; Ben Romdhane *et al.* 2006), the isolates presenting a similarity of 100% between them in each cluster obtained by PCR-RFLP 16S rRNA analysis were studied by PCR-RFLP of 16S-23S rRNA region (Mahdhi *et al.* 2008). However, Zakhia *et al.* (2006) found that strains isolated from *R. raetam* grown in the infra-arid regions of Tunisia belonged to the branches containing the genera, *Bosea, Ochrobactrum, Starkeya, Microbacterium* and *Paracraurococcus,* but all these strains failed to nodulate their host of origin. None of them are phylogenetically related to type strain of *B. japonicum*.

Guerrouj *et al*. (2013) proposed the name sv. *retamae* for a novel symbiovar within genus *Bradyrhizobium* isolated from *Retama* root nodules collected in different regions from Spain and Morocco (Table 2). These species are distinguishable by housekeeping gene analysis *recA, glnII* and *atpD* which complements 16S rRNA gene analysis in taxonomic studies at species level (Tindall *et al.* 2010). However, several housekeeping genes have been used in *Bradyrhizobium* to elucidate taxonomic relationships among species (Appunu *et al.* 2008; Chahboune *et al.* 2012; Chang *et al.* 2011; Menna *et al.* 2009; Stepkowski *et al.* 2007; Vinuesa *et al.* 2005b; Wang *et al.* 2012) which have been found useful to differentiate between closely related species and to select the species for DNA-DNA hybridization experiments (Chahboune *et al.* 2011-2012; Ramirez-Bahena *et al.* 2009; Vinuesa *et al.* 2005b). Therefore*, B. retamae* is present in different *Bradyrhizobium* species of group II. It is the first time that a species of this group is described in *Retama* nodules. The nodulation tests performed revealed nodules in the *Retama* plants, but no nodules were observed in soybean plants (Guerrouj *et al.* 2013).

Conclusion and future prospects

Retama genus species are scattered in the Mediterranean basin areas. Obviously, there is no doubt on the positive impact and the role they played on the fertility of degraded soils by coping with adverse environmental conditions such as temperature, pH, salinity and sunlight. This plant has been commonly used for the revegetation of degraded soils to create “fertile islands”, thanks to its root system that makes nodules and appears to contain bacteria of the *Rhizobiaceae* family that live in symbiosis with the plant and provide it with nitrogen.

Studies, based on the restriction fragment length polymorphism of PCR-amplified fragments of the 16S rRNA gene, the IGS region between the 16S and 23S rRNA genes, and the symbiotic genes related to *Retama*-rhizobia symbiosis field in various regions of different climates of the Mediterranean basin (Algeria, Morocco, Tunisia and Spain) have proved that the three species of the genus *Retama* (*R. monosperma, R. raetam* and *R. sphaerocarpa*) are able to enter into symbiosis with various nitrogen fixing bacteria, such as *Rhizobium, Sinorhizobium, Phyllobacterium* and especially with genus *Bradyrhizobium*, that is dominant and more prevalent. This leads us to think that much remains to be done in this area, to identify and characterize many bacterial isolates and classify them in a specific genus related to the *Retama* genus. Further studies related to the diversity of these bacteria, to climatic conditions, soil properties and their geographical distributions, have to be undertaken.

Studies on the *Retama*-rhizobia symbiosis are becoming more and more common. There must be indeed, a correlation between the host plant *Retama* and the microsymbiont rhizobia chemotaxis which involve molecular interactions necessary to determine the chemical nature and physiological aspect of the plant, the bacteria and the genes responsible. The use of such bacteria may be recommended as a biofertilizer to improve the productivity of legume species by cross inoculations; this would avoid the excessive use of expensive polluting chemical fertilizers.

It is now necessary to establish a Mediterranean program on the *Retama* genus, native of the Mediterranean basin, and to better determine the relationship between the genetic diversity of rhizobia and their geographical distribution, in order to have better infective bacterial strains and more efficient biological nitrogen fixation.

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Persistence of *Centaurea pumilio* L., a rare sand dune species

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Abstract

The persistence of C. pumilio *L. (Asteraceae) in time is an issue which is fundamental for conservation measures since the species is rare and often endangered. Therefore we tried to evaluate persistence as a consequence of plant longevity and its survival capacity. We estimated species'life-span by counting the number of rings present in root. Because species survival in time is guaranteed by availability of seeds in the habitat and their presence in soil seed banks, we studied the germination capacity of old seeds under light and in the dark and therefore their potential to remain viable through time.*

For better understanding of C. pumilio*'s germination strategy, we additionally studied germination of two sand dune species commonly found together with* C. pumilio*:* Cakile maritima *Scop. and* Medicago marina *L. for comparison.*

According to our results the persistence of C. pumilio *is guaranteed by the long-living mother plant, since we recorded specimen older than 50 years. On the other hand, species'rarity is the result of lacking mechanisms, which would prevent* C. pumilio *seeds to germinate at high rate under sunlight and thereby exposing seedlings to extreme conditions.*

Keywords: *Cakile maritima*, *Centaurea pumilio*, germination, *Medicago marina*, persistence, root annual rings

Introduction

Specific environmental conditions and overall rarity of coastal sand dunes are the reasons for rarity of plants which are capable of surviving there. We chose to study a rare sand dune species *Centaurea pumilio* L. (Asteraceae). It is distributed on sandy coasts in eastern Mediterranean from northern Africa through Libya and Egypt to Syria and it is found in two remnant locations, one in southern Greece on the island of Crete and one in Apulia in Italy (Greuter 1973; Marchiori et al. 1996; Kamari & Matthäs 1986; Zareh 2005; Youssef *et al.* 2009). In the southern part of the Mediterranean the coastal plain of Libya consists of sandy beaches, salty marshes and rocky coasts. On Jabal Akhdar *C. pumilio* is found in association with *Elytrigia juncea* subsp. *juncea* (El-Rtaib 2011). Further east, *C. pumilio* is a rare species along the deltaic Mediterranean coast of Egypt, found on coastal dunes – a habitat type with the highest number of unique species there (Boulos 1995; Shaltout & Al-Sodany 2008). In Israel *C. pumilio* is listed on the national Red list of plants (Sapir *et al.* 2003). Coastal sand dunes in the north-eastern part of the Mediterranean (east of Apennine Peninsula) are rare because of steep rocky shorelines and cliffs, which do not enable the establishment of dunes (e.g. Croatia, southern Albania and many Greek islands; Doody 2001). Notable exceptions are locally distributed smaller dunes in the Adriatic; a few remains on Croatian islands, the largest are found on island Mljet (Alegro *et al.* 2003). Sand dunes in Albania are associated with river deltas like Seman river or Drin river. In the eastern part of the Mediterranean, extensive dunes are found in the western Peloponnesus in Greece (Amvrakikos gulf, Acheloos river delta and Kotychi lagoon; Spanou *et al.* 2006). Dunes can also be occasionally present in bays of a few Greek islands, most notably on Crete and Rhodes. On Crete *C. pumilio* can be found in *Elytrigia juncea-Medicago marina* association characterized by ammophilous species. In this part of the Mediterranean sand dunes are endangered mostly because of heavy tourism pressure. In Turkey the dunes are extensive and in some places they can be again found close to river deltas (Doody 2001). Sand dune areas on the southern coast of Turkey are fragmented, narrow lined, extending parallel to the coastline and are under heavy cultivation pressures which also increases the possibility of invasion by alien plant species (Çakan *et al.* 2011). Additionally, sand dunes at river deltas are threatened by other human activities like building of dams, river canalization processes or sand and gravel exploitation (Spanou *et al.* 2006). This is why coastal sand dunes are priority habitats for conservation and *C. pumilio* is among vulnerable species occurring there. Besides habitat destruction, *C. pumilio* is also endangered by harvesting. In some regions, like Egypt, roots are collected for traditional medicinal use (Batanouny 1999).

Both environmental conditions and stability of the dune change along the coast-inland gradient. This is a strong environmental gradient, where huge changes over short distances occur. According to this, spatial distribution of plant communities changes and they are highly differentiated according to the stability of the dune. This is why we can find endemic as well as common coastal halophytic species in such habitats. Moreover, sand dunes represent stressful and highly disturbed environment for plants, which means that plants need special adaptations to survive. Besides salt spray and high irradiances at high temperatures, sand depositions also influence plants'survival. We wanted to focus on wind erosion, which represents a physical disturbance that can work in two directions: plants can be covered by sand (burial) or the opposite; their root system can be exposed. Plants exhibit various kinds of tolerance: some tolerate burial, others tolerate moderate deposits of sand or erosion when roots are not exposed, while some species can tolerate root exposure only and some species are not tolerant of any kind of burial. Plants which tolerate being covered by sand must be capable of fast growing rates when they are covered by allocating biomass from below-ground storage organs to above-ground shoot (Harris & Davy 1987; Harris & Davy 1988).

Centaurea pumilio is found on flat dunes within the pioneer vegetation at the strandline (Cakiletalia) and further away from the sea in the foredune and mobile dune communities (Ammophiletalia). *Centaurea pumilio* plants are often seen covered with sand. When buried, *C. pumilio* plants can enhance their growth with allocation of nutrients from the root. Increased growth, following frequent disturbances, formation of flowers and formation of seeds each season depend on reserves accumulated in the root. The same reserves determine the current persistence and life span of a species (persistence in time) as well. Additionally, the persistence of species in time can be guaranteed also with seeds if seeds are long-living. Such seeds could remain viable in the soil seed bank for longer time and form a persistent soil seed bank.

In our study we tried to evaluate the persistence of *C. pumilio* in time, first by estimating the age *C. pumilio* plants can reach. Therefore we studied the anatomy of roots, since recent findings suggest that most of the dicotyledonous perennial herbs in the seasonal climates develop annual rings in the roots or subterraneous stems (Dietz 2002). Further on, we investigated the viability of old seeds with germination studies under various conditions. For better understanding of *C. pumilio*'s germination strategy, we additionally studied germination of two common sand dune species *Cakile maritima* Scop. and *Medicago marina* L. for comparison. Both species were growing in close proximity to *C. pumilio* and are commonly found in phytosociological associations together with *C. pumilio* (Sýkora *et al.* 2003).

Methods

Study species

Chamaephyte *Centaurea pumilio* L. belonging to Asteraceae family is a small (4-20 cm high) acaulescent rosette plant with fleshy pinnate leaves overgrown with white trichomes. Flower heads are 2-3 cm in diameter and consist of sterile pinkish outer flowers and paler fertile central flowers. Prominent anthers are dark purple in color (for more detailed description see Marchiori *et al.* 1996). Plants have a thick root growing deep in the sand. Its diploid chromosome number is 2n = 22 (Kamari & Matthäs 1986).

Root anatomy

Roots were collected in June 2009 from part of a sand dune in Falasarna (Crete, Greece) where *C. pumilio* was growing in the *Medicago marina-Pancratium maritimum* community. Habitat type belonged to young mobile dunes – white dunes. This location suffers all year long disturbances by tourists, especially by creating trails to the sandy beach. We observed many dead *C. pumilio* roots from plants, which were either trampled to destruction or which were exposed to an extent that caused their end. Because of the rarity of species, we collected three samples, just enough to roughly estimate the species'life span. We chose a very thick (10 cm), medium (5.5 cm) and a very narrow root (2 cm), expecting that the diameter of the root corresponds with plant's age. Part of the root 1 cm below the transition zone with stem was sectioned and allowed to soak up in fixative FAA (formalin-acetic acid-alcohol) where we retained it until the analysis. Voucher material, preserved in FAA, is deposited in the herbarium of the Faculty of Natural Sciences and Mathematics, University in Maribor (Slovenia). Microscopic slides were performed by hand and observed in water. We performed cross-sections and longitudinal (radial) sections and studied them under the Nikon Eclipse 50i microscope. Phloroglucinol dissolved in ethanol and concentrated HCl was used for the histochemical reaction with lignin indicated by red color of lignified cell walls (Dietz & Ullmann 1998). In the root, such cells can be found in vessels and lignified parenchyma cells. We studied dyed sections to describe the occurrence pattern of lignified vascular tissue in the secondary xylem and to recognize annual rings, which we counted to estimate the age of a plant. We counted the number of growth rings on 10 slides and calculated the average age and measured the diameter of larger vessels as well.

Germination studies

Ripe seeds of *C. pumilio* were collected at the same occasion as roots and were stored dry at room temperature until the beginning of the germination study in March 2012. Additionally, for comparison of germination with *Cakile maritima* and *Medicago marina,* their fruits were collected from the same site and were stored in the same way as previously described for *C. pumilio*. Seeds were extracted from fruits right before the germination study. In *C. maritima* we distinguished between two types of seeds – whether originating from the upper or lower part of the fruit, as both types have shown differences in germination before (Barbour 1970). We performed germination tests without prior sterilization of seeds to exclude possible effects of sterilization on germination behavior. Twenty seeds (*C. maritima* and *M. marina*) or ten seeds (*C. pumilio*) germinated in Petri dishes on 2 layers of filter paper watered with 10 ml of deionized water in six replicates. Petri dishes were stored in a growth chamber with 16 h days and 8 h nights at 21/18 °C. Half of them were covered with aluminum foil to simulate dark conditions (seeds buried by sand). We checked for germinated seeds every two days and germinated seeds were removed to prevent mold. Seeds in the dark were checked under green flashlight not to induce germination by light.

Results

Root anatomy

Root cross-sections of *C. pumilio* exhibited characteristics, which could be used for the age estimation of individuals. In most cases we could distinguish annual growth rings. However, the distinctiveness between growth rings was gradually lost towards more recently produced vascular elements and the interpretation of single growth ring became

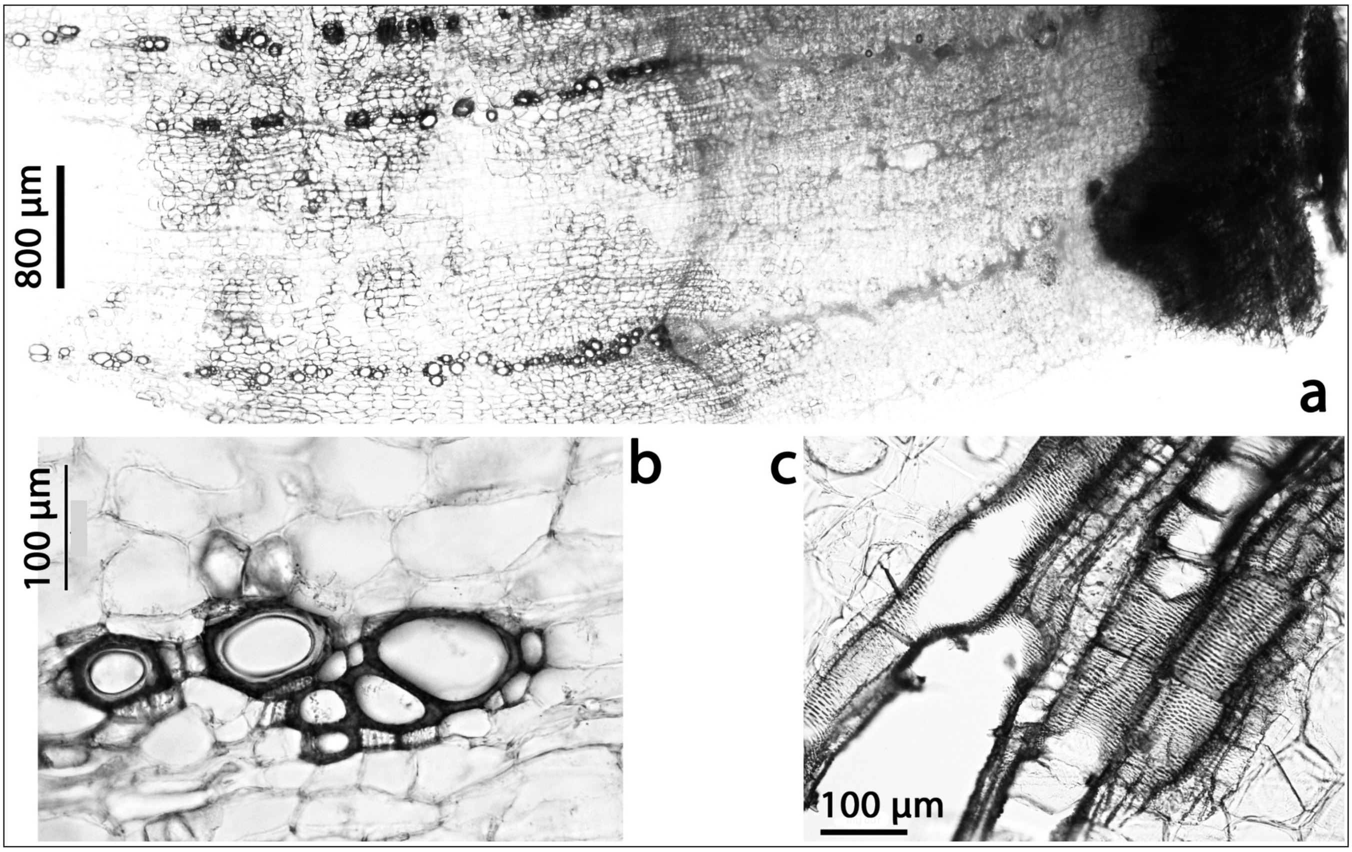

Figure 1 – Anatomical features of **Centaurea pumilio** *root. Red color is the result of histochemical reaction of phloroglucinol with lignin contained in cell walls. (a) Cross-section of the root. (b) Group of vascular elements in one growth ring of one vessel ray. (c) Longitudinal (radial) section of the root revealed the presence of reticulate type of secondary vessel wall pattern.*

difficult (Fig.1a). We could recognize growth rings according to groups of large-sized vessels which were distributed over the entire growth ring, but vessel rays were narrow and not branched. The number of vessels among growth rings fluctuated. We found groups consisting of several vessels to just a single vessel within a vessel ray (Fig. 1b). We could not distinguish earlywood and latewood. The diameter of the largest vessels did not vary considerably among young and old root. The average diameter of vessels in the middle length of the cell measured at the longitudinal section was 50.2 ± 3.5 µm. Within single specimen the diameters of the vessels differed between 3 to 15%. We found only vessels with reticulate secondary wall thickenings (Fig. 1c).

The thickness of the root fits with the age of the plant. However, the estimated age is most likely underestimated because thick roots have the primary xylem torn, resulting in a hollow root (Fig. 2). Additionally, age underestimation can be caused by difficult delineation of growth rings in younger wood layers. Average of ten counts showed that the youngest specimen collected was 26 ± 2 years old, followed by 42 ± 3 years, and the oldest specimen was 55 ± 3 years old.

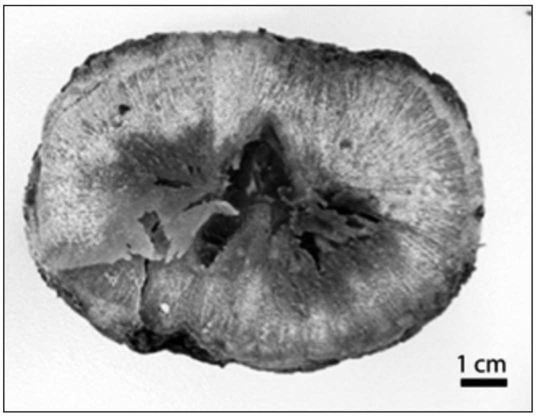

Figure 2 – Cross-section of the 55-years old specimen showing damage in the primary xylem, resulting in a hollow root.

Germination characteristics

Three-year old seeds of *C. pumilio* reached a germination rate of 100% in 12 days under light and in 9 days when in the dark, where germination velocity was greater (Fig. 3). First seeds germinated after 5 days, without regard to the presence or absence of light. *Centaurea pumilio* was the only species, among studied species, which reached 100% germination rate under light.

Comparison with *C. maritima*'s germination under light and in the dark showed significant differences between germination of both seed types – from upper and lower fruit part (Fig. 3). Old seeds from the upper part of silique showed similar germination pattern regardless of light/dark conditions and in each experiment, the maximum germination rate reached was 80%. Behavior of the seeds from the upper part of the fruit was similar to germination pattern of *C. pumilio* seeds. Old seeds from the lower part of the fruit, which in natural conditions remain on the dead mother-plant, germinated significantly better in the dark, reaching germination rate of 100% in 7 days, while only 50% of seeds germinated after 12 days when exposed to light. In both seed types, germination occurred very fast regardless of light/dark – after 2 days. 50% of seeds from the lower fruit part germinated in that time.

Old seeds from *M. marina* germinated very slowly compared to *C. pumilio* and *C. maritime* (Fig. 3). After 20 days, only about 15% of seeds germinated unrelated to presence or absence of light. Maximum germination rate reached after 55 days was 50% and 80% after 70 days in one replicate exposed to light (data not shown).

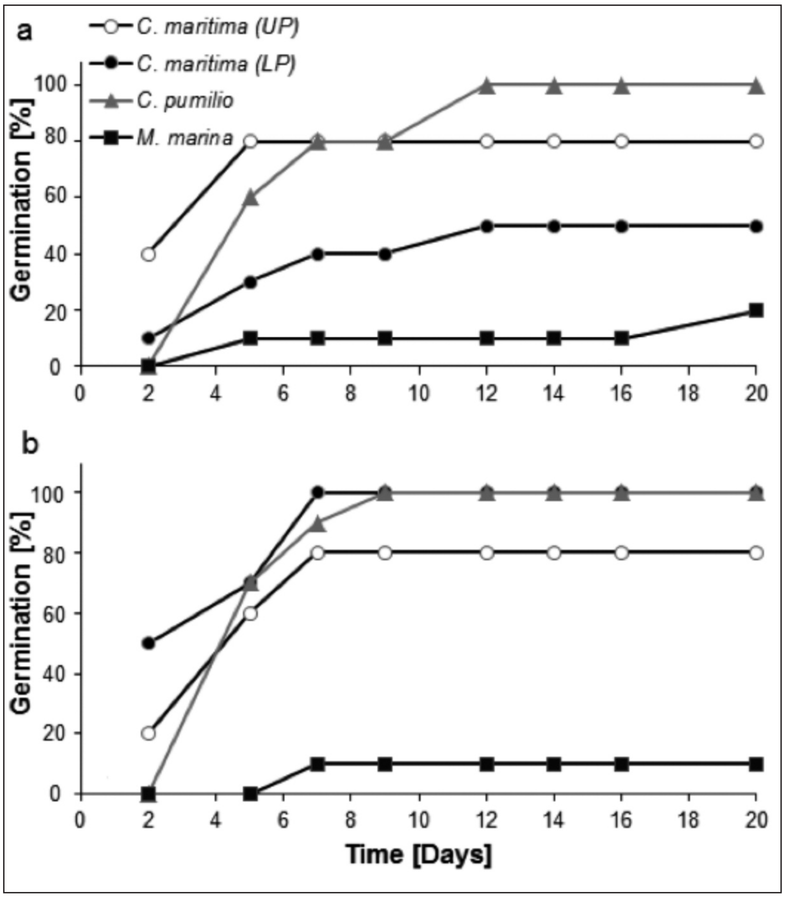

Figure 3 – Germination characteristics (average values) of 3-year-old seeds of Centaurea pumilio, Cakile maritima *(UP – upper part of the fruit, LP – lower part of the fruit), and* Medicago marina *under light (a) or in the dark (b).*

Discussion

Mediterranean sand dunes are under immense human pressure even though they harbor many rare species. For sand dune species protection we must gain knowledge about persistence of these species. According to persistence traits we can propose a reliable evaluation of their response to threats, which is crucial for the implementation of suitable protection management. The re-establishment of coastal sand-dune species and their survival is constrained not only by human disturbances, but by environmental stresses as well. Stressful conditions are imposed by wind-driven burial in sand or excavation, salt spray, high irradiance correlated with high temperatures, desiccation and low nutrient levels (Maun 2004).

Our results show that the persistence of rare *C. pumilio* is first of all guaranteed by thick root ensuring the plant's lifespan of 50 years and more. In general, demographic characteristics like growth, probability of survival and flowering, as well as reproductive output of perennial plants are strongly size-dependent (Metcalf *et al.* 2003). Because of very limited sampling and the damaged central part consisting of primary and partly secondary xylem, the estimated age is most likely underestimated. However, for crude estimation of age, the diameter of the root could be used in the field. Anatomical structure of the root revealed low secondary growth. This is a result of harsh environment enabling only the production of narrow growth rings. Reticulate secondary wall thickenings of vessels which we observed reinforce the vessel in transverse and vertical direction, making the vessel unable to extend with the growth of surrounding cells. Therefore, such vessels are present in organs where primary elongation has ceased (Mauseth 1988). This is in congruence with the role of *C. pumilio*'s roots as storage organs which do not elongate or grow in case of burial in sand, but allocate resources to aboveground organs. Therefore, plants with deep roots are better adapted to sand coverage as well as to substrate erosion (Miyanishi & Johnson 2007). When we compare *C. pumilio's* strategy for persistence with *C. maritime*, a biennial pioneer species, we see that *C. maritime's* recolonization is, in large part, determined by the regenerative ability from seeds (Hesp & Martinez 2007).

Three-year old seeds from all three studied sand dune species, no matter if they are common or rare, exhibit germination characteristics adapted to burial in sand. They germinate well and fast if buried in sand and all reach germination rate above 60%, except *M. marina* which germinated much slower, probably because of the impermeability of the seed coat.

Therefore, the *C. pumilio's* persistence is guaranteed by seed longevity, as well. It is widely accepted that with higher unpredictability and harshness of the environment, the persistence of seeds in the soil seed bank is increased. According to our germination study, the longevity of *C. pumilio* seeds is at least 3 years when no favorable conditions for germination exist before that. Germination rate of 3-year-old seeds reached 100% in the laboratory. If almost all seeds would germinate in nature, this would mean that in suitable conditions no seeds would be left in the soil seed bank. If additionally the survival and the establishment of seedlings is very low, this would be the cause of only few to no seedlings being established in some seasons, adding to rarity of *C. pumilio*. However, according to long lifespan of *C. pumilio,* the species'survival is still guaranteed even if seedlings are not established each year. Furthermore, results show that *C. pumilio* is among the fastest germinating species we studied and that it reached maximal germination rate, meaning that seedlings emerge during favorable conditions and are more likely to establish successfully.

Three-year-old seeds from *C. pumilio* have similar germination behavior as old seeds from *C. maritime* from the upper part of the fruit. These seeds also reached high germination rate quickly, regardless of light/dark. However, *C. maritime* is not a rare species, because it develops another seed morph in the lower part of the fruit which ensures survival despite short lifespan. Seeds from lower fruit germinate faster and twice as good in the dark as they do under light. This suggests that seeds from the lower part of the fruit might possess mechanisms which reduce germination under light (Thanos *et al.* 1991). High irradiance is also represented by higher temperatures and drought, therefore preventing germination under light would also prevent the growth of seedlings under less favorable conditions. Seed dimorphism ensures that *C. maritime* seeds are able to exploit a broader range of environmental factors, since both seed types have different purpose. The upper silique is released when ripe and dispersed from the mother plant, while the lower part stays attached to dead plant and is more likely to be covered by sand (Barbour 1970). Lower fruit is dispersed from the dead mother plant only if dried branches break off. Reported viability for 10-year-old dry-stored seeds of *C. maritime* seeds exists (Davy *et al.* 2006).

Conclusion

The simplest way for sand dune species protection seems to be the collection of seeds, however, our germination results show considerable variation among species even though they co-exist in a habitat. Especially for the rare species seed collecting alone is not sufficient. According to our results we could conclude that persistence of *C. pumilio* is guaranteed by the long-living mother plant, while species'rarity is the result of lacking mechanisms, which would prevent *C. pumilio* seeds to germinate at such high rate under sunlight and thereby exposing seedlings to extreme conditions. High germination rate regardless of light/dark prevents an establishment of persistent soil seed bank after favorable conditions passed.

Without a persistent soil seed bank, the re-establishment of *C. pumilio* and its survival could be self-sustained only in populations containing mature, older specimen, which are able to form seeds. This would mean a very time-consuming and difficult restoration management and this is why populations of long-living *C. pumilio* plants should require regular monitoring, especially concerning the information about population demography and factors contributing to population aging. In populations of long-lived plant species one can easily overlook the possibility of extreme risk that these species is already paying its extinction debt right in front of our eyes.

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Trait-driven *vs.* syndrome-driven diversification in the Mediterranean woody flora

Diversification déterminée par les traits vs. *syndromes dans la flore ligneuse méditerranéenne*

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Abstract

In the woody flora from the Mediterranean basin there are two character syndromes which differ in diversification rate: the sclerophyll and the nonsclerophyll syndrome; the latter has the highest diversification rate mainly due to rampant speciation. The cause of this increased diversification rate in nonsclerophylls could be the overall and complex interaction between their syndrome traits (conspicuous flowers, dry fruits, small seeds, non-animal dispersal, fire-induced germination) and environmental pressures (pollinator competition, summer drought, poor soils, frequent fires). Alternatively, one or very few of the syndrome traits could be responsible of most of the difference in diversification rate (trait-driven diversification). This work examines the relative role of syndrome traits on nonsclerophyll diversification using ANCOVA analyses for the flora of Western Andalusia (Spain). The results point that the increased diversification rate typical of the nonsclerophyll syndrome is largely caused by one single trait: the obligate seeder strategy (that is, fire-induced germination in fire-killed shrubs). This is the only trait whose consideration erases the difference in diversification rate between both syndromes. This result cannot be explained as the effect of altitudinal range as a potentially confounding variable. Furthermore, obligate seeder genera show a much higher diversification rate than the other genera and account for most of the species richness here considered. Thus the origin of this Mediterranean flora can be better understood as the outcome of trait-driven (seeder strategy) instead of syndrome-driven diversification. The role of fire in the evolution of this regional flora stands out over the other possible factors here considered.

Keywords: biodiversity, fire ecology, Mediterranean region, seeders, sclerophyll.

Résumé

Au sein de la flore ligneuse du bassin méditerranéen, le taux de diversification du syndrome (faisceau de traits) « sclérophylle » diffère de celui de « non-sclérophylle » ; ce dernier est le plus élevé, essentiellement à cause d'une importante spéciation. Le taux de diversification plus élevé chez les non-sclérophylles pourrait s'expliquer par une interaction complexe entre l'ensemble des traits du syndrome (fleurs colorées, fruits secs, petites graines, dispersion non animale, germination induite par le feu) et les pressions de l'environnement (concurrence pour les pollinisateurs, sécheresse estivale, sols pauvres, incendies fréquents), ou bien par l'action de quelques traits seulement (diversification entraînée par les traits).

Ce travail étudie le rôle relatif des traits du syndrome sur la diversification des espèces non-sclérophylles de la flore d'Andalousie orientale (Espagne) en utilisant des analyses de type ANCOVA. Les résultats indiquent que le taux de diversification élevé du syndrome « non-sclérophylle » est essentiellement dû à un seul trait : la régénération obligatoire par graines (dont la

Mots clés : biodiversité, écologie du feu, régénération obligatoire par graines, région méditerranéenne, sclérophylle.

germination est induite par le feu dans les arbustes incendiés). C'est le seul trait dont la prise en compte annule les différences de taux de diversification entre les deux syndromes. Ces résultats ne peuvent pas être expliqués par l'effet du gradient altitudinal comme possible variable de confusion. De plus, les genres qui ont une régénération obligatoire par graines montrent un taux de diversification plus grand que les autres genres et constituent la plus grande partie de la richesse spécifique étudiée ici.

L'origine de cette flore méditerranéenne peut ainsi être mieux comprise et apparaît comme étant le résultat d'une diversification induite par un seul trait (la régénération obligatoire par graines) et non par un syndrome de traits. Le rôle des incendies dans l'évolution de cette flore régionale ressort nettement parmi les autres facteurs possibles pris en compte dans cette étude.

Introduction

The Mediterranean region stands out as an important plant diversity area within temperate latitudes, harboring remarkable species and endemic richness out of the tropics (Raven 1973; Quézel 1995; Cowling *et al.* 1996; Blondel & Aronson 1999; Thompson 2005; Kier *et al.* 2009). As any regional species assemblage, the rich Mediterranean flora is the result of a diversification process which depends on the interplay between speciation and extinction rates (Rosenzweig 1995). In the Mediterranean woody flora there are two contrasting character syndromes which differ in diversification rates (Herrera 1992; Ackerly 2009; Verdú & Pausas 2013). The first one is the so-called sclerophyll syndrome: plants usually displaying evergreen and though leaves; small, unisexual and dull-colored flowers, vertebrate-dispersed large seeds in fleshy fruits, and resprouting post-fire strategy (Verdú 2000). The second one, the nonsclerophyll syndrome, is characterized by the opposite trait combination, that is: nonsclerophyll and deciduous (summer or autumn deciduous) leaves; big, hermaphroditic and conspicuously colored flowers, small seeds in dry fruits, and fire-induced germination (seeder strategy) (Verdú 2000). Diversification rates tend to be higher for lineages belonging to the nonsclerophyll syndrome, and this increased diversification is mainly due to a higher speciation rate (Verdú & Pausas 2013).

Nonsclerophylls may be more prone to diversification than sclerophylls as a consequence of the interaction between environmental factors and their syndrome traits. For example, the evolution of unusually high plant diversity in Mediterranean-climate areas is usually addressed as the outcome of multiple environmental factors (summer drought, poor soil, fires) which favors certain plant trait combinations (small and dry fruits, seeder strategy) which facilitate genetic isolation and so speciation (Cowling *et al.* 1996; Verdú & Pausas 2013). From this perspective, the higher diversification rate of nonsclerophylls comes from their tied syndrome traits (syndrome-driven speciation). However, it is difficult to believe that each syndrome trait has the same role as a promoter of genetic isolation, even if we accept they are evolutionarily interwoven. So it deserves consideration the opposite option that one single trait within the syndrome could be the main responsible of the difference in diversification between sclerophylls and nonsclerophylls (trait-driven speciation). Theory and data suggest single traits typical of nonsclerophylls may increase their speciation rate as follows:

a) Big and conspicuously colored flowers: these are notorious displays to attract animal pollinators, so I will consider animal pollination as the possible speciation-prone trait underlying these floral features. The role of animal pollination on speciation is controversial, with positive as well as negative evidence in the literature (Eriksson & Bremer 1992; Givnish 2010; Kay & Sargent 2009). Anyway, the potential for divergent selection of floral traits is higher in animal-pollinated than in wind-pollinated plants, and in this way animal pollination could facilitate genetic isolation and speciation. In the Mediterranean region this effect could be enhanced by the unusual diversity of bees. Bee species richness seems to peak in the Mediterranean basin within the temperate zone of the Palaearctic - an abnormally high diversity of bees is a general trend among mediterranean-climate regions (Michener 1979; 2000).
b) Hermaphroditic flowers: unisexual flowers could difficult speciation as long as they are proper of dioecious plants, which tend to diversify more slowly than monoecious lineages (Kay *et al.* 2006). Lowered diversification rates could originate from two particular issues of dioecy: first, dioecious plants require two individuals of different

sexes in order to reproduce, a necessity which may decrease their colonization ability, increase their extinction risk in small populations, and originate smaller effective censuses. Apart from that, dioecy is often accompanied by reduced and generalist flowers, so flower specialization may also be difficult in these plants (Givnish 2010). By accumulating most of the genera with unisexual flowers, the sclerophyll syndrome may be less prone to speciation, thus leaving the nonsclerophyll syndrome with a higher speciation rate.

c) Small seeds and no endozoochory: these traits may be tied with each other by biological constraints and by causing poor seed dispersal and so limited gene flow across populations, thus promoting speciation. The biological constraint is best understood by focusing on endozoochorous genera in the Mediterranean basin; they have fleshy fruits big enough to be eaten by vertebrates and so to contain relatively big seeds; therefore endozoochory and seed size could be positively related (Herrera 1992). Vertebrate dispersal in these plants is carried on largely by migratory birds, in some cases during autumn migration (Herrera 1995), so the usual distance covered by a seed from a fleshy fruit in the Mediterranean region is probably much larger than that of a dry fruit. Poor seed dispersal in the non-endozoochorous, small-seeded nonsclerophylls is thus a possible cause of increased speciation.

d) Seeder strategy: the link between fire-induced germination and speciation was first proposed by Wells (1969), who noticed that the most species-rich genera (*Arctostaphylos* and *Ceanothus*) of the mediterranean-climate shrublands of California (chaparral) have abandoned the resprouting strategy to become in many cases obligate seeders, that is, fire-killed shrubs whose seeds massively germinate after fires. In these shrubs, the mean lifespan of generations is shortened by the frequent return of fires. Shorter generations are expected to accelerate the evolutionary rate of obligate seeders compared to resprouters. Furthermore, the high density of seedlings after fire means stronger competition and thus intense natural selection. Shorter generations and enhanced natural selection facilitate speciation in seeders, in theory at least. The influence of this mechanism in speciation rate has been supported by some works (Wisheu *et al.* 2000; Segarra-Moragues & Ojeda 2010) but not by others (Verdú *et al.* 2007; Segarra-Moragues *et al.* 2013), all of them referred to Mediterranean-climate regions.

The objective of this work is to examine the relative influence of each of the previous traits on the increased diversification rate of nonsclerophylls compared to sclerophylls, in order to discern between syndrome-driven and trait-driven speciation in the origin of the Mediterranean woody flora.

Methods

The woody flora of Eastern Andalusia (SE Spain) was chosen as the study region. Only those genera whose species are largely phanerophytes, chamaephytes, or both, were considered for analysis; exclusively riparian genera were not included (e.g. *Alnus, Fraxinus, Populus, Salix, Ulmus*) because their summer moist habitat makes them not good representatives of the Mediterranean-climate (summer drought) flora and its overall evolutionary history.

For each genus I searched in the literature the following information: regional species richness, pollination mode (1 = animal pollination, 0 = wind pollination), flower sexuality (1 = unisexual, 0 = hermaphroditic), seed size (1 = length x width > 2.25 mm^2, 0 = length x width < 2.25 mm^2), seed dispersal mode (1 = endozoochory, 0 = other), post-fire strategy (1 = obligate seeder, 0 = other), and geological age in the area (oldest age available from the European fossil record, from molecular clocks, or from both). The diversification rate, *d*, of each genus was estimated as the per-capita birth rate in the following pure birth macroevolutionary model (Nee 2006):

$$S = 2^{dt}$$

being *S* extant genus species richness and t the geological age. Taking logarithms and rearranging, *d* is calculated as $\log_{10}(S)/[t \log_{10}(2)]$. Genera with incomplete or unreliable information were ruled out from the analysis.

All these data were taken from Blanca *et al.* 2011 (general information on the flora, species richness), Guzmán *et al.* 2009 (ages for *Cistus, Fumana, Halimium* and *Helianthemum*), Palamarev 1989 (many ages for genera based on the European fossil record of Paleomediterranean woody species; I considered the age of a genus as the intermediate age of the geochronological unit where its oldest Paleomediterranean species appears), Paula *et al.* 2009, Paula & Pausas 2009 (post-fire strategies; the strategy I assigned to each genus is that which can be deduced from the records of their species in the BROT database), and Verdú & Pausas 2013 (trait states and ages from the references they provide from molecular clocks for the genera *Dianthus, Helichrysum, Juniperus, Lavandula, Phlomis, Pinus, Rosa, Ruta, Satureja, Sideritis, Teucrium, Thymus* and *Viburnum*).

Each genus was classified into the sclerophyll or nonsclerophyll syndrome according to its coordinate (dim1) in the nonmetric multidimensional scaling of life-history and reproductive traits carried on by Verdú & Pausas (2013) with many Mediterranean woody plants from the Iberian Peninsula, following the original but less inclusive analysis by Herrera (1992). Syndromes are defined as genera clusters separated by a large gap in dim1 which Verdú & Pausas (2013) found at 1; this is the cutting point I selected to separate sclerophylls (high dim1) from nonsclerophylls (low dim1). A one-way ANOVA was carried on to confirm the difference in diversification rate between both syndromes, using genera as analytical units. Phylogenetically independent comparison are not recommended in this case due to the poor statistical power resulting from the few character changes observed in the phylogeny of Mediterranean woody flora (Verdú 2000). The phylogenetic bias in the approach here adopted is well known since the most diversified among nonsclerophyll genera belong to a few families in the Mediterranean region (namely *Cistaceae, Fabaceae* and *Lamiaceae*), whereas species-poor genera tend to be widely distributed along many different families (Verdú & Pausas 2013). This feature must be taken into account when interpreting the results.

The role of single traits of the nonsclerophyll syndrome on the origin of its increased diversification rate was detected through ANCOVA analyses for diversification rates of sclerophylls *vs.* nonsclerophylls with each variables described above as covariate (i.e. animal pollination, flower sexuality, seed size, endozoochory, and seeder strategy). If the significant difference in syndrome diversification rate disappears in any of these analyses, then the corresponding covariate will be taken as a driver of the difference and so of speciation. If two or more covariates erase the difference, their respective effect size will be measured by dividing their ANCOVA p-values by that of the ANOVA. To confirm the effect of any covariate, the mean diversification rates of its two states were compared (one-way ANOVA).

Positive results for any trait may respond to a hidden variable and not to the trait states. This would happen if the diversification-prone state happens to be correlated to another trait which would be the real driver of speciation. In this regional flora, such a confounding trait (if present) is likely to be a restricted altitudinal distribution, because many small shrubs in Western Andalusia are mountain endemics (speciation in "mountain-islands") (Giménez *et al.* 2004). If this is a confunding variable, then any positively supported diversification-prone trait is expected to correlate with the ratio of mountain species per genus species. This possibility will be tested by examining the significance of the Pearson correlation between the ratio of mountain species and any supported traits revealed in the ANCOVA tests. Here I consider as a mountain species that whose altitudinal range belongs entirely to the supra-mediterranean (1,400-2,000 m), oromediterranean (2,000-2,800 m) or cryoromediterranean (> 2,800 m) thermotypes, or combinations of all of them, according to Blanca *et al.* (2011) (regional altitudinal distribution of thermotypes following Giménez *et al.* 2004). All the statistical analyses were performed using OpenStat software, with the significance level set at $\alpha = 0.05$ as usual.

Results

The initial selection of 124 genera was thinned to 40 genera with complete information, especially about post-fire strategy and a reliable geological age (Table 1). These genera contain the most speciose and the commonest in the region; they sum 246 species, about 59% of this woody flora, so the final dataset can be taken as a reasonably comprehensive sample of the species assemblage under scrutiny. There are 16 genera which belong to the sclerophyll syndrome and 24 in the nonsclerophyll syndrome.

The one-way ANOVA yields a very significant difference in diversification rate (p-value = 0.002). This difference with respect to the fixed factor (syndrome) disappears in only

Table 1 – Dataset with information on woody plant genera from Western Andalusia (Spain). Species, regional species richness. PM, pollination mode (1, animal; 0, wind). FS, flower sexuality (1, unisexual; 0, hermaphroditic). SS, seed size (1, length x width > 2.25 mm^2; 0, length x width < 2.25 mm^2). SD, seed dispersal (1, endozoochory; 0, other). PFS, post-fire strategy (1, exclusively seeder; 0, other). Age (Ma), oldest geological age of the genus in Europe (from the fossil record or molecular clocks). DR, diversification rate (per-capita birth rate in a pure birth model). dim1, coordinate in the nonmetric multidimensional scaling of life-history and reproductive traits (> 1, sclerophyll syndrome; < 1, nonsclerophyll syndrome). MS, number of mountain species in the genus (species whose altitudinal range in the region is at or above the Supramediterranean thermotype, i.e. about > 1,400 m.a.s.l.).

Genera	Species	PM	FS	SS	SD	PFS	Age (Ma)	DR	dim1	MS
Arbutus	1	1	0	1	1	0	26.0	0.00	0.27	0
Buxus	2	1	1	0	0	0	11.6	0.09	4.39	0
Ceratonia	1	0	0	1	0	0	26.7	0.00	2.01	0
Chamaerops	1	1	1	1	1	0	36.0	0.00	4.02	0
Cistus	8	1	0	0	0	1	1.7	1.76	–1.73	0
Colutea	2	1	0	1	0	1	19.5	0.05	–1.44	0
Coriaria	1	0	1	1	1	0	26.0	0.00	4.02	0
Daphne	3	1	0	1	1	0	11.6	0.14	0.27	1
Dianthus	10	1	0	0	0	1	1.6	2.08	–1.30	0
Ephedra	3	0	1	1	1	0	30.4	0.05	4.33	0
Fumana	9	1	0	1	0	1	2.0	1.58	–1.44	1
Genista	17	1	0	1	0	0	3.0	1.36	–1.44	2
Halimium	6	1	0	0	0	1	2.1	1.23	–1.73	0
Helianthemum	25	1	0	0	0	1	11.6	0.40	–1.73	2
Helichrysum	2	1	0	0	0	1	3.6	0.28	–0.55	0
Ilex	1	1	1	1	1	0	3.9	0.00	3.28	0
Jasminum	1	1	0	1	1	0	3.9	0.00	–0.61	0
Juniperus	6	0	1	1	1	0	43.7	0.06	5.08	2
Laurus	1	1	0	1	1	0	26.0	0.00	3.27	0
Lavandula	6	1	0	0	0	1	5.7	0.45	–1.48	0
Lonicera	8	1	0	1	1	0	11.6	0.26	–0.73	3
Myrtus	1	1	0	1	1	0	26.0	0.00	0.27	0
Nerium	1	1	0	1	0	0	11.6	0.00	–0.13	0
Olea	1	0	0	1	1	0	26.0	0.00	4.21	0
Periploca	1	1	0	1	0	0	36.0	0.00	–0.13	0
Phillyrea	2	0	1	1	1	0	11.6	0.09	5.08	0
Phlomis	3	1	0	1	0	0	4.7	0.43	–1.01	1
Pinus	5	0	1	1	0	1	96.0	0.02	4.68	1
Pistacia	2	0	1	1	1	0	31.0	0.03	4.42	0
Quercus	8	0	1	1	0	0	26.0	0.12	4.33	0
Rhamnus	7	1	1	1	1	0	36.0	0.08	4.02	3
Rosa	10	1	0	1	1	0	3.8	0.87	–1.02	3
Ruta	3	1	0	1	0	1	19.0	0.08	–1.01	0
Satureja	2	1	0	0	0	1	6.7	0.15	–1.30	0
Sideritis	20	1	0	0	0	1	5.4	0.80	–1.23	2
Smilax	1	1	1	1	1	0	42.9	0.00	1.89	0
Teucrium	40	1	0	0	0	1	6.4	0.83	–0.98	1
Thymelaea	10	1	1	0	0	0	14.1	0.23	2.28	1
Thymus	12	1	1	0	0	1	2.2	1.64	–0.25	2
Viburnum	3	1	0	1	1	0	26.0	0.06	–0.39	1

one of the ANCOVA tests, that with the obligate seeder strategy as covariate (Table 2). Obligate seeders are almost absent in the sclerophyll group, whereas the nonsclerophyll group contain obligate and facultative seeders and resprouters. There is a clear difference in diversification rate between obligate seeders and all the other genera (p-value < 0.001 in one-way ANOVA), which confirms the link between this post-fire strategy and increased diversification rate.

The seeder strategy and the ratio of mountain species per genus species are weakly correlated ($r = –0.19$) and their association is anyway not significant ($p = 0.23$) – see the last column in Table 1 for the raw number of mountain species per genus. Thus the increased diversification rate detected for seeders cannot be attributed to a hidden correlation between the seeder strategy and altitudinal restriction.

***Table 2** – Results of the ANCOVA tests (diversification rates of sclerophylls* vs. *that of nonsclerophylls) and effect size of each covariate. The latter is obtained as the p-value of the corresponding ANCOVA divided by the p-value of the ANOVA between diversification rates of sclerophylls and nonsclerophylls. The covariates are pollination mode (PM), flower sexuality (FS), seed size (SS), seed dispersal (SD) and post-fire strategy (PFS), as these variables are described in the caption of Table 1.*

Covariate	p-value	Effect size
PM	0.021 *	10.5
FS	0.004 **	2.0
SS	0.016 *	8.0
SD	0.024 *	12.0
PFS	0.085 n.s.	42.5

* Significant (p-value from 0.05 to 0.01)
** Very significant (p-value from 0.01 to 0.001)
n.s.: not significant

Overall, these results support the view that the difference in diversification rate between sclerophyll and nonsclerophyll syndromes is mainly due to the presence of speciation-prone obligate seeder lineages in the sclerophyll syndrome.

Discussion

The results here obtained point that fire has been the main promoter of speciation in the Mediterranean woody flora but only within a few lineages (mainly *Cistaceae* and *Lamiaceae*). From a total of 246 species included in this survey, 150 (61%) belong to obligate seeder genera, so fire-induced diversification could underlie the evolutionary development of a significant part of this regional flora at least. The link between fire and diversification was previously considered as an important factor in the origin of plant diversity in some Mediterranean-climate regions (Cowling *et al.* 1996; Wisheu *et al.* 2000), but not in the Mediterranean basin (Segarra-Moragues *et al.* 2013). This is largely because fire is comparatively more infrequent and inconstant in the Mediterranean basin compared to the situation in California, Cape and SW Australia, three regions where plants display outstanding fire-adapted traits with respect to the former (Cowling *et al.* 1996; Dallman 1998).

The other possible main drivers of diversification have not been supported in the analyses, although this does not mean their role on plant speciation has been negligible during the evolution of the Mediterranean flora. For example, pollinator specialization and shifts may have happened, thus contributing to diversify animal-pollinated lineages – in fact many pollinator shifts have been noticed in the diversification of *Gladiolus* in South Africa (Valente *et al.* 2012). Since all the covariates reduce the difference in diversification rate between the sclerophyll and nonsclerophyll syndromes (Table 2), then they could all have contributed to some extent to speciation, in spite that the overall difference can be attributed to one of them only. The largest effect size after that of post-fire strategy corresponds to seed dispersal mode, so the hypothesized negative influence of bird seed dispersal on speciation may be strong enough to be detected in the Mediterranean flora using other methods. Preliminary works yielded negative results for the opposite idea, namely that endozoochory has promoted plant diversification in general (Herrera 1989).

The contribution of the traits which define the nonsclerophyll syndrome on the origin of its higher diversification rate is clearly unequal. Facilitated speciation could depend on many of these traits, but only one stands out as the main responsible, so trait-driven diversification seems to be a more accurate image than syndrome-driven diversification for the origin of this Mediterranean woody flora. Fire-induced diversification through the seeder strategy not only erases the difference in diversification rate between sclerophylls and nonsclerophylls, but also reveals a new difference (seeders tend to diversify faster) and would account for the development of more than half of the species richness here taken under scrutiny. Thus the role of fire in the evolution of the Mediterranean basin flora seems be more important than previously considered.

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Cork oak (*Quercus suber* L.) forests of western Mediterranean mountains: a plant community comparison

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Abstract

*Cork oak landscapes hold high socio-economic and biodiversity values. In the western Mediterranean they comprise open wood pastures as well as the denser forest stands that occur particularly in mountain regions. The aim of the current study was to compare the cork oak (*Q. suber*) forest vegetation of the Serra de Monchique (southern Portugal) with the more extensive formations of the Sierra del Aljibe (southern Spain). In particular, we sought to understand the degree of similarity of plant species composition and diversity components – species richness, endemicity and taxonomic singularity – between the two areas, with a view to establishing the importance of this vegetation type in its regional setting. We analyse vegetation plot data on vascular plant occurrence in the forests of the study areas through ordination and cluster analysis. Species richness, endemicity and taxonomic singularity are examined for the forest areas as well other common vegetation types in their vicinity. We find an overlap in species composition across Portugal and Spain, but also important local differences. In both areas, endemicity levels are low in comparison with other common vegetation types, but total and woody species richness is relatively high. We discuss these results in relation to previous comparisons between Aljibe and similar communities in the Tingitanian peninsula of northern Morocco. We conclude that the cork oak forests of this western Mediterranean region represent a conservation priority. They are faced with multiple threats, and their survival depends on a range of conservation approaches.*

Keywords: plant species composition, diversity, endemicity, taxonomic singularity, priority habitat, vascular plant.

Introduction

The cork oak tree (*Quercus suber* L.) is of exceptional international importance for its economically valuable cork product (Pausas *et al.* 2009). Across its western Mediterranean range, the tree is also a significant 'framework species' of savannah-like formations (*dehesas* in Spain and *montados* in Portugal), an increasingly threatened agro-silvo-pastoral ecosystem (Pereira *et al.* 2009) (figure 1a). The matrix of trees, pastures and occasional cropping support not only an economically productive multi-use system, but also a rich fauna and high levels of vascular plant species diversity. For example, Maranón (1988) noted as many as 130 species of legumes and annual grasses per 0.1 ha in dehesa grasslands.

Less well known and studied for their conservation significance are the relatively closed-canopy forest stands of cork oak (figure 1b). By virtue of climatic constraints and land-use history, these forests are largely restricted to hilly and mountainous environments within their range. Key strongholds for the cork oak forests in the western Mediterranean are the mountains of Aljibe in southern Spain, the Tingitanian peninsula of northern Morocco and Monchique of southern Portugal. As other mountain environments, these areas are characterised by strong climatic and edaphic singularity. The biogeographic significance of Aljibe and Tangier also rests on their positioning to the north and south of the Strait of Gibraltar: a marine gateway between the Atlantic Ocean and Mediterranean Sea that has acted as both a barrier and a bridge for species migration between the European and African Continents (Lavergne *et al.* 2013).

Figure 1 – Cork oak landscapes range from open wood pastures (a) to denser forest stands (b).

The plant species composition and diversity of cork oak forests and other vegetation types of Aljibe and Tangier have been compared and contrasted (Ajbilou *et al.* 2006; Arroyo 1997; Deil 1997; Galán de Mera and Vicente Orellana 1997; Marañón *et al.* 1999; Ojeda *et al.* 1996). Wider phytogeographical comparisons of the western Iberian Peninsula and north-west Morocco have also been undertaken (e.g. Galán de Mera, Latorre, & Vicente Orellana 2003). Additional studies have been made within the smaller confines of the Los Alcornocales Natural Park (Andrés and Ojeda 2002; Arroyo and Marañón 1990; Coca Pérez 2007; Jurado 2002; Ojeda *et al.* 2000, 1995) and Tangier (e.g. Abourouh *et al.* 2005; Frosch 2010). This literature provides fascinating insights into the processes – operating across evolutionary, ecological and human historical timescales – that have shaped these analogous and rich plant communities.

Building on this earlier literature, and using new vegetation plot data from Aljibe and the Serra de Monchique of southern Portugal, the aim of this current study was to understand the specialness of the cork oak forest vegetation in a wider, regional context. Specifically, we sought to answer the following questions: 1) how similar is plant species composition across analogous forest areas in these Spanish and Portuguese study sites; and 2) do the high biodiversity values of the cork oak forests of Aljibe also apply to Monchique? Ordination and clustering methods are first applied to the Aljibe and Monchique plot data to compare and contrast their plant species composition. For Monchique, we then analyse three biodiversity components – species richness, endemicity and taxonomic singularity – of the cork oak forests in relation to other vegetation types, and discuss the results in the context of similar published comparisons for Aljibe and Tangier. In order to provide greater context to this vegetation analysis, we describe the wider biodiversity values of cork oak forests, the threats they face, and conservation priority and actions they demand in the western Mediterranean region.

Methods

Study area

Aljibe and Tangier cover a latitudinal gradient of c. 160 km north-south across the Strait of Gibraltar, whilst Monchique lies 300 km west-north-west of Aljibe in the Algarve province of Portugal (figure 2). The areas of Aljibe and Tangier comprise the Baetic-Rifean floristic region (Valdés 1991) and contribute to one of ten centres of particularly high plant biodiversity recognised for the Mediterranean basin (Médail and Quézel 1997). Local topographic ruggedness and oceanic influences provide areas of climatic stability and important refugia for species, in the otherwise dynamic conditions of the western Mediterranean during the last few million years (Rodríguez-Sánchez *et al.* 2008).

Both the Aljibe and Tangier Mountains are composed of Oligocene-Miocene siliceous sandstones, surrounded by Eocene limestones and marls (Ojeda *et al.* 2000, 1995). The sandstone-derived soils are acidic (pH 4-5), poor in nutrients and have high levels of assimilable aluminium and other metals toxic to plants (Arroyo 1997; Ojeda *et al.* 1995). In the Tangier peninsula the sandstones are fragmented into 17 small islands and cover an area of 1,836 km^2, a somewhat smaller coverage than in Aljibe (table 1, figure 2). The Serra de Monchique is also typified by generally acidic, nutrient-poor soils, but here they derive from a rare nephelene syenite rock (a granitic composition of nephelene and alkali feldspar). The syenite massif has an expanse of 80 km^2 and is intruded into the surrounding carboniferous metasediments.

The Mediterranean climate of the study region is tempered by strong oceanic influence. Orographic effects, and western Atlantic rain fronts (Arroyo 1997) contribute to a mean annual rainfall in Aljibe of 665-1,700 mm across its elevational range, corresponding to a humid to hyperhumid ombrotype (Rivas

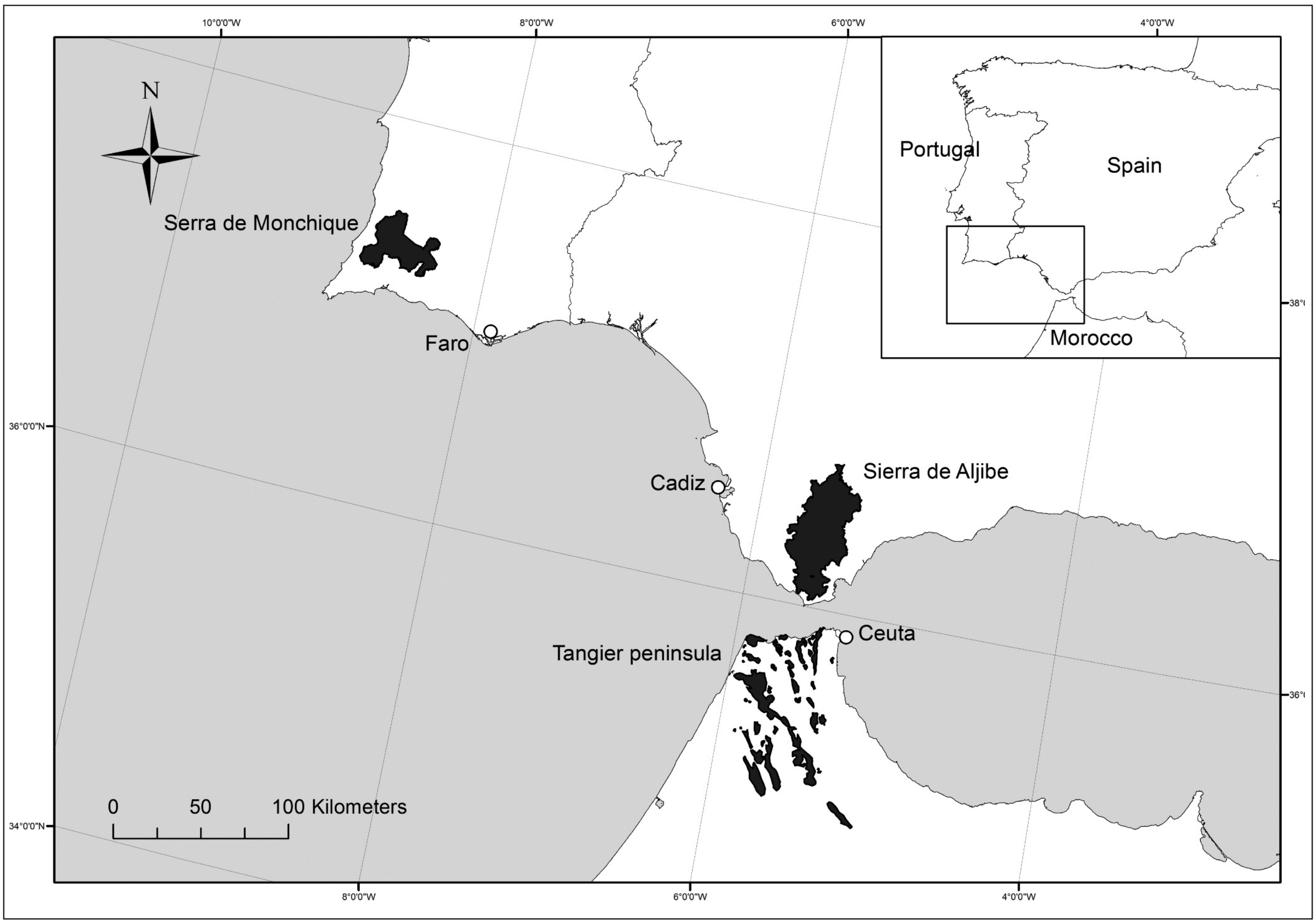

Figure 2 – Map of southern Iberia and the western end of the Mediterranean Sea, showing the location of the mountain complexes of the Serra de Monchique (Portugal), Sierra del Aljibe (Spain) and Tangier peninsula (Morocco).

Table 1 – Characteristics of three mountain areas in the western Mediterranean.

	Aljibe	Tangier	Monchique
Area (km^2)	2,276	1,836	750
Highest altitude (m)	1,092	1,705	902
Coordinates	36°03'-36°45' N 5°20'-5°45' W	35°00'-35°55' N 5°00'-6°15' W	37°16'-37°20' N 08°29'-08°39' W
Rainfall range (mm)	665-2,170	494-2,169	471-1,526
Population	2,500	c. 30,000*	6,045
Land tenure	Large-scale municipal and private forest estates	Complex mix of private and common lands	Small-scale private forests and farms Large-scale commercial plantations
Land uses	Large-scale cork forestry Woodland grazing Nature tourism Deer hunting**	Grazing (goats, cattle, sheep) Timber and fuel harvesting	Tourism Eucalyptus, pine and acacia plantations Small-scale subsistence farming and cork harvest
Estimated total vascular plant flora	1,046***	1,174†	492††
Trees and arborescent shrub flora	40*	38*	25††

Sources: * (Ajbilou *et al.*, 2006), ** (Seng, 2003), ***(Valdés *et al.*, 1987), † (Valdés *et al.*, 2006), †† (Malato Beliz, 1982).

Martínez *et al.* 1990). The average temperature here is 15.7°C with an average annual maximum of 34.3°C and minimum of 2.8°C (Coca Pérez 2007; Ojeda *et al.* 1995). Similar rainfall gradients and temperature patterns are to be found in Tangier and Monchique (table 1).

Natural vegetation types vary across the three areas. In Aljibe, the cork oak forms the most extensive forests, whilst the deciduous Algerian oak (*Q. canariensis* Willd), replaces it in the more humid, nutrient-richer conditions to be found in the valley bottoms and north-facing slopes. Areas of relict lauroid shrubs and trees form specialised communities in the shady and moist valleys (*canutos*) (Ojeda *et al.* 1995), whilst the sandstone ridges are covered by heathland communities dominated by *Cistus populifolius* L., *Erica australis* L. and *Chamaespartium tridentatum* (L.) P.E. Gibbs. The forest formations of Tangier are similar to those of Aljibe. Mixed evergreen forests (*Quercus suber*, *Q. coccifera* L. and *Q. rotundifolia* L.) and deciduous forests (*Quercus canariensis* and *Q. pyrenaica* L.) dominate the landscape, whilst small thickets of *Cedrus libani* (Endl.) Carrière subsp. *atlantica* and small stands of the endemic *Pinus pinaster* Aiton ssp. *hamiltoni* var. *maghrebiana* are present at high altitudes (Ajbilou *et al.* 2006). In Monchique, the cork oak dominates the forests, with remnant areas of the Algerian oak in more humid situations, where ancient coppices of sweet chestnut (*Castanea sativa* Miller) also occur. Heathlands are common on the highest slopes and ridges, whilst shrublands are common on lower slopes.

Population size, and historical and current land uses, are also contrasting across the three areas (table 1). Whilst depending on cork production for a large proportion of their local economic activity, other silvicultural uses of the mountain regions are important. In Monchique, commercially important trees are sweet chestnuts (wood and nuts), *Arbutus unedo* L. (berries), pine (mostly *Pinus pinaster*, wood) and eucalyptus (*Eucalyptus globulus* Labill.). In Aljibe, the Algerian oak was as a major source of wood for charcoal production that served the energy needs of much of the Cadiz province until the 1960s (Urbieta *et al.* 2008). Slashing and cutting of trees for fuel and wood continues in Tangier (Ajbilou *et al.* 2006; Ojeda *et al.* 1996); fuelwood and fodder are the main products collected by local communities (Ellatifi, 2009). In terms of agricultural and pastoral uses, a once highly significant but now almost absent reliance on subsistence cultivation of terraced fields (Monchique) contrasts with still-active grazing of cattle (Aljibe) and sheep and goats (Tangier). Eco-touristic activities have been gaining importance in Monchique and Aljibe in recent years. Both areas are protected as

Special Areas of Conservation (SACs) under the EU Habitats Directive (Directive 92/43/EEC), whilst Aljibe is also designated the Los Alcornocales Natural Park (area 1,700 km^2) and managed for deer hunting and other recreational uses.

Vegetation data collection

Vegetation data were collected between 1992 and 2011 for 267 plots, distributed in Monchique (188) and Los Alcornocales (79). All vascular plant occurrence data were highly comparable: being taken from plots of equal size (10 x 10 m), by the same recorder, and always according to the cover-abundance values of the Braun-Blanquet ordinal scale (Braun-Blanquet, 1932). The only potential bias that could not be avoided was the effect of varying climatic conditions on the presence, and particularly abundance, of plants within the plots. Plots were located through preferential sampling of representative patches of vegetation, avoiding edges and areas showing obvious recent disturbance. Prior to multivariate analyses (see below) the cover-abundance data were converted to percentage cover values based on Braun-Blanquet's (1964) conversion quoted in Maarel (1979). This followed the precedent of an earlier analysis of part of the dataset (Mitchell *et al.* 2009). Analyses were performed in R 2.14.2 (R Development Core Team, 2012).

Plant species composition

Similarity of plant communities of cork and Algerian oak forests between Aljibe and Monchique was studied by cluster analysis and ordination of plot inventory data for woody species. Plant co-occurrence data for sweet chestnut (*Castanea sativa*) plots in Monchique were also included, as here they occupy topographic and micro-climatic environments that are apparently similar to those of the less common Algerian oak. The percentage cover values for 53 plots from Monchique and 79 plots from Aljibe were included in a nonmetric multidimensional scaling (NMDS) ordination using the function *metaMDS* in the R package *vegan* (Oksanen *et al.* 2010). NMDS is regarded as one of the most robust unconstrained ordination methods in community ecology, accommodating nonlinear species responses to environmental variables (Minchin 1987). Bray-Curtis was selected as the dissimilarity measure. Visual interpretation of the results was aided by cluster analysis of the plot data (*hclust* function in R, using average linkage algorithm and Bray-Curtis dissimilarities) and graphing the obtained classes in the ordination space of the two NMDS dimensions. The influence of key tree, shrub and liana species on the spread of plots in the ordination was investigated by plotting the respective vectors.

Plant diversity components

Plant species diversity of the forests and other vegetation communities of Monchique was studied following the approach adopted for Aljibe and Tangier comparisons (Ajbilou *et al.* 2006; Arroyo & Maranon 1990; Arroyo 1997; Marañón *et al.* 1999; Ojeda *et al.* 1995, 1996, 2000). Both woody and non-woody species were included in the analysis of 93 plots within semi-natural vegetation and 34 plots within plantations. From the mountains we included upland heathland (n = 15), rock outcrop (16), cork oak forest (36), humid *Castanea sativa*/*Quercus canariensis* forest (16), and shrubland (10), which develop where the canopy of evergreen oak has been removed and where the *Arbutus unedo* is managed for the harvesting of its berries. Wetland areas (riparian, rhododendron) and other rarer habitats were not included. The *Castanea*/*Q. canariensis* forests comprise old coppices of sweet chestnuts abutting and sometimes mixed with remnant areas of formerly more extensive Algerian oak on north-facing slopes of Picota. They are analogous to the much more extensive patches of the deciduous oak in Aljibe. The upland plantation plot data originated from monospecific production of pine (*Pinus pinaster*, *P. radiata* D. Don and *P. brutia* Ten.; n = 11), eucalyptus (*Eucalyptus globulus*; 13) and black acacia (*Acacia melanoxylon* R. Br.; 10).

Three biodiversity components were analysed: species richness, geographical range (endemicity), and taxonomic singularity (an indicator of distinctiveness). Together they are useful for assessing the conservation value of different habitats (Ojeda *et al.* 1995). Species richness was simply the species number per plot. Endemicity was calculated based on a prior classification of species into one of eight chorological types based on Ojeda *et al.* (1995) and Coca Pérez (2007): Mediterranean-Eurosiberian (ME), Circum-Mediterranean (CM), Western Mediterranean-Macaronesian (WMM), Western Mediterranean (WM), Iberian (IB), Ibero-North African (INA), Southwestern Iberian-Tingitanian (SIT) and Gibraltarian (G). Endemics were considered as belonging to one of the four most geographically restricted chorological types (IB, INA, SIT and G) and endemicity levels for plots were calculated as the proportion of all species that were endemics.

Taxonomic singularity is the inverse of the infra-generic diversity. In the absence of phylogenetic information for many Mediterranean species, it provides an effective alternative measure of the distinctiveness of species, and is useful for seeing whether habitats are offering refuges for relict Tertiary flora elements, or harbour modern highly speciated genera (Ojeda *et al.* 2000). For each species in the co-occurrence dataset, the number of co-generic species for Iberia was recorded, based on the Flora iberica (Castroviejo 1986-2012), or in cases where this was incomplete, the Flora Europaea (Tutin *et al.* 1964-1993). Updated taxonomic treatment for some groups in the more recent flora may have had some effect on these infra-generic diversity values. The values were averaged for all species in each plot before conversion into the index of taxonomic singularity.

Significant difference in the three biodiversity components between community types was tested using one-way ANOVA, and multiple post-hoc comparisons by HSD Tukey's tests for unequal sample sizes. Diagnostic plots were inspected to confirm data normality and homoscedasticity.

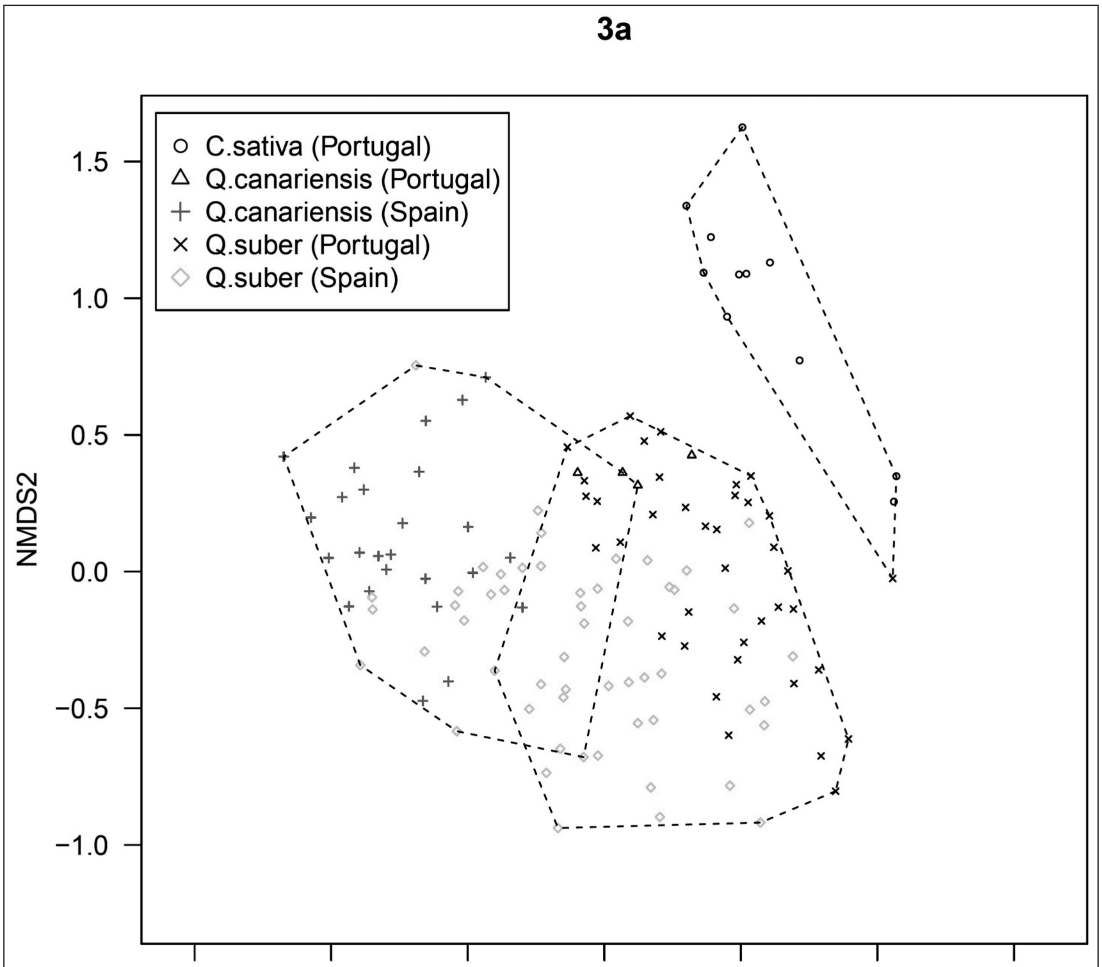

*Figure 3a – NMDS ordination diagrams showing Monchique and Aljibe plots in the ordination space of the first two NMDS axes. (a): plant community composition of the woody species (*C. sativa* = sweet chestnut;* Q. suber *= cork oak;* Q. canariensis *= Algerian oak). Dashed lines show the three classes obtained from the cluster analysis of the species data.*

Results

Similarity of plant community composition

The ordination of woody vascular plant species data for forest plots from Aljibe and Monchique reveals variability in the cork oak floras, but also a degree of similarity with some plots sharing the same ordination space (figure 3a). Cork and Algerian oak dominated plots also intermingle in the ordination diagram, although in Aljibe there is a pattern of differentiation with the deciduous oak plots having the lowest axis 1 scores. The sweet chestnut coppices of Monchique, whilst in close geographical proximity to oak forests on some northern slopes, form a distinct cluster in the ordination diagram.

Differences between plots can be explained not just in terms of principal canopy trees (figure 3b), but also other plant functional types (figures 3c-e). *Phillyrea latifolia* L. and the strawberry tree *Arbutus unedo* are important

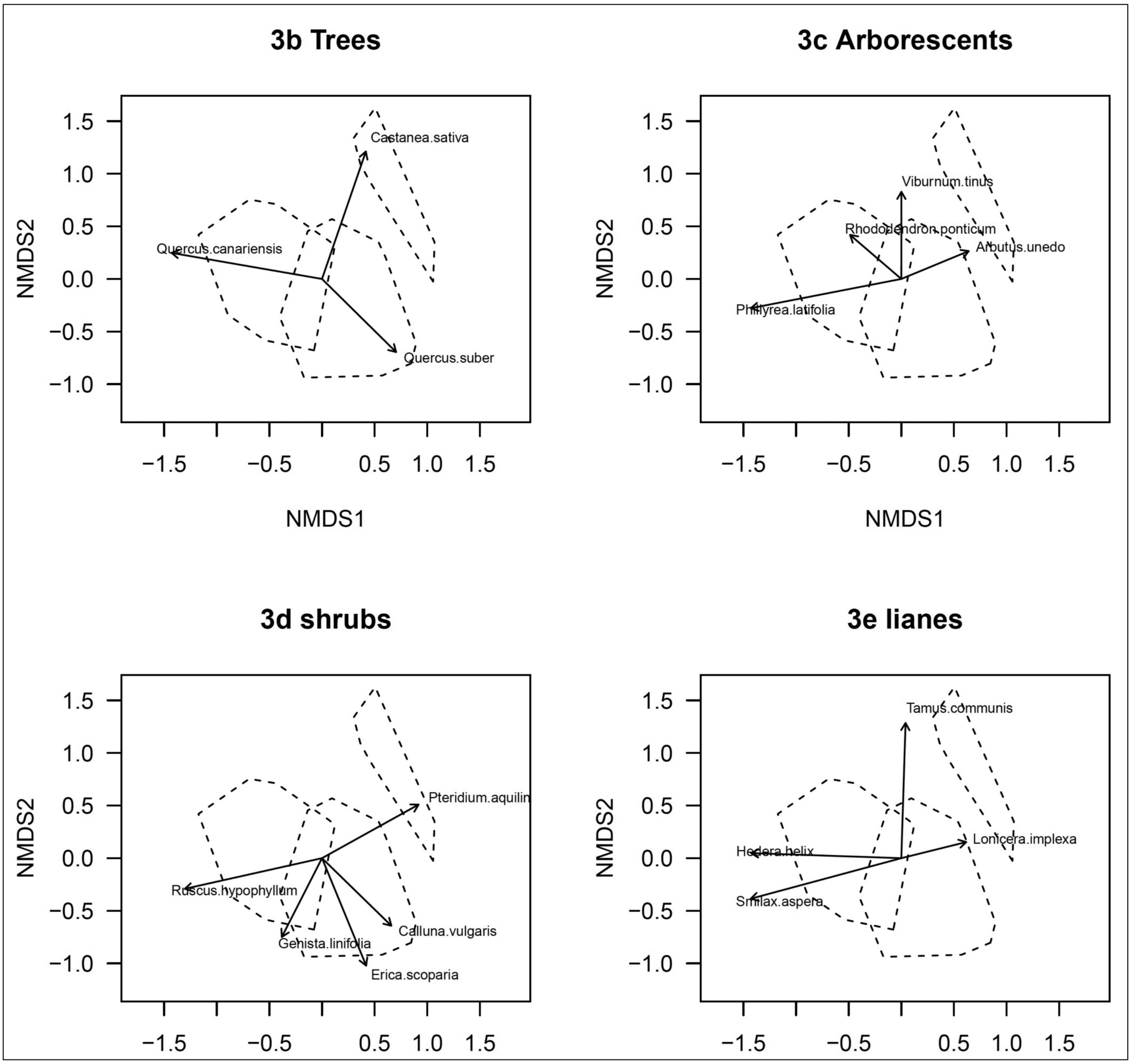

Figure 3b-e – NMDS ordination diagrams showing Monchique and Aljibe plots in the ordination space of the first two NMDS axes. (b-e): Interpretation of the NMDS ordination of woody species data using posterior fitting of biplot arrows for selected trees (b), arborescent shrubs (c), shrubs (d) and lianes (e).

species separating the Spanish and Portuguese cork oak plots along the first NMDS axis (figure 3c). The strawberry tree is common in the understorey of cork oak patches in Monchique, as well as dominating some *maquis* communities resulting from the loss of the canopy layer. Instead, *Phillyrea latifolia*, which is absent from Monchique, is the more common suppressed tree in the subcanopy of the Spanish oak forests; *Arbutus unedo* is widespread here but rarely attains high cover values. Separating the oak plots along the second NMDS axis, *Viburnum tinus* L. and – to a lesser degree – *Rhododendron ponticum* L. are the more important arborescent species.

Plotting vectors for common lower-growing shrub species helps to explain the differentiation along the second ordination axis (figure 3d). The heathers *Erica scoparia* L. and *Calluna vulgaris* (L.) Hull and gorse *Teline linifolia* (L.) Webb & Berthel suggest more open canopy conditions for the plots of low axis 2 scores. Also of note amongst the differentiating shrub-layer species are ‘butchers broom’ *Ruscus hypophyllum* L., and bracken *Pteridium aquilinum* (L.) Kuhn. Regarding the lianas (figure 3e), there is a strong association of two species (*Smilax aspera* L. and *Hedera helix* L.) with the Spanish *Q. canariensis*-dominated plots at low axis 1 scores. *Lonicera implexa* Aiton is more important for those plots with high axis 1 scores, whilst *Tamus communis* L. has a strong diagnostic value for plots of high axis 2 scores.

Plant diversity components

Of the semi-natural plant communities of Monchique, total species richness was highest in the cork oak forests, chestnut coppices and rock outcrops (figure 4). The chestnut coppices had a high density of herbaceous species, including the ferns *Asplenium onopteris* L. and *Polypodium australe* Fée and saxifrage *Saxifraga granulata* L.. The rock outcrops had a significant component of chasmophytes in the flora, including the three stonecrop species *Sedum album* L., *S. brevifolium* DC. and *S. forsteranum* Sm., mostly confined to soil-filled crevices and weathered seams in the rock. For both Monchique and Aljibe, woody species richness peaked in the cork oak forests, with slightly lower levels for chestnut coppices. The shrublands were also relatively rich in woody species including *Cistus ladanifer* L., *Erica australis, Lavandula stoechas* L., *Phillyrea angustifolia* L., *Lithodora diffusa* (Lag.) I.M.Johnst. and *Quercus lusitanica* Lam. Upland heathlands of Monchique were particularly depauperate in species compared to equivalent communities in Aljibe, and were dominated by generalist and ubiquitous species such as *Cistus salvifolius* L., *Rubus ulmifolius* Schott and *Pteridium aquilinum*. Total and woody species richness of Monchique cork oak forests was significantly higher than eucalyptus, pine and acacia plantations (results not shown).

In Monchique, endemicity within the total species as well as woody species pools was found to be highest in rock outcrop, shrubland and heathland communities, and lowest for cork oak forest and chestnut coppices (figure 4). Endemicity levels of these latter semi-natural formations were not higher than for eucalyptus, pine and acacia plantations (results not shown). Taxonomic singularity between habitats did not differ, except for the high levels to be found in shrublands (figure 4). Contributing to the high scores for this habitat were species of low diversified genera, including the shrubs *Calluna vulgaris*, *Lithodora diffusa*, *Helichrysum stoechas* (L.) Moench, *Arbutus unedo* and *Phillyrea angustifolia*, the herbaceous legume *Astragalus baeticus* L., and parasitic plant *Cytinus hipocistus* (L.) L..

Discussion

Similarity of cork oak plant communities

This study has established the Monchique cork oak forests as being comparable communities to the formations of Aljibe, whilst at the same time showing some distinctiveness. The degree of similarity is indicated by the overlap of plots in the ordination (figure 3a). A similar comparison for Aljibe and Tangier, using detrended correspondence analysis (DCA), also revealed a mixing of communities, interpreted in terms of similarity of species composition and abundance (Marañón *et al.* 1999).

The spread of plots in both study areas reflects a range of understorey conditions and vegetation characteristics, ranging from more shaded and undisturbed environments with a predominance of arborescent shrubs and lianas creating multi-layered vegetation structure, and sunnier, warmer environments with a preponderance of lower shrubs associated with heathlands. *Arbutus unedo* is considerably more common in the Monchique than the Aljibe communities, and this may be at least partly due to its local protected status as a valuable source of berries in the former area. *Rhododendron ponticum* was generally more prevalent in the Aljibe *Quercus canariensis* plots. This species is a Tertiary relict that is associated with the more mesic and fertile end of the environmental gradient (Marañón *et al.* 1999). It is most common along the mountain streams and *canutos* of Aljibe (Jurado 2002),

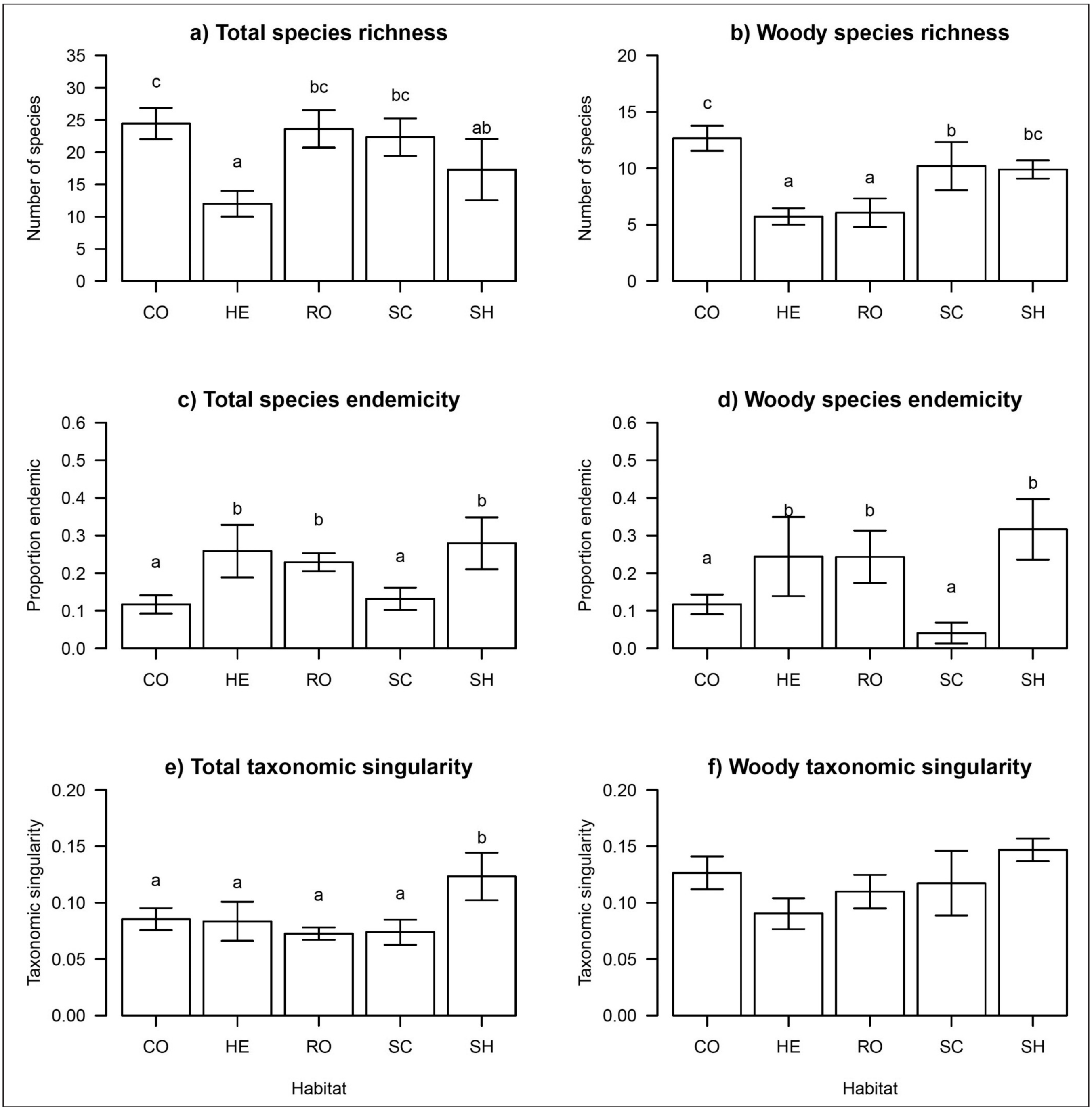

***Figure 4** – Biodiversity components of cork oak and other vegetation communities of Monchique. CO = upland cork oak (*Quercus suber*) forest (36 plots), HE = heathland (15), RO = rock outcrop (16), SC = sweet chestnut (*Castanea sativa*) coppice (16), SH = shrubland (10). Significant differences (p<0.05) between habitats revealed by Tukey HSD tests on one-way ANOVA results are indicated by different letters.*

filling a niche identical to that occupied by *Prunus lusitanica* L. in N. Morocco (Ajbilou *et al.* 2006). Also of note amongst the differentiating shrub-layer species are 'butchers broom' *Ruscus hypophyllum* and bracken *Pteridium aquilinum*. The *Ruscus* is typical of shaded forest sites in Spain (Pérez-Ramos *et al.*, 2008) but is absent from the Portuguese communities. Bracken has fire-resistant rhizomes, deep litter and a dense frond canopy; it is a successful invader, especially of disturbed areas, and is often negatively correlated with plant species diversity (Coca Pérez 2007). *Tamus communis*, another typical species of shaded forest sites (Pérez-Ramos *et al.* 2008), has a strong suggested diagnostic value for plots of high axis 2 scores in both Monchique and Aljibe.

These similarities and differences are reflected in the phytosociological treatment of these forests. Belonging to the alliance of *Quercion broteroi* (order *Quercetalia ilicis* and class *Quercetea ilicis*), a distinction is made between the cork oak *Teucrio baetici-Quercetum suberis* and Algerian oak *Rusco hypophylli–Quercetum canariensis* associations of Aljibe, and the *Poterio agrimonioidis–Quercetrum suberis* and *Euphorbo monchiquensis–Quercetum canariensis* associations of Monchique (Rivas-Martínez *et al.* 2001; Seng 2003). Nevertheless, the phytosociological and ecological interpretation of the Portuguese communities is best served by treating them as the western variants of more extensively distributed communities on the other side of the border (Malato Beliz 1982).

Plant diversity significance of cork oak forests

In relation to plant diversity components, our study of the Monchique cork oak woodlands and associated habitats showed similar patterns to those previously documented for Aljibe. In particular, at the plot level, cork oak forests show a high richness of woody and total species relative to other vegetation types (figure 4a-b). In Aljibe, an environmental gradient of increasing fertility has been observed from open heathlands on dry, acidic sites, through *Q. suber* forest on intermediate sites, to *Q. canariensis* forest on the most mesic sites (Ojeda *et al.* 1996). Woody species richness was found to peak in the intermediate conditions of the cork oak forests (Marañón *et al.* 1999; Ojeda *et al.* 1995). Within the spectrum of *Q. suber* forests studied by Coca Pérez (2007), richness and diversity of the woody species flora increased from lowland, more xeric sites, to high altitude, more humid sites with greater cover of *Pteridium aquilinum* and woody species. *Q. canariensis* forest has been found to be more diverse than *Q. suber* forest in herbaceous species, which comprise many woodland ephemerals that benefit from the deciduous nature of the canopy. *Q. suber* forests, on the other hand, are more diverse in woody species (Ojeda *et al.* 2000). Similar trends in woody species richness have been found for Moroccan communities, although the plant communities are generally impoverished in comparison with the Spanish ones, with more generalist species and over-domination of *Erica arborea* L. (Marañón *et al.* 1999; Ojeda *et al.* 1996).

In terms of endemicity, in Aljibe there is a gradient of increasing herbaceous and woody species endemicity from *Q. canariensis* plots, through *Q. suber* forest to heathlands (Marañón *et al.* 1999; Ojeda *et al.* 2000, 1995). In these communities, vegetation of geographical wide distribution and of pre-Pliocene evolution is replaced with more diversified taxa, of recent evolution (post-Pliocene) and restricted/local distribution (Coca Pérez 2007). Plants here are also subjected to high selective pressures by adverse conditions of acidity and nutrient limitation (Marañón *et al.* 1999), thereby promoting speciation (Ojeda *et al.* 1995). Whilst endemicity levels in the Monchique heathlands were not low, the notable paucity of their flora (figure 4) may reflect degradation from frequent fires and overgrazing, and a more recent origin compared to the heathlands of Aljibe, where diversification of the flora is thought to have proceeded for some 70,000 years (Arroyo and Marañón 1990).

Within the mountains of Aljibe, a gradient of taxonomic singularity exists from *Quercus canariensis* forest (highest levels), through *Quercus suber* forest to heathlands (lowest levels) (Marañón *et al.* 1999; Ojeda *et al.* 1995, 1996, 2000). The general lack of significant differences in taxonomic singularity between the habitats of Monchique may be because this index of plant diversity was calculated at the Iberian scale; the patterns for Aljibe, considered at the Western Andalusian scale, disappeared when re-analysed at the Ibero-North African or Mediterranean basin scales (Ojeda *et al.* 1995). The Aljibe mesic woodlands harbour taxa belonging to less-diversified genera: *Hedera* and *Ruscus* (at the worldwide scale), *Rubus, Ilex, Viburnum, Smilax* and *Rhododendron* (outside of Mediterranean) (Marañón *et al.* 1999; Ojeda *et al.* 1996). The moister and shadier conditions have probably acted as a refuge for these pre-glaciation relict taxa; modern, truly Mediterranean taxa, belonging to highly diversified genera (and thus less singular), are less able to colonise those habitats (Ojeda *et al.* 2000).

Conclusion: cork oak forests as a conservation priority

Our work associates the cork oak forests of Monchique of southern Portugal with those bordering the Strait of Gibraltar as a regional vegetation unit of importance for its flora. The Monchique communities have similarly high species richness as the Aljibe forests, and are especially notable in their woody plant species composition. Whilst endemicity levels were not high, a number of notable South-west Iberian–Tingitanian (e.g. *Paeonia broteroi* Boiss. & Reut. and *Rhododendron ponticum*) and Iberian (*Hyacinthoides hispanica* (Mill.) Rothm., *Saxifraga granulata* and *Senecio lopezii* Boiss.) plants were recorded. The range of vegetation structures created by cork oak formations ranged from heathy understories under relatively open canopies, to dense multi-layered forests with young trees, arborescent shrubs (*Arbutus unedo, Erica arborea, Myrtus communis* L., *Pistacia lentiscus* L., *Viburnum tinus*) and lianas filling the space under the mature canopy. These latter vegetation structures are particularly unusual in a regional context, and their structural complexity is likely to create an important variety of niches for animals (Brokaw and Lent 1999).

In terms of the animal biodiversity of cork oak ecosystems, the greatest focus has been on wood pastures, and some authors have suggested these are more important than the denser forests (Díaz 2008; Díaz *et al.* 1997). These wood pastures represent ecotonic habitats supporting both open and forest specialists (Díaz 2008; Godinho and Rabaça 2010; Tellería 2001). Nevertheless, the significance of cork oak forest for wildlife should not be underestimated. They are potential habitat for forest-adapted birds (Díaz 2009; Pereira *et al.* 2012), butterflies (Verdasca *et al.* 2012), and mammals (Díaz 2009; Rosalino *et al.* 2009). Some 96 species protected by European environmental legislation are supported by this habitat type (Díaz *et al.* 2009). At the landscape scale, forests complement the savanna matrix in enhancing overall (gamma) diversity of a number of taxonomic groups. Some animals, such as the Iberian lynx (*Lynx pardinus*) and Eurasian black vulture (*Aegypius monachus*), seek shelter in denser forested habitats whilst feeding in more open areas (Carrete and Donazár 2005; Gonçalves *et al.* 2011).

Whilst cork oak forests and wood pastures are biodiverse, they also face a range of threats, including climate change, disease, and the commercial trend towards cork-alternatives as wine bottle stoppers that challenge the sustainability of a finely-tuned cultural ecosystem (Bugalho, Caldeira, Pereira, Aronson, & Pausas 2011; Pereira *et al.* 2009; Pinto Correia 1993). Cork oak die-back (*[l]a seca*) and regeneration failure are now widespread in forests and wood pastures alike (Vericat *et al.* 2012), and are resulting in their gradual replacement by persistent shrublands (Acácio *et al.* 2009).

Important differences exist between the Monchique, Aljibe and Tangier study areas in relation to predominant threats to the cork oak forests. In Monchique, fragmented forest patches are vulnerable to catastrophic fires facilitated by plantation forestry of eucalyptus and pine (Simonson *et al.* 2013). In Aljibe, the high deer population and mechanical clearance of understories leads to widespread recruitment failure for the cork oak as well degradation of sub-canopy vegetation (Marañón 2009). Meanwhile, in Tangier, the high human population density and reliance on the forests for fuelwood provision and pasturage has led to unsustainable levels of slashing, cutting and grazing, leading to aridification of the landscape and poor vegetation recovery (Abourouh *et al.* 2005; Ajbilou *et al.* 2006; Bugalho, Plieninger, Aronson, Ellatifi, & Gomes Crespo 2009; Laaribya 2006).

In the face of such threats, we advocate urgent conservation action for cork oak forests. These forests are recognised as habitats of community importance under the EU Habitats Directive (habitat code 9330), but concerted action is required under this framework to achieve the goal of favourable conservation status. A range of conservation approaches are required, including site-level management (Vallejo *et al.* 2009), payments for ecosystem services (Bugalho *et al.* 2011), and ecoregional approaches and policies to bolster and improve livelihoods and markets for forest products (Berrahmouni *et al.* 2009; Laaribya 2006). Threats from fire and overgrazing – whether by livestock in Morocco or deer in Aljibe – are particularly important to address. As we have seen, much of the floristic interest of cork oak woodlands lies in the woody plants, and their sprout and seed banks can become exhausted by the constant disturbance caused by these impacts. Management plans for Aljibe forests already include large-scale fencing within priority management actions (Urbieta *et al.* 2008), whilst temporary exclosures can also be effective in encouraging tree and shrub regeneration (Abourouh *et al.* 2005). Fuel reduction strategies designed to control fire risk need to be balanced with the retention of late successional multi-layered forest stands supporting high levels of biodiversity, through appropriate zonal planning at the landscape level.

The contribution of our current work is to highlight in particular the diverse plant communities associated with cork oak forests, establishing their importance alongside the more widespread wood pasture systems of southern Iberia. The structurally and compositionally rich forest communities make an important contribution to regional biodiversity and natural heritage, and represent a vegetation unit of high priority for conservation and restoration.

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Climatic Patterns in the Mediterranean region

Modèles climatiques dans la région méditerranéenne

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Abstract

Climate and vegetation patterns in the Mediterranean region are known to be highly correlated and a summary of the major studies in this topic is provided. Many of the studies rely on simple indices based on simple climatic variables such as monthly averages of temperature and precipitation. The availability to the public of data from FAO and World Climate with 30 year averages of monthly temperatures and precipitation for 2,086 weather stations around the Mediterranean provided a good basis to model their geographical distribution. Again, simple variables were used as explanatory variables, as latitude, longitude, elevation and distance to coast. Models of the linear or logistic type were used to explain monthly and annual average temperatures and precipitation indicating that, in many situations, the simple models provided can already be used to understand the general patterns of climate and vegetation in the Mediterranean Region. A small exercise illustrates the possibilities of these models to simulate the general effects of major climatic changes in the changes of the geographical limits of Mediterranean species and vegetation.

Résumé

Dans la région méditerranéenne, le climat et la distribution de la végétation sont connus pour être hautement corrélés et une synthèse des principales études sur le sujet est présentée ici. Pour la plupart, les études s'appuient sur des indices simples fondés sur des variables climatiques simples comme les moyennes mensuelles de la température et des précipitations. La disponibilité pour le grand public de données de la FAO et de World Climate comprenant des moyennes trentennales de températures et de précipitations pour 2 086 stations météorologiques autour de la Méditerranée a fourni une bonne base pour modéliser leur distribution géographique. Des variables simples ont été utilisées comme variables explicatives, comme la latitude, la longitude, l'altitude et la distance à la mer. Des modèles de type linéaire ou logistique ont été utilisés pour expliquer les moyennes des températures et des précipitations mensuelles et annuelles, indiquant que, dans de nombreux cas, les modèles simples proposés peuvent d'ores et déjà être utilisés pour comprendre la caractérisation spatiale du climat et la distribution de la végétation en région méditerranéenne. Un petit exercice illustre les potentialités de ces modèles pour simuler les effets des principaux changements climatiques sur les variations des limites géographiques des espèces et de la végétation méditerranéenne.

Introduction

Climate and vegetation

Mediterranean vegetation has been studied for a long time and its geographical distribution has been represented in several papers, as in the very influential work by Tomaselli (1977 *in* de Montgolfier 2002) shown in Figure 1.

Keywords: Mediterranean region, climate, climate interpolation.

Mots clés : région méditerranéenne, climat, interpolation climatique.

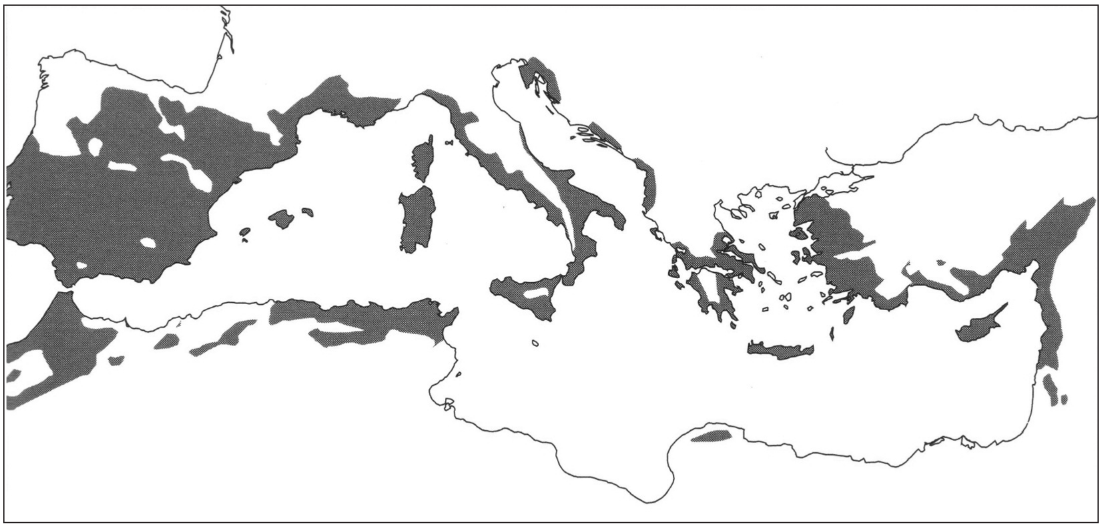

Figure 1 – Distribution of the Mediterranean matorral (maquis) (Tomaselli 1977 in *de Montgolfier 2002).*

Most early bioclimatic studies were characterized by the search of synthetic expressions of climate to produce maps of homogeneous climatic regions and to assess climate-vegetation relationships (e.g. Lang 1915; de Martonne 1926a, b, 1942) and several of those studies were performed in the Mediterranean region (Emberger 1930; Giacobbe 1949; Daget 1977). In most cases, climatic variables (in particular precipitation, evaporation and temperature) were combined to allow climatic patterns to be correlated with observed vegetation patterns and to provide some quantitative expressions of climatic conditions such as aridity and winter cold (Mazzoleni *et al.* 1992).

Mediterranean vegetation was always considered to be associated with a specific type of climate – the Mediterranean climate. In fact, climate has an obvious direct influence on vegetation, and the influence of other natural factors on vegetation is related with climate as soil development or fire regimes. Even the effect of topography is not independent of climate because of the influences of elevation and aspect on temperature and precipitation.

This close association between climate and vegetation results in that the geographical limits of the Mediterranean ecosystems are commonly defined by climatic parameters (e.g. Emberger 1930; Gaussen & de Phillips 1958; Quezel 1977; de Montgolfier 2002).

The different climatic indices in the Mediterranean

A popular approach for the explanation of the distribution of species in the Mediterranean was that of Emberger (1930), who proposed a system with two axis, one related with the cold limit (represented by the average of the minimum temperatures of the coldest month – m in ºC), and one coefficient (Q) related to average annual precipitation (P in mm), m and to the average of the maximum temperatures of the warmest month (M in ºC):

$$Q = 2000\ P/[(M + m)(M - m)]$$

In a comparative study, Daget (1977) concluded that Emberger's (1930) system was the best for defining Mediterranean climates, and the approach was disseminated in several Mediterranean countries (e.g. Quézel 1977 or Mhirit 1999).

However, in spite of the wide use of the Emberger system in the Mediterranean, other alternative systems were proposed based on simple and more readily available data as monthly averages of temperature and precipitation.

One popular approach is the displaying of climatic patterns as a combined double-scale representation of temperature and precipitation values throughout the year (Bagnouls & Gaussen 1957; Gaussen 1956; Walter 1955). The use of these climatic diagrams was very successively extended to the complete world in the Klimadiagramm-Weltatlas (Walter & Lieth 1960).

In this system, a dry month was defined by the simple relation P/T < 2, where precipitation (P in mm) was less than two times the average temperature (T in ºC). This approach allowed for the calculation of the number of dry months, which was the basis of the approach taken by Gaussen and de Phillips (1958) in the preparation of the bioclimatic map of the Mediterranean (UNESCO-FAO, 1963).

Many other authors, using the same method, agree in that the Mediterranean climate is characterised by the presence, in the warm season, of a dry period of at least one month (de Montgolfier 2002).

In spite of the obvious criticisms for the oversimplification of these empirical approaches based on Walter temperature rainfall diagrams, these are still very much used as did Rivas-Martinez (1981) in his climatic classifications linked to phytosociological categories. Rivas-Martinez further extended Gaussen's concepts, suggesting the use of ratios between the sum of precipitations (P_i in mm) for a period of n months and the sum of the corresponding positive monthly temperatures (T_i in ºC):

$$I_n = \Sigma_n P_i / \Sigma_n T_i$$

The period can range from one month, where the index is the same as that of Gaussen, a period of n summer months (Iosn), or the total year (Io). As before, the value of 2 for the ratio between precipitations and temperatures in summer months is the limit of a dry period. The values of Io allow for the classification of the climate as humid (above 3.6), dry (2.0-3.6), semi-arid (1.0-2.0), or arid (below 1.0). Originally used in Spain, this system has been more recently applied in other regions of the world such as South America (Rivas-Martinez & Navarro 1994), or North America (Rivas-Martinez *et al.* 1999).

Regardless of the indices used, monthly average temperatures and precipitation are the basis for many analyses of climate and its correlation with vegetation. It is important now to understand the factors associated with those climatic variables.

The factors associated with temperature and precipitation

Temperature and precipitation are known to vary with spatially predictable patterns. They vary also in function of the elevation. If precipitation has a relatively complex relationship with elevation, temperature decreases linearly according to elevation, following a mean lapse rate of – 6 to – 10 °C km^{-1} (MacArthur 1984; Friend & Woodward 1990; Waring & Running 1998).

It is also well known that proximity to oceans or other large water bodies of water that are heat reservoirs has a great moderating effect on temperature; the interiors of continents, far from oceans, are said to have a "continental" climate, having lower temperatures in winter and higher temperatures in summer.

The issue of the timescales in modelling temperature and precipitation is important and it has been addressed by various authors. Timescales used vary from daily (Johansson & Chen 2003), to monthly (Goodale *et al.* 1998), or annual (Briggs & Lemin Jr 1992).

For annual precipitation, it has been long indicated that global rainfall patterns in relation to latitude can only be understood on the basis of major atmospheric circulation processes. Global circulation patterns have been described by scientists since Halley in 1683 or Hadley in 1735 following observations made in the discovery voyages throughout the oceans. Full explanations for such patterns are complex but good approximations are presented in various books (e.g. MacArthur 1984).

The information of the average annual precipitation is however not enough to describe features of extreme relevance for the Mediterranean Region. In particular, it does not enable us to determine the degree of water scarcity in the summer months. It is therefore necessary to understand the processes associated with the seasonal fluctuations of precipitation.

In Europe and North Africa the atmospheric circulation is established in the presence of permanent cyclonic centers, the Icelandic Low and the Azores High, located around latitude 30ºN in January and moving north towards the British Isles in July. The Mediterranean type climate corresponds exactly to this latitudinal belt north of the deserts, where winters are rainy (above 30ºN) and summers are dry (below 45ºN).

The effect of location (distance to the coast and longitude) on precipitation can be easily understood by inspection of any European map of rainfall distribution (e.g. EEA & Bourdeau 1995).

The increase in precipitation with elevation is evident worldwide, and commonly approximate a linear form (Osborn 1984). However, because of the various interactions of elevation with wind direction, topography, latitude and distance to the coast, it is very difficult to provide a simple way to represent the independent effect of elevation, and authors as Daly *et al.* (1994) proposed a statistical-topographic model for use over mountainous terrain where precipitation-elevation regressions were estimated in independent slopes. These authors further indicate that the coefficients of the different regressions can be quite variable, ranging from increases of precipitation of 250 mm per kilometer of elevation in low precipitation regions to more than 2,000 mm/km in high precipitation areas. As a consequence, the authors proposed that the regression slopes could be expressed as a proportion of the average precipitation of the area, indicating increases in precipitation in the range of 0.6 to 1.3 km^{-1}.

The above discussion refers to general patterns, as local topography influences local climate patterns, therefore a portion of the variability of temperature and precipitation may be explained using topoclimatic models (Dobrowski *et al.* 2009). These models allow the use of both regression modeling and interpolation methodologies for climatic dataset creation. In particular, multiple regression statistics have proved to be useful in examining climate data and can be used to develop relationships between topographic variables and temperature and precipitation at locations of measured climate data. These relationships can then be applied to areas possessing appropriate topographic data but lacking measured climate information (Brown & Comrie 2002).

This study examines the relationship between terrain and location variables with average monthly temperature and precipitation by estimating multi-regression models. The approach aims to use simple models for a better understanding of the exogenous factors that can lead to an explanation of climatic patterns.

Going a step further, we discuss how the models developed may be useful to define the boundaries of the Mediterranean region taking into account the limits of temperature suggested by Pavari (1954) and the relationships between temperature and precipitation proposed by Gaussen and de Phillips (1958) in the preparation of the bioclimatic map of the Mediterranean (UNESCO-FAO, 1963).

The analysis is based on data from the Food and Agriculture Organization of the United Nations (FAO) and World Climate.

Methods

Study area

While the focus of the research is the Mediterranean region, the network of meteorological stations used in the analysis was defined as the area from 25° to 70°N and 35ºW to 50°E (Figure 2) to cover neighboring regions, so that possible edge effects arising from interpolation were minimized.

The study region is characterized by extremely varied physiology, ranging from isolated and extended mountain ranges to low-elevation deserts.

Climate data

Monthly mean temperature (°C) and total precipitation (mm) data were obtained from FAO and World Climate Data, as averages for periods varying between 30 and 90 years in the last century, for a total of 2,086 weather stations around Europe and North Africa (Figure 2). FAO data accounted for one third of the stations considered and included almost all the stations in Europe. Stations located in North Africa and Euro-Asia were taken from World Climate. In instances, where individual reporting stations contained partial or no data (e.g. a missing monthly value), they were omitted from the analysis.

Explanatory Variables

Using the geographic information system ArcGIS, an initial set of terrain and location variables were developed in order to be used as regression predictor variables. The 1 × 1 km DEM developed by the United States Geological Survey, the gtopo30 DEM, was used to provide topographic data for the study region. However due to the great extension of the study area, a resample of 10 x 10 km proved to be the manageable solution for variables development. Latitude and longitude were also calculated at 10 × 10 km resolution for each grid cell using the DEM grid as a ref-

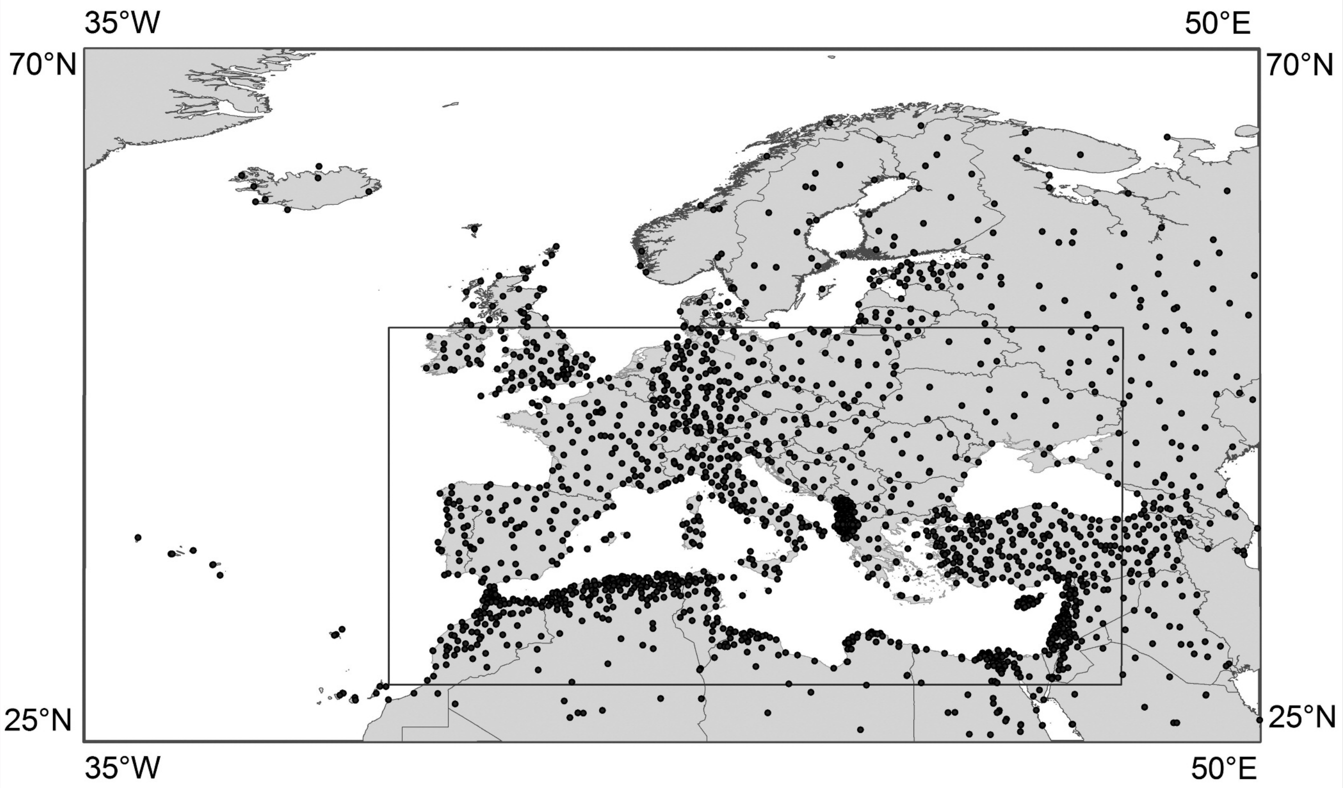

Figure 2 – The study area encompasses the Mediterranean region, with data also collected from portions of the surrounding countries. Locations of FAO and World Climate weather stations are shown.

erence. Using an ArcGIS extension, the near distance to coast line was also calculated.

Summary statistics of latitude, longitude, elevation and distance to coast are provided in Table 1.

Table 1 – Summary statistics of explanatory variables used in model development.

	Mean	Minimum	Maximum	Std. Deviation
Latitude (ºN)	45.7	25.5	69.7	13.5
Longitude (ºE)	11.5	–31.1	50.0	28.1
Elevation (m)	228.3	0.0	3109.0	493.6
Distance (km)	132.5	0.0	964.0	206.4

Results

Temperature Model

The strong relationship expected between average annual temperature and latitude is very dominant in our dataset (Figure 3).

The effect of latitude (Lat in ºN) was thus modeled as a constant cooling rate. The "continentality" was expressed by two variables, distance to the coast (Dist in km), and longitude (Lon in ºE), and also assumed as having a linear effect. Finally, as discussed above, the effect of elevation (Elev in km) was assumed to be linear.

The average monthly temperatures (and annual average) were then estimated with SPSS Statistics for Windows, Version 22.0 (IBM Corp. 2013) by a weighted multiple linear regression using the area of Thiessen polygons as weight, because the stations are not uniformly distributed across the study area.

The independent variables used in the regression models were latitude, longitude, elevation, and distance to coastline, as a stepwise selection method, using $p = 0.05$, indicated that all independent variables should be included in the model. In fact, all variables were statistically highly significant (p lower than 0.001).

The analysis was performed for every month and for the annual average. The linear equations fitted to the temperature data from the 2086 weather stations was of the form:

$$\text{Temp (ºC)} = a + b\ \text{Lat (ºN)} + c\ \text{Lon (ºE)} + d\ \text{Dist (km)} + e\ \text{Elev (km)}$$

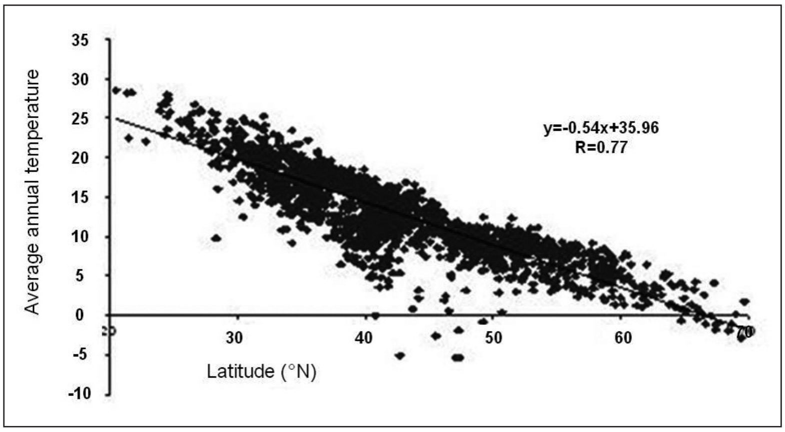

Figure 3 – Decrease in average annual temperature with latitude based on data from the 2,086 weather stations analyzed. A reasonable good fit of the equation (R square 0.77) indicates a linear trend with a general decrease of 0.54°C per degree of latitude.

Table 2 shows the regression parameters estimated for each month, and for the annual average, as well as the corresponding coefficient of determination.

The analysis of the parameters estimated indicates that the intercept (a) behaves as expected, following the seasonal variation of the temperatures, with the highest values in August and September.

The negative effect of latitude in temperature (b) is clear throughout the year, but less pronounced in summer.

The two variables associated with "continentality", longitude (c) and distance to the coast (d) show the same seasonal pattern, with positive values (higher temperatures) in summer and negative values (lower temperatures) in winter, as expected.

The effect of elevation (e) in decreasing temperature is also obvious throughout the year but, as with latitude, the effect is also less pronounced in summer. The values estimated, a decrease of temperature between 3.5 ºC and 6.5 ºC per kilometer of elevation are only a little lower than the "moist adiabatic lapse rate" suggested by MacArthur (1984) to be around 6 ºC km^{-1}.

Overall, the fit of the models can be considered good (R square always above 0.89).

Globally, the exercise showed that simple models can really be used as a general approximation to the distribution of temperatures throughout the year.

The models were used, as explained below, to build the final maps.

Precipitation Model

The data from 2,086 weather stations around Europe and North Africa allow for a good demonstration of the influence of latitude on annual precipitation (Figure 4).

A preliminary exploratory analysis confirmed a non-linear relationship between annual precipitation total and latitude (Figure 4). Different non-linear alternatives were explored and selection was made based on the known relationships between precipitation and explanatory variables discussed above. The component of latitude was modeled as an equation of the logistic type:

$$\exp \{a/[1 + \exp (b * (Lat – c))]\}$$

Table 2 – Parameters of the equations relating temperature with latitude, distance to coast, longitude, and elevation for the various months, based on the 2,086 weather stations analyzed. Coefficients of all variables are highly significant (p < 0.001).

Month	a (°C)	b (°C/°N)	c (°C/°E)	d (°C/km)	e (°C/km)	R square
January	35.7	– 0.62	– 0.16	– 0.0082	– 6.28	0.924
February	36.5	– 0.63	– 0.14	– 0.0058	– 6.23	0.912
March	37.0	– 0.61	– 0.09	– 0.0020	– 5.79	0.924
April	37.4	– 0.56	– 0.02	0.0037	– 5.81	0.937
May	38.0	– 0.51	0.03	0.0066	– 5.19	0.931
June	39.7	– 0.48	0.06	0.0069	– 4.75	0.915
July	41.3	– 0.47	0.07	0.0059	– 3.48	0.892
August	43.5	– 0.52	0.05	0.0045	– 3.97	0.902
September	43.9	– 0.57	0.01	0.0016	– 5.10	0.932
October	42.4	– 0.60	– 0.03	– 0.0022	– 5.97	0.936
November	38.9	– 0.61	– 0.08	– 0.0050	– 6.17	0.946
December	36.2	– 0.60	– 0.12	– 0.0078	– 6.53	0.936
Annual	**39.2**	**– 0.56**	**– 0.04**	**– 0.0002**	**– 5.44**	**0.942**

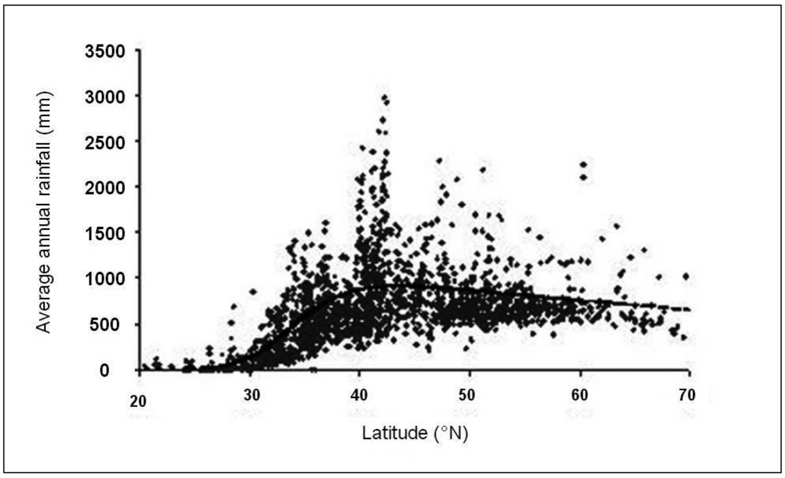

Figure 4 – Average annual rainfall in 2,086 weather stations in Europe and North Africa as related to latitude between 20° and 70°N. It is clearly apparent the latitude of the deserts below 30°N.

where a, b and c are fitted parameters. The value of c has units of latitude and is related with the latitude of the Azores High.

The components related to location and to elevation assume a multiplicative effect, with the parameters d, e, and h indicating proportional increases, or decreases:

$$(1 + d * Lon + e * Dist) * (1 + h * Elev)$$

The variables Lat, Lon, Dist, Elev are the same as in the Temperature Model.

A full non-linear model with all the components was then used. As for temperature, and because weather stations were not uniformly distributed across the study area, we used the area of Thiessen polygons as a weight variable. The contribution of all variables was highly significant (p lower than 0.001). Model fitting was done using the Non-Linear Model Option in SPSS and the Levenberg-Marquardt method.

The full model is of the form:

$$\text{Prec (mm)} = \exp \{a/[1 + \exp (b * (Lat - c))]\} * (1 + d * Lon + e * Dist) * (1 + h * Elev)$$

In Table 3, we show fitted parameters as well the coefficient of determination (R^2). These models were used, as explained below, to build the final maps.

It is concluded from this analysis that precipitation is more predictable during the summer months June, July and August (R square > 0.77) than in other periods of the year. Precipitation patterns are very much determined by the value of the parameter c, reflecting the changes in the latitudinal position of the cyclonic centers. Changes in summer precipitation patterns based on changes of the latitudinal position of the Azores High can now be predicted.

The influence of "continentality", represented by the parameters associated to longitude (d) and to distance to the coast (e) show that the negative effect is much more pronounced in winter.

The values for the parameter associated to the effect of elevation (h) are generally lower than those presented in the literature, probably because of the large area considered in this study, except for the summer months, where the values are similar to the lower limit of the range of values suggested by Daly *et al.* (1994).

Table 3 – Parameters of the equations relating precipitation with latitude, distance to coast, longitude, and elevation for the various months, based on the 2,086 weather stations analyzed. Coefficients of all variables are highly significant (p < 0.001).

Month	a	b	c (°N)	d (°E^{-1})	e (km^{-1})	h (km^{-1})	R square
January	4.59	– 0.35	25.3	– 0.0128	– 0.000307	0.205	0.635
February	4.36	– 0.30	25.2	– 0.0124	– 0.000319	0.337	0.630
March	4.37	– 0.28	26.3	– 0.0120	– 0.000271	0.290	0.661
April	4.10	– 0.31	28.9	– 0.0103	0.000004	0.527	0.702
May	4.06	– 0.40	32.8	– 0.0100	0.000226	0.786	0.762
June	4.10	– 0.34	34.9	– 0.0077	0.000543	0.783	0.791
July	4.22	– 0.22	34.9	– 0.0047	0.000384	0.780	0.779
August	4.44	– 0.21	33.2	– 0.0081	0.000117	0.343	0.770
September	4.49	– 0.40	32.2	– 0.0089	– 0.000148	– 0.186	0.606
October	4.70	– 0.26	26.8	– 0.0085	– 0.000496	– 0.049	0.561
November	4.56	– 0.26	23.2	– 0.0088	– 0.000597	0.452	0.562
December	4.58	– 0.30	24.2	– 0.0100	– 0.000487	0.324	0.591
Annual	**6.88**	**– 0.21**	**23.5**	**– 0.0101**	**– 0.000104**	**0.235**	**0.700**

Discussion on the possible uses of the models

On understanding the limits of the Mediterranean vegetation

The geographical distribution of sclerophyllous species of some typical Mediterranean genus as *Olea*, *Laurus*, or *Ceratonia*, has been studied by various authors. One of the most well-known studies of the distribution of *Olea* in relation to the number of dry months was presented by Desfontaines (1975 *in* de Montgolfier 2002) and shown in Figure 5.

Applying our models to the DEM grid (10 x10 km), it was possible to predict average monthly and annual temperature and precipitation for the whole area, and to use specific thresholds to estimate the geographical limits of the Mediterranean climate. In order to estimate such geographical limits it was considered, based on the literature already mentioned, that the threshold for the "cold limit" could be set as 4 ºC for the average temperature of the coldest month. For the "aridity limit", the approach by Rivas Martinez (1981) was followed, and the threshold of 2 for the ratio between the total annual precipitation (in mm) and the sum of all positive monthly temperatures (in ºC) was used. The result for the geographical distribution of the Mediterranean climate based on our models and the above thresholds can be seen in Figure 6. These limits are in general agreement with the distribution of the Mediterranean "maquis" by Tomaselli (1977 *in* de Montgolfier 2002) represented in Figure 1, and with other studies about the Mediterranean climate or the distribution of Mediterranean genus as *Olea* represented in Figure 5.

On predicting the consequences of climatic changes

The models can also be used as a first approximation to estimate the effects of climate change in the Mediterranean region. In fact, during the 20th century, with an evident acceleration since 1970, climate change has already led in the Mediterranean to an average increase of temperatures of about 2 °C in the south-western Europe (Iberian Peninsula, southern France) and North African territories and rainfall decreased up to 20% in some regions of southern and eastern Mediterranean (FAO 2013).

It is also expected that ongoing climate changes continue and increase in the Mediterranean region in the next decades, mainly affecting air and sea temperatures and pre-

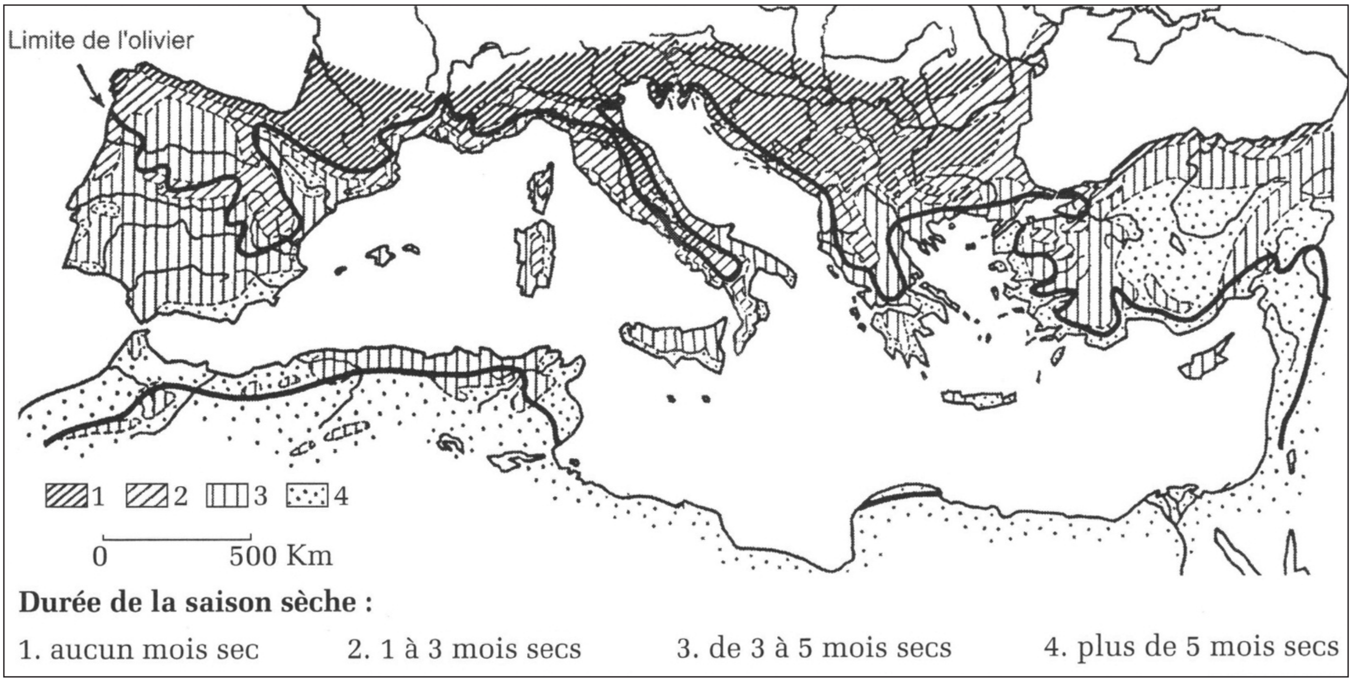

Figure 5 – Geographical distribution of the number of dry months in the Mediterranean region as compared with the limits of* Olea *(Desfontaines 1975* in *de Montgolfier 2002).
1 = no dry months; 2 = one to three dry months; 3 = three to five dry months; 4 = more than five dry months.

cipitation patterns as described in many texts as in the Strategic Framework for Mediterranean Forest (FAO 2013). By 2100, the Mediterranean climate is set to continue to change with temperatures rising further by an average of 2°C to 4°C, while rainfalls drop by 4% to 30% (IPCC 2007; FAO 2013). In accordance with the predictions, a scenario of a general increase of 2ºC and a decrease of 20% in precipitation was used resulting in a different geographical distribution of the Mediterranean climate, as shown in Figure 7.

It is apparent that aridity increases in the south and east, shifting the dry limit of the Mediterranean climate to the north. On the other hand, new areas in the north will change to a Mediterranean type of climate, from the French Landes to large areas in Turkey.

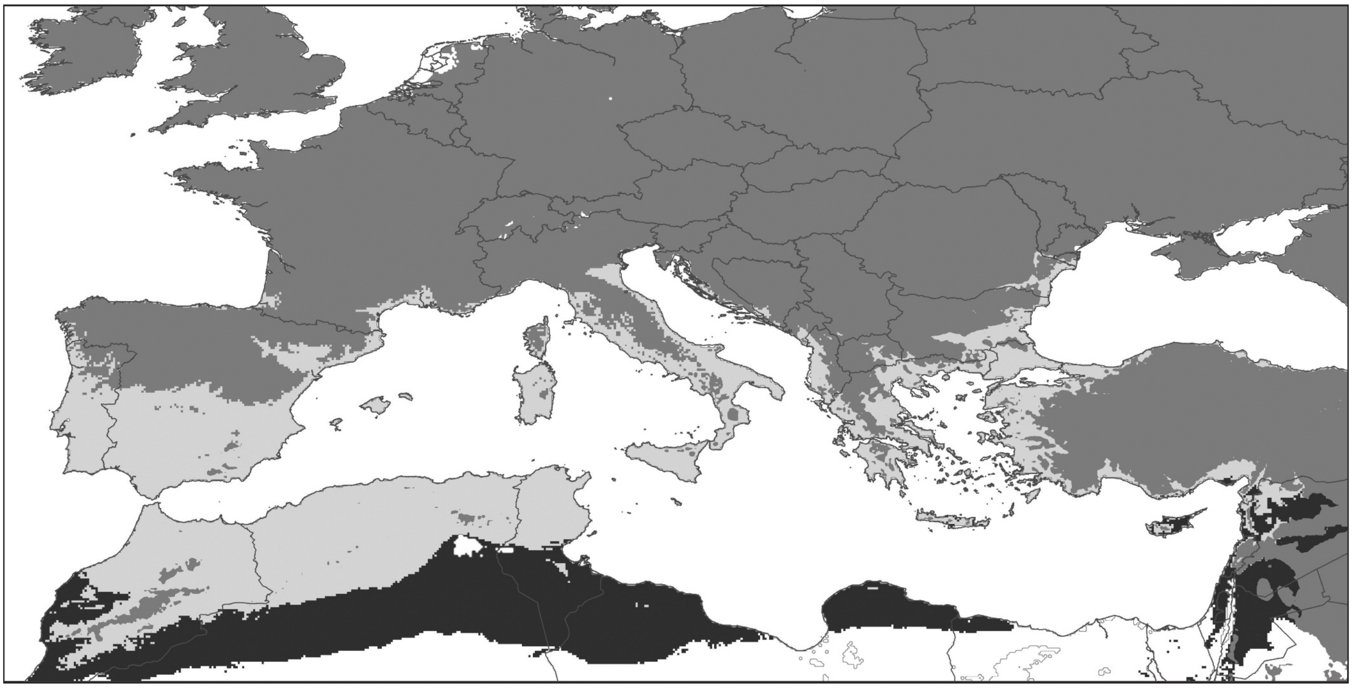

Figure 6 – Current geographical distribution of the Mediterranean climate resulting from the models developed using the temperature and aridity limits mentioned in the text.

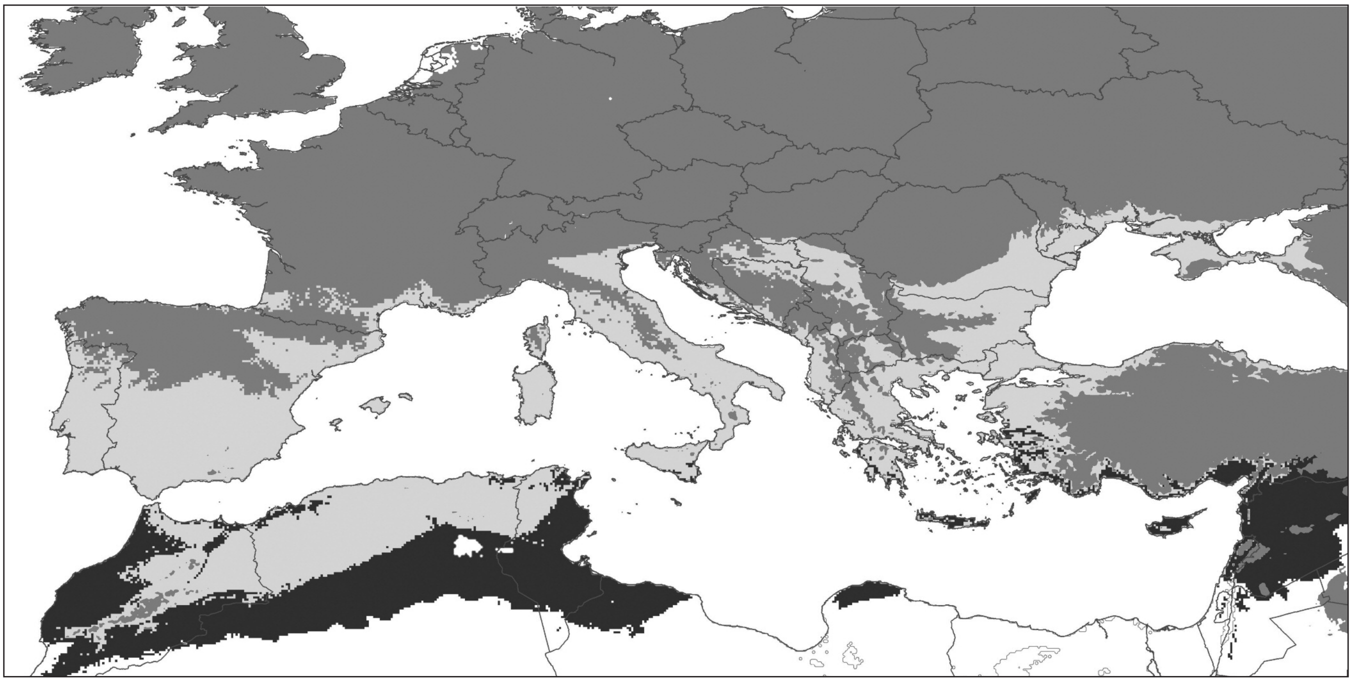

Figure 7 – Scenario of climate change with increased temperature and decreased precipitation as described in the text.

Other possible uses of the models

These models can also be used, for example, to assist in predicting future distribution of species using, for example, niche-based models of species climatic envelops as proposed by Thuiller *et al.* (2005). These distributions are commonly associated to thresholds in average temperature or precipitation in specific periods (months or seasons). Using this type of models it is possible to evaluate the spatial distribution of a species as a function of geographic location, distance to coast and elevation.

The results confirm, at the scale of the Mediterranean region, that simple equations can explain a relatively important proportion of the variations of temperature and precipitation in the Mediterranean region. The simplicity of these models relies on the fact that they use spatial variables that are widely available or computed in GIS (latitude, longitude, elevation, and distance to the coast), and that they confirm the general effects of those variables in temperature and precipitation. This is particularly important when global models tend to be so complex that it becomes difficult to decode the relative importance of the various factors involved in the vegetation distribution.

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Approche syntaxonomique et écologique des formations à Genévrier thurifère (*Juniperus thurifera* L.) dans les Alpes françaises

Syntaxonomic and ecological approach of Juniperus thurifera *L. stands in the French Alps*

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Résumé

*Le Genévrier thurifère (*Juniperus thurifera *L.) des montagnes de l'ouest de la Méditerranée a fait l'objet de plusieurs études phytosociologiques sur l'ensemble des Alpes françaises. Sa répartition dessine un croissant continu allant du sud du massif des Bauges à la Tinée épousant l'ancien front glaciaire, quelques stations colonisent les vallées internes de l'Oisans et la Haute Durance. Une analyse de 213 relevés phytosociologiques stratifiés réalisés sur l'ensemble de son aire alpine française, couplée à une analyse des conditions climatiques nous permet de proposer une cartographie et une synthèse syntaxonomique de ses populations. À l'étage de végétation supraméditerranéen inférieur, le Genévrier thurifère ne fait qu'effleurer la série du Chêne vert (*Quercus ilex *L.) de la classe du* Quercetea ilicis *et de l'alliance du* Quercion ilicis*, alors qu'à l'étage supraméditerranéen et méditerranéo-montagnard il domine dans l'aire du Chêne pubescent (*Quercus pubescens *Willd.) avec ou sans le Buis (*Buxus sempervirens *L.) qui correspond à la classe du* Querco roboris-Fagetea sylvaticae *et de l'alliance du* Quercion pubescenti-sessiliflorae*. Les formations primaires arbustives associées de la classe du* Crataego monogynae-Prunetea spinosae *et de l'alliance du* Berberidion vulgaris *se retrouvent sur l'ensemble de sa répartition alpine alors que dans l'étage montagnard des Alpes internes sèches, les pinèdes sylvestres à Genévriers* spp. *appartiennent à la classe oro-méditerranéenne du* Pino sylvestris-Juniperetea sabinae *et de l'alliance du* Juniperion thuriferae *décrite d'Espagne et indiquée comme présente en France par le Prodrome des végétations de France (Bardat* et al. *2004) et des cahiers d'habitats Natura 2000.*

Abstract

*The thuriferous juniper (*Juniperus thurifera *L.) phytosociology of the western part of Mediterranean Basin and French Alps has been well studied. Its distribution within the French Alps is crescent shaped. It follows the last glacial maximum delimited by the French pre-Alps range (from the Bauges mountain to the Tinée region); some scattered populations persist along the dry continental valleys of Oisans and High-Durance. Our work is to draw up a syntaxonomic synthesis and a cartography of French alpine populations. Thuriferous juniper of the supramediterranean range belongs to the class of White oak (*Quercus pubescens *Willd.) and associated shrubs vegetation (*Querco roboris-Fagetea sylvaticae*:* Quercion pubescenti-sessiliflorae*; and* Crataego monogynae-Prunetea spinosae*:* Berberidion vulgaris*). In mesomediterranean range it belongs closely to the Evergreen Oak (*Quercus ilex *L.) class (*Quercetea ilicis*:* Quercion ilicis*), but in dry valleys of the mountain range it belongs to the class of* Pino sylvestris-Juniperetea sabinae*:* Juniperion thuriferae *described from Spain and indicated in the French phytosociological nomenclature (Bardat* et al. *2004).*

Mots clés : bioclimatique, flore des Alpes, *Juniperus thurifera* L., *Juniperion thuriferae*, orophytes, phytosociologie.

Keywords: *Juniperus thurifera* L., *Juniperion thuriferae*, flora of the Alps, orophytes, bioclimatic, phytosociology.

Introduction

En 1787, sur la commune de Mont-Dauphin, Dominique Villars signale pour la première fois le Genévrier thurifère sous le nom de *Sabina arborescens*. Il faudra attendre une centaine d'années pour que l'espèce soit reconnue en France sous le nom de *Juniperus thurifera* L. var. *gallica* de Coincy (de Coincy 1898). Depuis, sa connaissance systématique, chorologique et écologique s'est considérablement améliorée. L'intérêt des forestiers dès le début du XX^{e} siècle pour la prestigieuse forêt de Saint-Crépin est à la base de nouvelles études qui, jusqu'aux années 1950, ont concerné principalement sa distribution. Braun-Blanquet (1922) indique que la végétation herbacée de Saint-Crépin paraît « tout à fait indépendante du Genévrier thurifère ». Guinier (1929) indique : « Saint-Crépin est une forêt très claire de petits arbres épars, le sol intensément pâturé ne porte qu'une végétation pauvre et discontinue. » Widmann (1950) dans son étude très complète sur les Genévriers thurifères (*Juniperus thurifera* L.) des Hautes-Alpes apporte des données nouvelles sur son écologie, sa biologie et sa répartition. La phytosociologie est abordée par Archiloque & Borel (1965) ; dans les Alpes-de-Haute-Provence, ils indiquent les « caractéristiques présumées ou locales du groupement » et proposent pour les Alpes du Sud de rattacher les habitats de l'espèce dans une série du Genévrier thurifère, incluse dans la série supraméditerranéenne du Chêne pubescent (*Quercus pubescens* Willd.), vicariant à cet étage de la série du Chêne vert (*Quercus ilex* L.). Ozenda (1966 ; 1981) ne reconnaît pas la série du Genévrier thurifère d'Archiloque et Borel, mais uniquement un faciès à Genévriers thurifères, voire une sous-série des chênaies pubescentes. Gamisans & Gruber (1980) décrivent dans la Drôme une association du *Buxo sempervirentis-Quercenion pubescentis* Br.-Bl. 1961 à Genévrier thurifère, et bien que plusieurs espèces indicatrices et préférentielles du *Pino sylvestris-Juniperetea sabinae* Rivas Martinez 1964 soient présentes, la balance floristique tranche en faveur du *Quercion pubescentis-sessiliflorae* Br.-Bl., *Buxo sempervirentis-Quercetum juniperetosum thuriferae* Gamisans & Gruber 1980.

De Foucault (1991) précise dans sa synthèse des végétations arbustives que l'on peut isoler les arbustes formant un fourré xérophile et primaire de corniches et de parois calcaires dans lequel le Genévrier thurifère est associé à *Juniperus communis* L., *Amelanchier ovalis* Medik., *Cotinus coggygria* Scop. ; il précise alors l'association : *Amelanchiero ovalis-Juniperetum thuriferae* (Archiloque & Borel 1965) de Foucault 1991.

Borel & Polidori (1983) indiquent que le boisement de Genévrier thurifère du vallon de Mollières (Alpes-Maritimes) s'individualise bien dans une lande à buis et Genêt cendré (*Genista cinerea* (Vill.) DC.) pictée de rares Chênes pubescents. Vers 1 400 m, il pénètre dans la pinède sylvestre, alors que dans les zones les plus basses, il est dans une buxaie dense à Chêne pubescent ; mais le cœur du peuplement constitue une formation originale où le Genévrier thurifère s'associe au Genévrier oxycèdre (*Juniperus oxycedrus* L.) et à la Bruyère arborescente (*Erica arborea* L.). Il est très rarement avec le Genévrier de Phénicie (*Juniperus phoenicea* L.) et le Chêne vert (*Quercus ilex*). Barbero & Quezel (1986) proposent plusieurs ensembles en considérant les situations écologiques et biogéographiques : (1) les thuriféraies supraméditerranéennes inférieures se développent entre 750 et 1 100 m et les espèces des boisements des chênaies vertes sont fréquentes ; malgré cela ils ne rattachent pas ces thuriféraies au *Quercetea ilicis* Br.-Bl. mais bien dans la série méditerranéenne inférieure du Chêne pubescent thermophile ; (2) les thuriféraies supraméditerranéennes typiques, préalpines, plus alticoles que la précédente ; ces thuriféraies dominent les espèces du *Quercion pubescentis-sessiliflorae* Br.-Bl. ; (3) les thuriféraies montagnardes en deux types, l'une des Alpes internes et l'autre oro-méditerranéenne. Cette dernière synthèse constitue la base de travail des cahiers d'habitats décrivant les boisements de Genévriers thurifères en France (Bensettiti *et al.* 2001). En 2008, Vagge & Biondi décrivent le *Junipertum communis-thuriferae* que nous évoquerons ci-après.

Depuis 1995, le Conservatoire botanique national alpin (CBNA) a initié plusieurs études : Lathuillière (1994) réalise une synthèse complète de l'espèce sur les Alpes ; Garraud & Villaret (2000) précisent son écologie et les cortèges floristiques associés ; puis Coussy (2008b) et Fertin (2010) étudient la dynamique des peuplements.

La répartition du Genévrier thurifère est aujourd'hui mieux connue, avec plus de 1 800 relevés floristiques dans les Alpes sur une période de 220 ans. L'espèce est présente sur six départements français (Isère, Drôme, Savoie, Hautes-Alpes, Alpes-de-Haute-Provence et Alpes-Maritimes) correspondant à 187 communes. Son aire de répartition dans les Alpes du Sud (figure 1) couvre 8 600 ha environ (Coussy 2008a) répartis sur trois secteurs biogéographiques bien connus mais aux limites mal définies : les Alpes internes schématiquement caractérisées par un climat froid et sec, les Préalpes méridionales au climat chaud et sec et les Préalpes septentrionales au climat frais et humide.

Disposant aujourd'hui d'un matériel phytosociologique plus conséquent et de données climatiques à l'échelle de l'aire de distribution de l'espèce, nous proposons une mise à jour des connaissances en précisant l'écologie et la phytosociologie de l'espèce à partir de 213 relevés phytosociologiques originaux, tout en mettant en perspective nos travaux avec ceux de nos prédécesseurs.

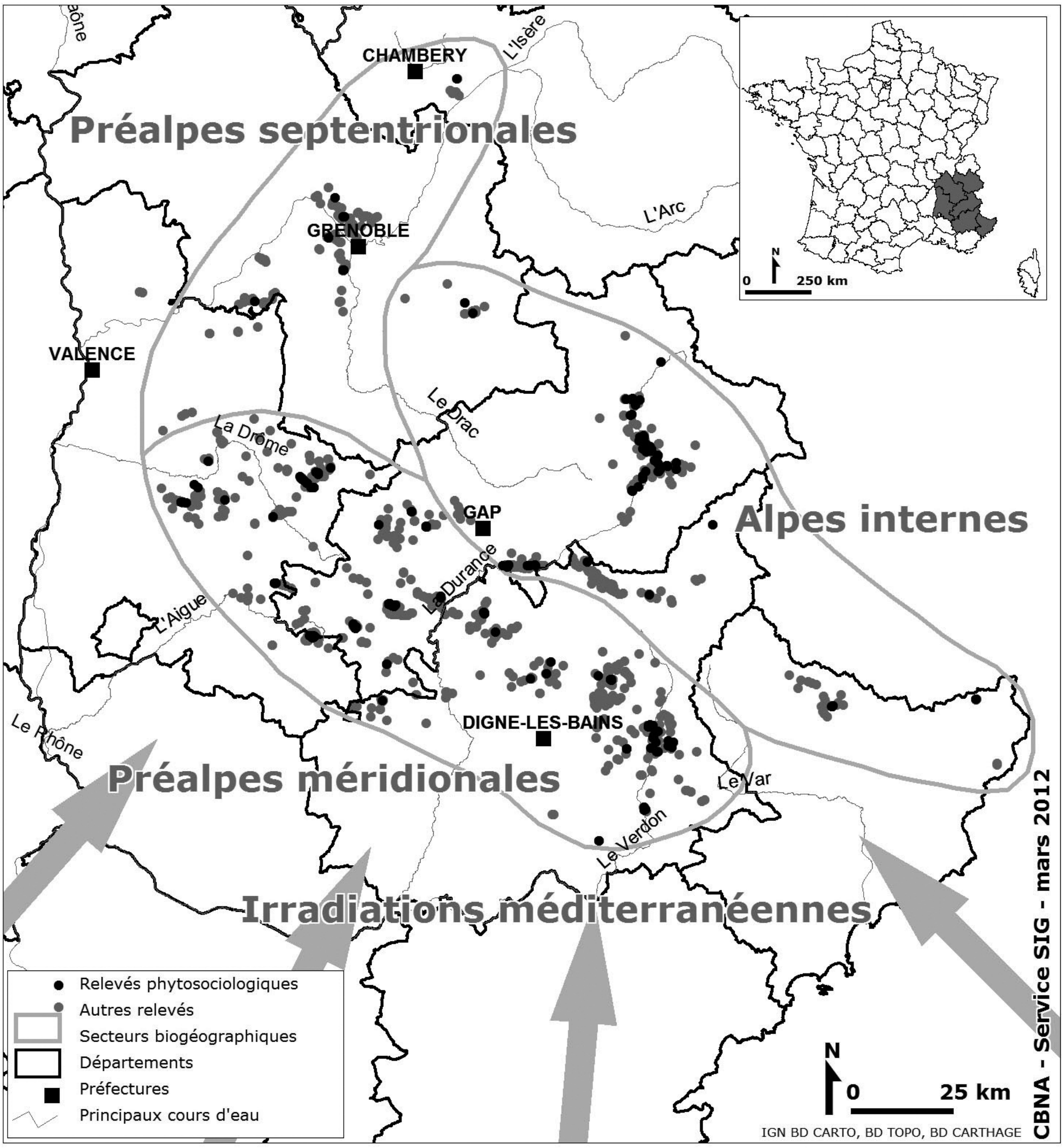

Figure 1 – Carte de répartition des relevés floristiques et phytosociologiques de *Juniperus thurifera* L.

Figure 1 – Distribution of phytosociological and floristical relevés of* Juniperus thurifera *L.

Méthodes

À partir des données existantes, nous souhaitons affiner l'écologie de *Juniperus thurifera*, déterminer quels sont les cortèges floristiques qui l'accompagnent mais aussi quelles sont les conditions climatiques qui lui sont favorables. En effet, de la Drôme méditerranéenne jusqu'aux vallées glaciaires des Alpes, sa répartition actuelle semble être héritée d'une succession de migrations liées aux différentes phases climatiques (glaciaire-interglaciaire). L'objectif est donc de faire émerger les différentes conditions écologiques en mettant en perspective les résultats des analyses phytosociologiques avec les conditions climatiques sur l'ensemble de son aire alpine française.

Analyses phytosociologiques

Le jeu de données initial comprend l'ensemble des relevés de végétation au nombre de 1 878. Ce lot compte 350 relevés phytosociologiques, mais nous n'avons retenu que les relevés phytosociologiques stratifiés. Il s'agit de relevés réalisés selon la méthode dite classique de l'école zuricho-montpelliéraine. Nous retiendrons cinq strates (arborée, arbustive, sous-arbustive, herbacée et muscinale) qui reflètent une bonne partie de la structure de végétation. Il nous paraît important de conserver cette approche stratifiée, afin de distinguer les relevés comprenant des Genévriers thurifères de classes d'âge différentes. Au final, 213 relevés phytosociologiques stratifiés sont retenus. Si l'on considère que les relevés existants reflètent la répartition actuelle de l'espèce, alors la population statistique recouvre bien l'aire de répartition (figure 1), puisque les relevés phytosociologiques, bien qu'en plus faible nombre, couvrent l'ensemble des populations recensées. Nous pouvons cependant noter des zones surprospectées correspondant au secteur de Saint-Crépin, considéré pendant longtemps comme la population de référence. Les peuplements sur pentes raides et parois des Préalpes méridionales sont par ailleurs sous-prospectés alors qu'ils concernent un grand nombre de populations de Genévrier thurifère. Nous précisons donc que l'échantillonnage n'est ni systématique ni stratifié, ce qui induit un biais dans l'analyse ; il est cependant spatialement bien réparti et moyennement représentatif.

Tableau 1 – Liste des variables climatiques issues du modèle Météo France AURELHY (Bénichou & Le Breton 1987) à 1 km de résolution, désagrégé à 100 m (W. Thuiller).

Table 1 – List of climatic factors from Météo France AURELHY model with a 1 km spatial resolution (Bénichou & Le Breton 1987), disaggregated to 100 m (W. Thuiller).

Bio1	Annual Mean Temperature
Bio2	Mean Diurnal Range (Mean of monthly (max temp-min temp))
Bio3	Isothermality (Bio2/Bio7) (* 100)
Bio4	Temperature Seasonality (standard deviation *100)
Bio5	Max Temperature of Warmest Month
Bio6	Min Temperature of Coldest Month
Bio7	Temperature Annual Range (Bio5-Bio6)
Bio8	Mean Temperature of Wettest Quarter
Bio9	Mean Temperature of Driest Quarter
Bio10	Mean Temperature of Warmest Quarter
Bio11	Mean Temperature of Coldest Quarter
Bio12	Annual Precipitation
Bio13	Precipitation of Wettest Month
Bio14	Precipitation of Driest Month
Bio15	Precipitation Seasonality (Coefficient of Variation)
Bio16	Precipitation of Wettest Quarter
Bio17	Precipitation of Driest Quarter
Bio18	Precipitation of Warmest Quarter
Bio19	Precipitation of Coldest Quarter

Ensuite, nous avons réalisé une classification phytosociologique à partir de la composition spécifique et des strates de végétation à l'aide du logiciel libre Juice 7.0. Le module Mulva-5 permet de réaliser une analyse statistique multivariée et une classification du jeu de données. L'analyse porte sur l'abondance des espèces au sein des relevés. Les similarités sont établies par une méthode d'ordination selon la distance de Chord et les groupes de l'arborescence définis par la méthode de Ward. Les indices de fidélité et de fréquence des espèces sont calculés pour chacun des groupes. Les espèces à forte fidélité représentent les espèces diagnostiques d'un groupe.

Analyses statistiques des données climatiques

Grâce au travail et à la collaboration de W. Thuiller (UMR 5553, Laboratoire d'écologie alpine), nous avons utilisé les données climatiques issues du modèle Météo France AURELHY à 1 km de résolution (Bénichou & Le Breton 1987), désagrégé à 100 m de résolution sur les Alpes françaises. Nous réalisons ensuite des analyses en composantes principales (ACP) et des diagrammes écologiques des données climatiques sur les résultats de la classification avec le logiciel libre de statistique R. Les ACP permettent de sélectionner les variables climatiques les plus significatives pour l'analyse car nombre d'entre elles apportent des informations redondantes (tableau 1). Quelles variables climatiques discriminent le mieux les groupes issus de la classification ? Afin de répondre à cette question, nous procédons à des analyses discriminantes (Carraro & Badea 2007 ; Dolédec *et al.* 1997). Cette méthode permet d'étudier ce qui distingue les différents groupes issus de la classification en tenant compte des variables climatiques simultanément. Elle permet au final de valider notre classification phytosociologique.

Résultats

Le dendrogramme (figure 2) illustre la classification phytosociologique et ordonne les relevés. Afin de conserver un maximum de précisions dans l'analyse, nous optons pour une classification en seize classes correspondant à un niveau de précision jusqu'au rang de la sous-association et même du faciès. Pour l'analyse phytosociologique détaillée, nous utilisons les seize classes, et pour l'analyse combinée des données climatiques les huit groupes (figure 2). Quatre grands embranchements se dégagent de la classification (figure 2) :

I – correspond aux anciens parcours, zones pâturées et anciennes pâtures en reconquête par *Juniperus thurifera*, essentiellement sur le secteur de Saint-Crépin ;

II – regroupe les fruticées d'amélanchier (*Amelanchier ovalis*), dont celles accompagnées du buis (*Buxus sempervirens*), avec un gradient d'ouverture du couvert végétal qui apparaît dans l'ordination : les relevés aux sols les plus écorchés correspondent aux embranchements situés le plus à droite ;

III – concerne les thuriféraies à Pin noir (*Pinus nigra* Arnold subsp. *nigra*) et Pin sylvestre (*Pinus sylvestris* L.) ;

IV – concerne les relevés atypiques de Saint-Genis et des Alpes-Maritimes qui se distinguent par des cortèges floristiques différents des autres groupes.

Le tableau synoptique résultant de la classification ordonne les espèces par leur fréquence et leur fidélité au sein des seize classes. Les tris permettent de diagonaliser le tableau et de faire émerger les espèces caractéristiques des classes (celles qui ont une forte fidélité). Cette table offre une lecture assez claire des cortèges floristiques, mais cette méthode seule ne permet pas de trancher sur des questions d'écologie et de rattachement syntaxonomiques.

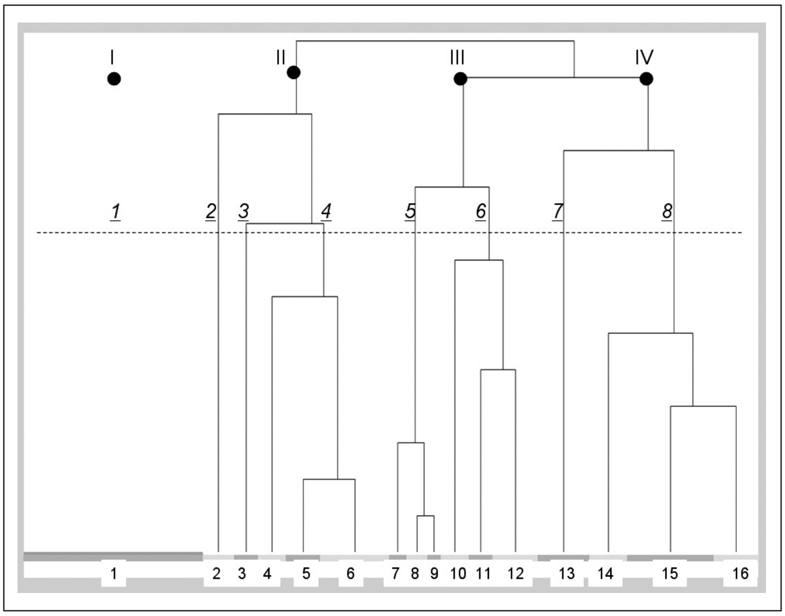

Figure 2 – Dendrogramme de la classification phytosociologique en 16 classes.
Numérotation de I à IV : les embranchements principaux ;
Numérotation de 1 à 8 en italique et souligné : les groupes sujets à l'analyse climatique ;
Numérotation de 1 à 16 : les classes issues de l'analyse phytosociologique détaillée.

Figure 2 – 16 classes of the phytosociological classification dendrogram.
In Roman letters, I to IV : main vegetation type classes.
1 to 8 numbers, italic and underline font : climatic analysis groups.
1 to 16 numbers : 16 classes from the detailed phytosociological analysis.

Nous croisons donc les résultats de la classification avec les données climatiques et réalisons des analyses discriminantes (figure 3) afin de déterminer quelles variables climatiques discriminent le mieux les huit groupes de la classification. Les précipitations annuelles (variable Bio12, en mm x 10), la température moyenne annuelle (variable Bio1, T °C x10) et la température moyenne du trimestre le plus froid de l'année (variable Bio11, T °C x10) sont celles qui discriminent le mieux les huit groupes retenus (figure 3, graphique "Canonicals weights"). Nous ajoutons à l'analyse la variable « altitude des relevés » car elle informe sur le caractère montagnard des cortèges floristiques.

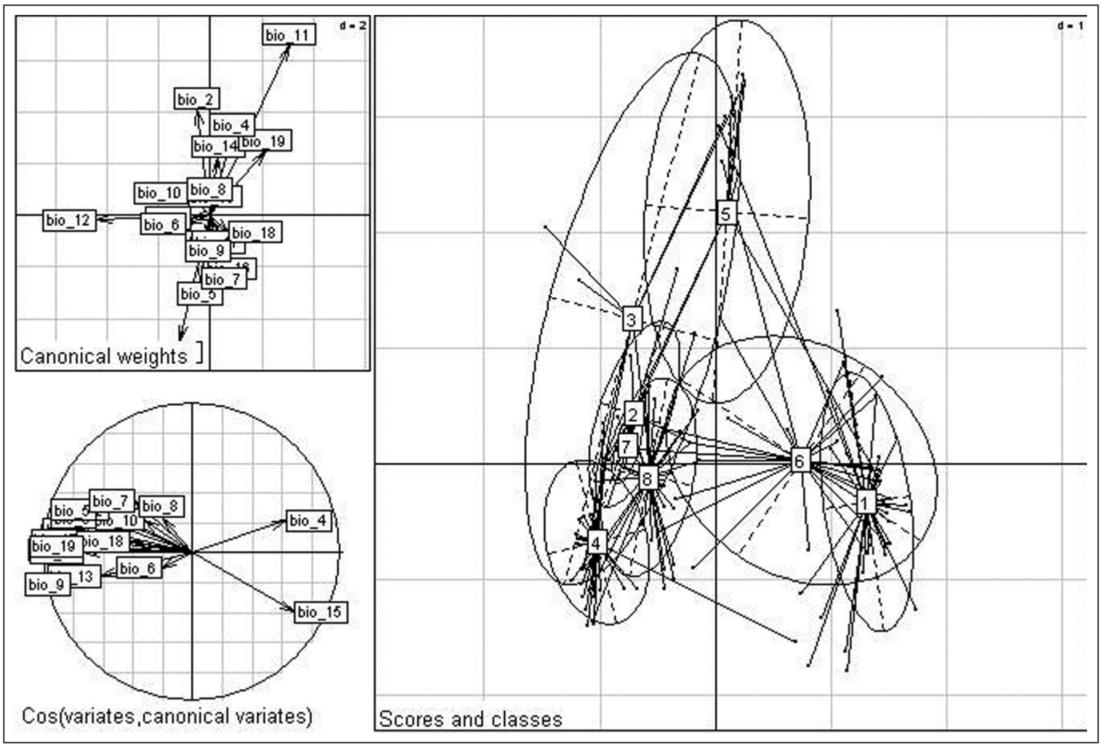

Figure 3 – Résultats graphiques de l'analyse discriminante. bio_1 à bio_19 correspondent aux variables climatiques (tableau 1). Les chiffres de 1 à 8 sont les groupes sujets à l'analyse climatique (figure 2).

Figure 3 – Graphics from discriminant analysis. bio_1 to bio_19 are the climatic factors (Table 1). Numbers 1 to 8 are the climatic analysis groups (Figure 2).

Caractéristiques climatiques des différentes thuriféraies

Les diagrammes représentant les précipitations annuelles (figure 4) et les indices d'aridité (figure 5) de De Martonne (De Martonne 1926) permettent de faire émerger les groupements soumis aux conditions climatiques les plus arides, avec des précipitations annuelles inférieures à 800 mm et des indices d'aridité (Iar-DM) inférieurs à 45,1 : groupes 1, 5 et 6.

Les groupes 2, 3, 4, 7 et 8 sont caractérisés par des précipitations annuelles d'environ 900 mm. Les diagrammes des altitudes et des températures moyennes annuelles (figure 4) font émerger les groupements alticoles (altitude supérieure à 1 050 m) et de conditions climatiques fraîches (température moyenne annuelle entre 7 et 8 °C), il s'agit des groupes 1, 6, 7 et 8. Les groupes 2, 3, 4 et 5 sont quant à eux caractérisés par des températures moyennes supérieures à 8 °C et des altitudes inférieures à 950 m. Le diagramme des températures moyennes du trimestre le plus froid de l'année (figure 4) permet de distinguer les groupes 1, 6 et dans une moindre mesure le 8 qui correspondent à des sites soumis à un climat montagnard marqué, avec des températures moyennes du trimestre très souvent négatives. Les groupes 2, 3, 4, 5 et 7 subissent des températures plus douces puisque comprises en moyenne autour de 1 °C. Ces conditions climatiques variées nous permettent de mieux distinguer et mieux spatialiser les stations de l'espèce. Nous avons affaire à deux ensembles : (1) les groupements des vallées internes et des Alpes-Maritimes (groupes 1, 6 et 8) caractérisées par des altitudes élevées, des précipitations faibles (groupes 1 et 6) et un climat montagnard marqué par un hiver froid (températures moyennes négatives du trimestre le plus froid) ; (2) les groupements situés globalement sur le croissant préalpin méridional et constituant l'aire de répartition principale de *Juniperus thurifera*, caractérisés par des altitudes légèrement inférieures, des précipitations plus abondantes et surtout une rigueur hivernale moindre traduisant un climat montagnard moins marqué. Grâce à cette approche climatique, nous appréhendons mieux l'écologie de l'espèce et clarifions ses appartenances phytosociologiques.

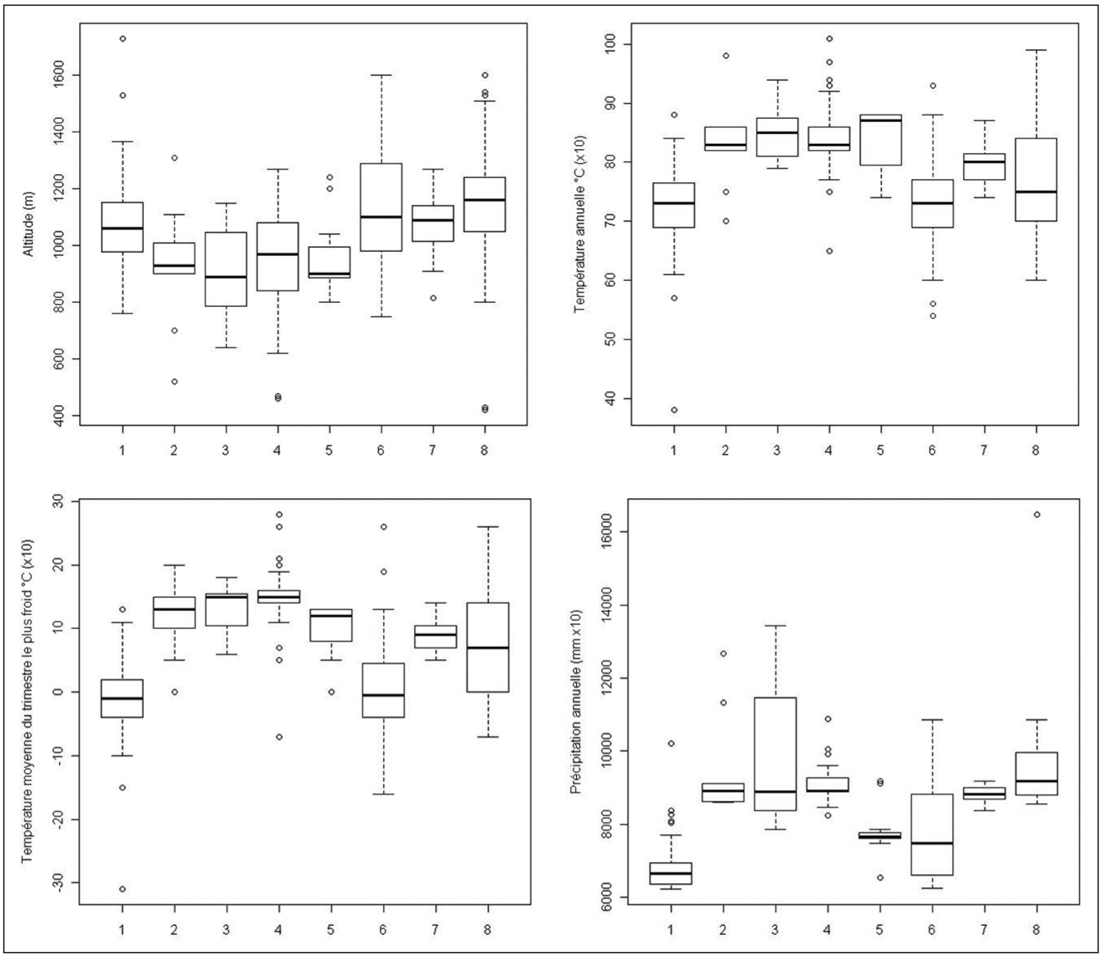

Figure 4 – Diagrammes climatiques des huit groupes issus de la classification phytosociologique concernant *Juniperus thurifera* L.

Figure 4 – Boxplots of the climatic analysis of the eight groups from the phytosociological analysis concerning* Juniperus thurifera *L.

Les habitats de *Juniperus thurifera* dans les Alpes françaises

Le tableau 2 synthétise les résultats de la classification des relevés, présente la description écologique et phytosociologique des seize classes qui figurent sur le dendrogramme figure 2. Notons que la physionomie des groupements végétaux ne facilite pas l'analyse. En effet, selon le contexte dynamique dans lequel *Juniperus thurifera* est situé, nous n'avons pas affaire aux mêmes alliances.

Des stades à fruticées jusqu'aux boisements clairs, les groupements sont à rattacher à l'alliance du *Berberidion vulgaris* Br.-Bl. (tableau 2, classes 2, 4, 6, 7 et 12), et cela indépendamment de l'âge des Genévriers thurifères. Il est fréquent que des individus de *Juniperus thurifera* aient une existence antérieure au cortège floristique environnant : nous avons relevé des fruticées dont l'ancienneté est évaluée à moins de 40 ans et qui abritent des arbres centenaires. Pour les jeunes groupements, les faciès de recolonisation, les fruticées et les landes boisées, nous soulignons d'une part l'indépendance chronologique possible entre les individus de *Juniperus thurifera* et leur environnement végétal et d'autre part la difficulté de trancher sur l'appartenance d'un groupement à une alliance préforestière plutôt que forestière. Dans l'alliance du *Berberidion vulgaris*, les groupements les plus fréquents sont les fruticées à *Amelanchier ovalis* et *Juniperus thurifera* des vires, parois et pentes rocheuses que nous rattachons à l'association *Amelanchiero ovalis-Juniperetum thuriferae* (Archiloque & Borel 1965) de Foucault 1991. Cette dernière se rencontre de 200 à 1 500 m d'altitude dans les étages collinéen, supraméditerranéen et méditerranéo-montagnard des Préalpes méridionales et septentrionales (figure 6). Dans une

Tableau 2 – Description des groupements à *Juniperus thurifera* L. des Alpes françaises.

Table 2 – Description of vegetation types for Juniperus thurifera *L. in the French Alps.*

	Description de végétation	Etages de végétation et altitudes	Répartition	Phytosociologie proposée	Espèces indicatrices	Groupes climatiques
1	Anciens parcours en voie de fermeture par les ligneux (landes à *Juniperus sabina*, garrigues et fruticées)	montagnard interne de 900 et 1600 m	Haute Durance	**Aucune:** À rapprocher du ***Juniperion thuriferae*** Rivas-Martinez 1969 et du ***Pino sylvestris - Juniperion sabinae*** (Rivas-God. 1946) Rivas-God. & Borja 1961.	*Juniperus sabina, Juniperus communis s. l., Pinus sylvestris, Berberis vulgaris.*	1
2	**Fruticée** primaire d'amélanchier à genévrier thurifère de vires et parois calcaires froides d'ubac.	du collinéen thermophile au supraméditerranéen de 200 à 1300 m	Sur l'ensemble de sa répartition : Préalpes du nord et du sud, Alpes internes et intermédiares	***Berberidion vulgaris*** Br .- Bl. ; ***Amelanchiero ovalis - Juniperetosum thuriferae*** (Archiloque & Borel 1964) De Foucault 1991	*Amelanchier ovalis*, *Saxifraga paniculata*, *Sesleria caerulea*, *Laserpitium siler*.	2
3	**Boisement** de chênes blancs et genévriers thurifères en fruticée d'Amélanchier sur vires et pentes rocailleuses thermophiles d'adret.	collinéen thermophile au supraméditerranéen de 650 à 1150 m	Verdon, moyenne Durance, Baronnies, bassin de Grenoble, Diois	***Quercion pubescenti-sessiliflorae*** Br.-Bl. 1932 ; ***Buxo sempervirentis -Quercenion pubescentis*** (Zölyomi & Jarkucs 1960) Rivas-Martinez 1972 ; ***Buxo sempervirentis-Quercetum juniperetosum thuriferae*** Gamisans et Gruber 1980	*Quercus humilis* subsp. *lanuginosa*, *Amelanchier ovalis.*	3
4	**Fruticée** primaire en buxaie claire d'amélanchier à genévrier thurifère des failles et vires de parois calcaires et pentes rocheuses thermophiles d'adret.	supraméditerranéen de 600 et 1250 m	Préalpes méridionales (Diois, Baronnies)	***Berberidion vulgaris*** Br .- Bl. 1950 ; ***Amelanchiero ovalis - Juniperetosum thuriferae*** (Archiloque & Borel 1964) De Foucault 1991	*Amelanchier ovalis*, *Buxus sempervirens*, *Thymus vulgaris, Lavandula angustifolia.*	4
5	**Boisement** de chêne blanc et genévrier thurifère en fruticée dense à buis et amélanchier sur vires et pentes rocailleuses thermophiles d'adret.	collinéen thermophile au supraméditerranéen de 700 à 1180 m	Préalpes septentrionales et méridionales en Diois, Baronnies, Buëch et Vercors	***Quercion pubescenti-sessiliflorae*** Br.-Bl. 1932 ; ***Buxo sempervirentis -Quercenion pubescentis*** (Zölyomi & Jarkucs 1960) Rivas-Martinez 1972 ; ***Buxo sempervirentis-Quercetum juniperetosum thuriferae*** Gamisans et Gruber 1980	*Buxus sempervirens*, *Amelanchier ovalis.*	4
6	**Boisement** clair de genévrier thurifère en fruticée dense à buis et Amélanchier sur vires, pentes rocheuses ou pieds de parois calcaires xérothermophiles d'adret.	collinéen thermophile au supraméditerranéen de 450 à 1250 m	Préalpes méridionales et septentrionales en Vercors, Diois et Baronnies	***Berberidion vulgaris*** Br .-Bl. 1950 ; ***Amelanchiero ovalis - Juniperetosum thuriferae*** (Archiloque & Borel 1964) De Foucault 1991	*Buxus sempervirens*, *Amelanchier ovalis*, *Thymus vulgaris.*	4
7	**Fruticée** dense mésoxérophile à cotoneaster du Dauphiné et Amélanchier sous couvert d'une pinède noire de reboisement sur pentes rocailleuses calcaires	supraméditerranéen au montagnard interne de 800 à 1240	Buëch, moyenne et haute-Durance	**Aucune: faciès de recolonisation.** À rapprocher du ***Berberidion vulgaris*** Br .- Bl 1950.		5
8 et 9	**Boisement** clair et résiduel de chêne blanc et genévrier thurifère en fruticée d'amélanchier et fustet, pistachier et staeline en mosaique d'un couvert d'une pinède noire de reboisement dense sur pentes rocailleuses marno-calcaires au supraméditerranéen inférieur (irradiation septentrionale du mésomediterranéen inférieur)	supraméditerranéen de 800 et 950m	moyenne Durance	***Quercion pubescenti-sessiliflorae*** Br.-Bl. 1932 ; ***Buxo sempervirentis -Quercenion pubescentis*** (Zölyomi & Jarkucs 1960) Rivas-Martinez 1972 ; ***Buxo semperviventis-Quercetum juniperetosum thuriferae*** Gamisans et Gruber 1980, faciès boisé en pinède de reboisement à *Pinus nigra* sur marnes.	*Amelanchier ovalis*, *Quercus humilis* ssp *lanuginosa, Cotinus coggygria, Onobrychis saxatilis, Aphyllanthes monspeliensis, Dorycnium pentaphylleum*, *Rubia peregrina, Juniperus oxycedrus,* Affinités méditerranéennes marquées par la présence de quelques espèces stenomediterranéennes *Juniperetosum oxycedrii.*	5
10	**Boisement** de pins sylvestres à genévrier thurifère sur lande à genévrier commun et au montagnard des vallées internes xérothermophiles	montagnard interne de 900 et 1600 m	Alpes internes : haute-Durance, Verdon, Haute-Bléone et Tinée et Guil	**Aucune: faciès de transition à Pinus sylvestris en recolonisation .** À rapprocher du ***Juniperetum communis – thuriferae*** (Vagge & Biondi 2008), du ***Juniperion thuriferae*** Rivas-Martinez 1969 ou du ***Pino sylvestris - Juniperion sabinae*** (Rivas-God. 1946) Rivas-God. & Borja 1961.	*Pinus sylvestris*, *Juniperus communis s. l.*, *Juniperus sabina, Arctostaphyllos uva-ursi.*	6
11	**Fruticée** pionnière à genévrier thurifère en reconquête par le pin sylvestre, sur terrasses et replats	supraméditerranéen au montagnard inférieur de 750 à 1100 m	moyenne et haute Durance, Ubaye	**Aucune: faciès de recolonisation.** À rapprocher du ***Pino sylvestris - Juniperion sabinae*** (Rivas-God. 1946) Rivas-God. & Borja 1961.	*Amelanchier ovalis*, *Pinus sylvestris*, *Cornus sanguinea, Crataegus monogyna, Juniperus communis s. l.*	6
12	**Boisement** clair et fruticée ouverte d'amélanchier et genévrier thurifère en lande à lavande sur pentes rocailleuses thermophiles	montagnard inférieur xérophile au méditeranéo-montagnard de 810 à 1460 m	Alpes internes et intermédiaires : Buëch, Oisans, haute Durance, Baronnies, haute Bléone,	**Aucune: faciès de transition.** À rapprocher du ***Berberidion vulgaris*** Br .-Bl. 1950 Faciès interne à *Lavandula angustifolia*	*Amelanchier ovalis*, *Lavandula angustifolia.*	6
13	**Fruticée** haute de genévrier thurifère à érable de Montpellier et Amélanchier en lande ouverte à lavande et armoise blanche sur vires et pentes rocheuses xérothermophiles	supraméditerranéen de 815 à 1270 m	Buëch	***Quercion pubescenti-sessiliflorae*** Br.-Bl. 1932 ; ***Buxo sempervirentis -Quercenion pubescentis*** (Zölyomi & Jarkucs 1960) Rivas-Martinez 1972, faciès à *Acer monspessulanum:* ***Aceri monspessulani - Juniperetum thuriferae ass. nov hoc loco***	*Acer monspessulanum*, *Amelanchier ovalis*, *Lavandula angustifolia, Teucrium aureum, Artemisia alba.*	7
14	**Fruticée** de genévrier thurifère colonisée par le genêt cendré et le genévrier commun au sein d'une chênaie blanche résiduelle thermophile sur vires et pentes rocheuses.	collinéen thermophile, supraméditerranéen et méditerranéo-montagnard de 420 à 1600m	Verdon, Buëch, Diois, Dévoluy, bassin de Grenoble	**Aucune: faciès de transition entre lande et boisement du *Quercion pubescenti-sessiliflorae* Br.-Bl. 1932**	*Amelanchier ovalis*, *Thymus vulgaris*.	8
15	**Boisement** de genévrier thurifère en fruticée claire à amélanchier, lavande et thym sur crêtes et pentes rocheuses de haut de versant xérothermophiles du supraméditerranéen au méditerranéo-montagnard	supraméditerranéen au méditerranéo-montagnard de 800 à 1330 m	Haute-Bléone, Dévoluy, Baronnies, Buëch et Diois, Haute-Durance.	***Quercion pubescenti-sessiliflorae Br.-Bl. 1932 ; Buxo sempervirentis-Quercenion pubescentis (Zölyomi & Jarkucs 1960) Rivas-Martinez 1972***, faciès à *Acer monspessulanum* : ***Aceri monspessulani - Juniperetum thuriferae ass. nov hoc loco***	*Acer monspessulanum, Amelanchier ovalis*, *Thymus vulgaris*, *Lavandula angustifolia.*	8
16	**Boisement** de genévrier thurifère à cade et bruyère arborescente sur pentes rocheuses siliceuses xérothermophiles du supraméditerranéen des Alpes-Maritimes	supraméditerranéen de 1100 à 1400 m	Tinée	**Aucune: faciès à *Juniperus oxycedrus* et *Erica arborea* sur substrats siliceux, marquant la transition entre l'étage méso et supra méditerranéen,** proche du ***Juniperion thuriferae*** Rivas-Martinez 1969 et du ***Quercion pubescenti-sessiliflorae*** Br.-Bl. 1932 ; ***Buxo sempervirentis -Quercenion pubescentis*** (Zölyomi & Jarkucs 1960) Rivas-Martinez 1972.	*Juniperus oxycedrus*, *Erica arborea*, *Satureja montana*, *Thymus vulgaris*.	8

moindre mesure elle pénètre aussi dans les vallées internes. Association thermophile à xérothermophile, elle présente plusieurs faciès selon les conditions hydrique, thermique et topographique : (1) un faciès à *Buxus sempervirens* L. (tableau 2, classes 4 et 6) dans les Préalpes les plus humides ; (2) un faciès à *Lavandula angustifolia* Mill. (tableau 2, classe 12) des vallées internes et secteurs méditerranéo-montagnards des Préalpes ; (3) un faciès « frais » des Préalpes septentrionales et vallées internes, des vires et parois calcaires d'ubac (tableau 2, classe 2) ; (4) des faciès de transition entre landes et boisements aux cortèges floristiques et aux limites mal définies (tableau 2, classes 7 et 14).

Les boisements plus ou moins denses, certaines fruticées hautes, plus âgées et accompagnées de peuplement mûrs, actuels ou hérités, sont à considérer comme des groupements forestiers. L'analyse des conditions climatiques distingue clairement les groupements des Alpes internes de ceux des Préalpes, appartenant respectivement aux alliances du *Juniperion thuriferae* Rivas-Martinez 1962 et du *Quercion pubescentis-petraea* Br.-Bl. 1932. La majorité des populations des Genévriers thurifères est située dans les Alpes externes dans le domaine du Chêne pubescent et appartient à la sous-alliance du *Buxo sempervirentis-Quercenion pubescentis* (Zólyomi & Jakucs 1960) Rivas-Martinez 1972 et à la sous-association *Buxo sempervirentis-Quercetum juniperetosum thuriferae* Gamisans & Gruber 1980. La sous-association se répartit sur l'ensemble du croissant préalpin (figure 6) de l'étage collinéen à supraméditerranéen de 600 à 1 300 m d'altitude (tableau 2, classes 3, 5, 8, 9 et 13). Elle se caractérise par la présence de *Juniperus thurifera* accompagné de *Buxus sempervirens* ou *Quercus pubescens* sur les pentes et vires suffisamment accueillantes pour permettre l'installation de boisements (figure 7). En contact avec les peuplements de *Pinus nigra* Arnold subsp. *nigra* et des boisements clairs d'autres essences, elle présente une grande variété : des faciès dégradés des chênaies pubescentes à *Juniperus oxycedrus* aux faciès boisés à *Pinus nigra* subsp. *nigra* (tableau 2, classes 8 et 9), jusqu'à ceux, tout à fait originaux, à *Acer monspessulanum* L. des Préalpes méridionales calcaires (tableau 2, classes 13 et 15). Nous proposons pour ce groupement la description d'une nouvelle association : *Aceri monspessulani-Juniperetum thuriferae ass.*

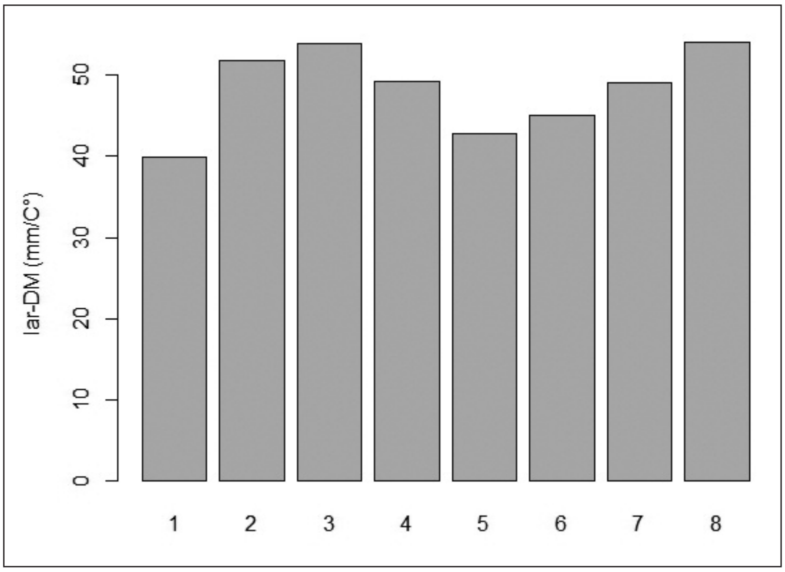

Figure 5 – Diagramme des indices d'aridité de De Martonne (1926) (Iar-DM = P/(Tm + 10)) des huit groupes issus de la classification phytosociologique concernant *Juniperus thurifera* L.

Figure 5 – Bar graph of De Martonne's aridity index (Iar-DM = P/(Tm + 10)) of the eight groups from the phytosociological analysis concerning* Juniperus thurifera *L.

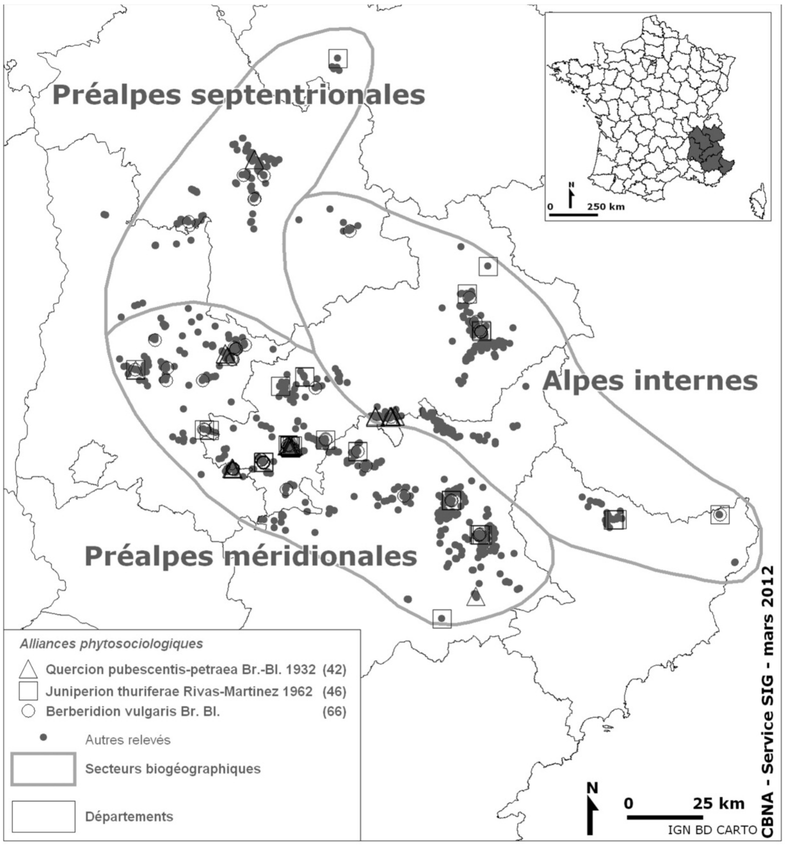

Figure 6 – Carte de répartition des alliances phytosociologiques pour *Juniperus thurifera* dans les Alpes françaises.

Figure 6 – Distribution map of phytosociological alliances for* Juniperus thurifera *in the French Alps.

Figure 7 – Boisement de *Quercus pubescens* et *Juniperus thurifera* en fruticée dense à *Buxus sempervirens* et *Amelanchier ovalis* (1 000 m, Drôme, Saint-André-de-Rosans). Classe n° 5 du tableau 2. Syntaxon le plus proche décrit : *Buxo sempervirentis-Quercetum juniperetosum thuriferae* Gamisans & Gruber 1980 (alliance du *Quercion pubescenti-sessiliflorae* Br.-Bl. 1932 ; sous-alliance du *Buxo sempervirentis-Quercenion pubescentis* (Zólyomi & Jakucs 1960) Rivas-Martinez 1972).

Figure 7 – **Quercus pubescens** ***and*** **Juniperus thurifera** ***woodlands with*** **Buxus sempervirens** ***and*** **Amelanchier ovalis** ***scrubs (1,000 m, Drôme, Saint-André-de-Rosans). Class n° 5 of table 2. Nearest described syntaxon :*** **Buxo sempervirentis-Quercetum juniperetosum thuriferae** ***Gamisans & Gruber 1980 (alliance du*** **Quercion pubescenti-sessiliflorae** ***Br.-Bl. 1932 ; sous-alliance of*** **Buxo sempervirentis-Quercenion pubescentis** ***(Zólyomi & Jakucs 1960) Rivas-Martinez 1972).***

Figure 8 – Boisement de *Pinus sylvestris* à *Juniperus thurifera* sur landes à *Juniperus sabina* et *Juniperus communis* s.l. (1 500 m, Alpes-de-Haute-Provence, Prads-Haute-Bléone). Classe n° 10 du tableau 2. Proche de l'alliance du *Juniperion thuriferae* Rivas-Martinez 1969).

Figure 8 – **Pinus sylvestris** ***and*** **Juniperus thurifera** ***woodlands with*** **Juniperus sabina** ***and*** **Juniperus communis** ***s.l. thickets (1,500 m, Alpes-de-Haute-Provence, Prads-Haute-Bléone). Class n° 10 of table 2. Near from alliance of*** **Juniperion thuriferae** ***Rivas-Martinez 1969).***

nov. hoc loco (figure 9) dont nous précisons l'écologie et la description dans le tableau 3.

Les thuriféraies des vallées internes ou d'affinités montagnardes qui se caractérisent par la rareté du Chêne pubescent et la présence de *Pinus sylvestris* sont à rallier au *Juniperion thuriferae* Rivas-Martinez 1962 (figure 6). Cette alliance se présente sous la forme de deux groupements riches en espèces du genre *Juniperus*. Le groupement le plus fréquent, celui typique des Alpes internes, associe *Juniperus thurifera*, *Pinus sylvestris*, *Juniperus communis* s.l. et *Juniperus sabina* (figure 8). Il est proche du *Juniperetum communis-thuriferae* (Vagge & Biondi 2008), mais ce dernier ne constitue selon nous qu'un faciès de transition à *Pinus sylvestris* en phase de recolonisation (tableau 2, classe 10). *Juniperus communis, Cotinus coggygria* et *Cytisophyllum sessiliflorum* sont citées comme espèces caractéristiques (Vagge & Biondi 2008), mais l'analyse de nos 213 relevés nous pousse à les classer comme espèces compagnes, présentes dans la majorité des groupements à *Juniperus thurifera* des pentes rocheuses. Le *Juniperetum communis-thuriferae* (Vagge & Biondi 2008) correspond plutôt à des formations de pentes et vires rocheuses calcaires d'adret, proches de groupements de l'*Amelanchiero ovalis-Juniperetum thuriferae* (Archiloque & Borel 1965) de Foucault 1991.

Figure 9 – Boisement à *Juniperus thurifera* et *Acer monspessulanum* sur crête rocheuse, avec *Amelanchier ovalis* et *Thymus vulgaris* (1 100 m, Hautes-Alpes, Saint-Genis). Classe n° 13 et 15 du tableau 2. Association du *Aceri monspessulani-Juniperetum thuriferae ass. nov. hoc loco*.

***Figure 9 –* Juniperus thurifera *and* Acer monspessulanum *woodlands on rocky ridge, with* Amelanchier ovalis *and* Thymus vulgaris *(1,100 m, Hautes-Alpes, Saint-Genis). Class n° 13 and 15 of table 2. Association of* Aceri monspessulani-Juniperetum thuriferae ass. nov. hoc loco.**

Tableau 3 – Description de l'association *Aceri monspessulani-Juniperetum thuriferae ass. nov. hoc loco.*

Table 3 – Description of association* Aceri monspessulani-Juniperetum thuriferae ass. nov. hoc loco*.

Association : *Aceri monspessulani-Juniperetum thuriferae ass. nov. hoc loco*.

Synonymes : –.

Unités supérieures : *Quercion pubescenti-sessiliflorae* Br.-Bl. 1932, *Buxo sempervirentis-Quercenion pubescentis* (Zólyomi & Jarkucs 1960) Rivas-Martinez 1972, *Quercetalia pubescentis-sessiliflorae* Klika 1933 corr. Moravec *in* Béguin & Theurillat 1984.

***Typus nominis* :** rel. Nº 9 du 07/05/2010, chrono nº 748321 de la de la BD Flore© du CBNA.

Physionomie : boisement clair de *Juniperus thurifera* L. et d'*Acer monspessulanum* L. sur crêtes et vires rocheuses.

Combinaison caractéristique d'espèces : *Juniperus thurifera* L., *Acer monspessulanum* L., *Amelanchier ovalis* Medik., *Lavandula angustifolia* Mill. subsp. *angustifolia*, *Thymus vulgaris* L.

Variations : forme plus saxicole, sur roches finement fracturées et lithosols, différenciée par l'abondance de *Teucrium aureum* Schreb. et *Sempervivum calcareum* Jord. et la moindre fréquence d'*Amelanchier ovalis* Medik. et *Acer monspessulanum* L.

Synécologie : boisement clair de l'étage supraméditerranéen thermophile (exposition sud-est à sud-ouest), calcicole, saxicole, sur vires et crêtes rocheuses.

Synchorologie : Préalpes méridionales (Buëch, Dévoluy, Baronnies, Diois, Préalpes de Digne, Haute-Bléone, Haut-verdon), atteint les Alpes internes (Haute-Durance).

Relevé phytosociologique stratifié : Nº 748321 de la BD Flore© du CBNA, relevé nº 9 (typus nominis), 07/05/2010, Sylvain ABDULHAK, Hugues FERTIN, commune de Saint-Genis, Hautes-Alpes, France. Alt. : 1 050 m. Exposition : sud. Pente : 20º. Surface : 200 m^2. Recouvrement des strates : arborescente : 15 % ; arbustive : 20 % ; sous-arbustive : 15 % ; herbacée : 5 %. Intitulé du milieu : « Crête rocailleuse à *Juniperus thurifera* et *Acer monspessulanum* en lande ouverte à *Lavandula angustifolia*, *Thymus vulgaris* et *Genista cinerea*, en lisière de chênaie-érablaie. Pente : 20°. Recouvrement total de végétation : 20 %. » Liste des espèces : strate arbor. : *Juniperus thurifera* L., 1753 (2), *Quercus pubescens* Willd., 1805 (+); strate arbust. : *Genista cinerea* (Vill.) DC. subsp. *cinerea* (2), *Acer monspessulanum* L., 1753 (2), *Amelanchier ovalis* Medik., 1793 (2), *Juniperus thurifera* L., 1753 (2), *Cotinus coggygria* Scop., 1771 (+) ; strate sous-arbust. : *Lavandula angustifolia* Mill. subsp. *angustifolia* (1), *Thymus vulgaris* L., 1753 (2) ; strate herb. : *Teucrium chamaedrys* L., 1753 (2), *Koeleria vallesiana* (Honck.) Gaudin, 1808 (1), *Trinia glauca* (L.) Dumort., 1829 (1), *Festuca marginata* (Hackel) K. Richt. subsp. *marginata* (1), *Carex halleriana* Asso subsp. *halleriana* (1), *Stipa eriocaulis* Borbás, 1878 (1), *Cerastium arvense* L. subsp. *suffruticosum* (L.) Ces., 1844 (+), *Helianthemum nummularium* (L.) Mill., 1768 (+), *Aethionema saxatile* (L.) R. Br. subsp. *saxatile* (+), *Helianthemum apenninum* (L.) Mill., 1768 (+), *Potentilla neumanniana* Rchb., 1832 (+), *Galium corrudifolium* Vill., 1779 (+), *Sedum anopetalum* DC., 1808 (+), *Argyrolobium zanonii* (Turra) P.W. Ball, 1968 (+), *Teucrium aureum* Schreb., 1773 (+), *Valeriana tuberosa* L., 1753 (+).

Dans les Alpes-Maritimes, les junipéraies primaires xérothermophiles de l'étage supraméditerranéen, évoluant sur des pentes rocheuses siliceuses, caractérisées par la présence de *Juniperus thurifera*, *Juniperus oxycedrus* et *Erica arborea* sont à intégrer à la sous-alliance du *Buxo sempervirentis-Quercenion pubescentis* (Zólyomi & Jakucs 1960) Rivas-Martinez 1972 (tableau 2, classe 16), avec la présence systématique du Chêne et du Buis. Ce groupement est à différencier des thuriféraies corses à *Erica arborea* de la sous-alliance du *Galio rotundifolii-Fagenion sylvaticae* Gamisans (1977) 1979.

Le caractère continental des vallées internes et le caractère montagnard sec des Préalpes font que ces associations décrites d'Espagne trouvent dans les Alpes du Sud un climat similaire marqué par une sécheresse estivale et des hivers froids. Bien que nous n'ayons pas encore procédé à des analyses phytosociologiques poussées visant à comparer les relevés d'Espagne avec ceux des Alpes françaises, nous jugeons les groupements très proches d'un point de vue floristique et écologique.

Discussion

L'analyse des relevés a montré combien il est ardu d'interpréter des résultats phytosociologiques pour le Genévrier thurifère. La physionomie de ses peuplements ne traduit pas clairement les dynamiques forestières, influencées ou non par des pratiques sylvopastorales actuelles ou passées. Cela complique l'approche phytosociologique aussi bien au niveau de la réalisation des relevés de terrain que dans l'analyse. L'analyse des groupements floristiques combinée à des informations climatiques a permis de mettre en lumière les différents cortèges bioclimatiques des boisements de *Juniperus thurifera* et de délimiter deux domaines : celui du croissant préalpin dominé par l'alliance du *Quercion pubescentis-petraea* Br.-Bl. 1932 et celui des vallées internes dominé par les alliances du *Juniperion thuriferae* Rivas-Martinez 1962 et du *Pino sylvestris-Juniperion sabinae* (Rivas-God. 1946) Rivas-God. & Borja 1961. Sur l'ensemble de son aire, les stades pionniers, préforestiers, boisements clairs et fruticées appartiennent à l'alliance du *Berberidion vulgaris* Br.-Bl. et à la sous-association *Buxo semperviventis-Quercetum juniperetosum thuriferae* Gamisans & Gruber 1980. Cette dernière constitue avec les associations *Amelanchiero ovalis-Juniperetum thuriferae* (Archiloque & Borel 1965) de Foucault 1991 et *Aceri monspessulani-Juniperetum thuriferae ass. nov. hoc loco* la toile de fond des thuriféraies des Alpes françaises en parois, vires et crêtes rocheuses.

Nous excluons l'appartenance des thuriféraies à la série du Chêne vert car bien que les deux espèces se côtoient dans les paysages, elles ne sont pas associées de façon significative dans les relevés comme l'avaient déjà remarqué Borel et Polidori en 1983. Enfin, nous proposons de rattacher les groupements des Alpes internes aux alliances du *Juniperion thuriferae* Rivas-Martinez 1962 et du *Pino sylvestris-Juniperion sabinae* (Rivas-God. 1946) Rivas-God. & Borja 1961. Pour ces dernières, un travail phytosociologique approfondi s'avère nécessaire pour mettre en perspective les résultats avec les travaux réalisés en Espagne afin de préciser les caractéristiques d'un *Juniperion thuriferae* français. Une analyse combinée des données climatiques sur les jeux de données espagnols et français aidera à mieux cerner les correspondances entre les cortèges végétaux de chaque pays.

Depuis Villars en 1787, les études se sont succédé sur le Genévrier thurifère, tout d'abord sur l'espèce puis sur ses habitats, sa phytosociologie. Aujourd'hui, le travail que nous avons conduit démontre que son écologie et son appartenance syntaxonomique sont encore mal connues. Plus encore, sa taxonomie dans les Alpes françaises a été mal examinée. En effet, il y a peu de zones où les trois taxons de la section *sabinae* sont en contact et il est communément admis que les populations de Genévriers thurifères des Alpes sont bien individualisées et isolées. Avant 2006 aucune forme intermédiaire ou d'hybride n'a jamais été mentionnée. Aparicio Rojo *et al.* (2006, 2009) décrivent deux hybrides en Espagne *Juniperus x cerropastoriensis* (*J. thurifera x J. sabina*) et *Juniperus x palancianus* (*J. thurifera x phoenicea*). En septembre 2011, *Juniperus x cerropastoriensis* est trouvé à Saint-Crépin (Hautes-Alpes) par L. Garraud et S. Abdulhak et en février 2012 *Juniperus x palancianus* à Saoû (Drôme) par D. Benefice et L. Garraud. L'interrogation des bases de données du Conservatoire botanique national alpin (base de données Flore 2011) montre qu'il existe sur le territoire étudié une cinquantaine de stations où se rencontrent à la fois le Genévrier thurifère et le Genévrier de Phénicie. À l'étage méditerranéo-montagnard, il existe plus d'une centaine de stations où Genévrier thurifère et Genévrier sabine sont en contact. L'étude de ces populations reste à entreprendre et l'on peut s'interroger sur la valeur taxonomique et les degrés d'introgression de certaines populations connues de *Juniperus thurifera*.

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Caractérisation de différentes espèces de *Pratylenchus* associées aux marcottières et aux plants greffés de MM106 en pépinières d'arbres à pépins en Tunisie

Characterization of different Pratylenchus *species associated with stoolbeds and grafted plants of the rootstock MM106 in apple tree nurseries in Tunisia*

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Résumé

Les Pratylenchus *(nématodes des lésions racinaires) sont des espèces qui peuvent parasiter plusieurs plantes hôtes annuelles et pérennes telles que les arbres fruitiers en vergers et en pépinières. Les pépinières des cinq principales zones de production de plants de pommier situées en Tunisie dans les régions de Bizerte, Testour (Béja), Jendouba, Kairouan et Kasserine sont prospectées. Les racines des plants de même vigueur de marcottes de MM106 ainsi que des plants de MM106 greffés par différentes variétés de pommier sont prélevées et les nématodes sont extraits par la technique de double centrifugation. Les individus femelles de* Pratylenchus *des différentes populations sont prélevés, fixés, montés dans de la glycérine, mesurés sur la base des caractères morphométriques et comparés aux différentes espèces de ce genre déjà décrites dans la littérature. Les résultats obtenus par l'analyse en composante principale et l'analyse discriminante montrent un effet de la région et de la plante hôte sur les caractères biométriques des femelles de* Pratylenchus. *L'analyse de la classification hiérarchique a permis de classer les différentes populations de nématodes par rapport aux espèces connues. La plupart des spécimens, notamment ceux provenant des régions de Jendouba et de Testour, se rapprochent soit des espèces* P. neglectus *et* P. brachyurus *avec quelques variantes, soit de l'espèce* P. vulnus. *Cependant, quelques individus isolés des racines de pommier des régions de Kairouan et Jendouba s'apparentent à l'espèce* P. jordanensis.

Mots clés : pépinière, porte-greffe, pommier, *Pratylenchus* spp., *Pratylenchus neglectus*, *Pratylenchus brachyurus*, *Pratylenchus vulnus*, *Pratylenchus jordanensis,* Tunisie.

Abstract

Pratylenchus *spp. (root-lesion nematodes) are nematodes that can parasitize numerous annual and perennial host plants, such as fruit trees in orchards and nurseries. Nurseries in the five main Tunisian areas of apple production in the regions of Bizerte, Testour (Beja), Jendouba, Kairouan and Kasserine were surveyed. Roots from plants of similar vigor from the MM106 rootstock alone and from the MM106 rootstock grafted to apple varieties were harvested and*

Keywords: nursery, apple rootstock, *Pratylenchus* species, *Pratylenchus neglectus*, *Pratylenchus brachyurus*, *Pratylenchus vulnus*, *Pratylenchus jordanensis,* Tunisia.

nematodes were extracted by the double centrifugation technique. Females of different Pratylenchus *populations were fixed, mounted in glycerol and measured. Morphometric and morphological characters were used to compare populations to known species. The results obtained by principal compound analysis and discriminate analysis showed regional and host plant effects on biometrical characters of* Pratylenchus *females. Hierarchical cluster analysis is used to classify different nematode populations in relation to known species. Most specimens, particularly those from the regions of Jendouba and Testour, were similar either to the species* P. neglectus *and* P. brachyurus *or to* P. vulnus*. However, a few isolated specimens obtained from apple roots in Kairouan and Jendouba were similar to* P. jordanensis*.*

Introduction

Pratylenchus Filipjev, 1963 est un genre qui regroupe des nématodes endoparasites migrateurs des racines (Subbotin *et al.*, 2008) également appelés nématodes des lésions racinaires. Certaines espèces de *Pratylenchus* sont polyphages et parasitent un large spectre d'hôtes alors que d'autres sont monophages. Ces nématodes infestent plusieurs cultures et notamment les arbres fruitiers à pépins (pommier et poirier) en pépinières et en vergers (Scotto La Massèse, 1989). Les espèces de *Pratylenchus* entraînent la formation de larges lésions dans le parenchyme racinaire des plantes car elles détruisent les cellules corticales durant leur migration à l'intérieur des racines, ce qui a pour conséquence un mauvais développement racinaire et une faible reprise des plants issus de pépinières et transférés en vergers (Askary, 2012). Ce même auteur rapporte que *Pratylenchus* est responsable du dépérissement des arbres en vergers et des "*die-back*", de la réduction de la croissance et du nanisme des arbres. Le nématode entraîne le jaunissement et le brunissement des feuilles et un stress hydrique pendant les heures chaudes de la journée ; cela est en rapport avec la diminution de la densité racinaire et la détérioration des racines nourricières. Certains auteurs considèrent que la mortalité des plants infestés par le genre *Pratylenchus* est liée aux complexes pathogènes qui lui sont associés (Bridge & Starr, 2007). Handoo et Morgan Golden (1989) ainsi que Frederick et Tarjan (1989) ont rapporté l'existence de 63 espèces de *Pratylenchus* réparties dans le monde entier. En Tunisie, Gillard (1985) a fait état de la présence de *P. penetrans* sur céréales, *P. scribneri* sur pomme de terre et *P. thornei* sur racines d'abricotier. Niang (1985) a identifié *P. thornei*, *P. neglectus* et *P. penetrans* sur céréales. Enfin Belkadhi (1986) a retrouvé *P. vulnus* sur pommier, poirier, amandier et pêcher et *P. neglectus* sur grenadier et figuier mais rarement sur *Citrus*. Le cycle de ces nématodes endoparasites migrateurs se fait en grande partie dans la région corticale des racines et paraît tributaire de la phénologie de la plante et des conditions agro-météorologiques.

L'objectif de ce travail est d'évaluer la fréquence et de déterminer les espèces de *Pratylenchus* associées au pommier en marcottières et en pépinières de plants greffés. Il est également d'aborder la relation entre la variabilité morphologique entre populations et, d'une part, les variétés greffées de pommier et, d'autre part, les conditions agro-météorologiques des principales régions de cultures de la Tunisie.

Matériel et méthodes

Cette étude a été effectuée dans les principales pépinières d'arbres à pépins de la Tunisie situées dans cinq gouvernorats, Bizerte, Testour (Béja), Jendouba, Kairouan et Kasserine. Dans les pépinières, les plants du porte-greffe MM106 sont produits en marcottières en plein champ. Les plants mères sont par la suite buttés avec du sable de carrière (profondeur supérieure à 4 mètres). Les plants rejets enracinés (marcottes) issus des pieds mères sont prélevés et installés en pleine terre et greffés par les différentes variétés. L'assolement dans ces pépinières est effectué avec une monoculture de céréale (blé) pendant 4 ans. Jendouba située au nord-ouest (étage bioclimatique subhumide) bénéficie d'une pluviométrie annuelle variant de 450 à 1 500 mm/an avec une moyenne de 800 mm et d'une température annuelle moyenne de 18 °C. Le gouvernorat de Bizerte situé au nord-est de la Tunisie appartient à l'étage bioclimatique subhumide inférieur avec une température moyenne de 22,8 °C et une pluviométrie moyenne de 632 mm/an. La région de Testour, septentrionale, appartient à l'étage bioclimatique méditerranéen semi-aride supérieur à hiver tempéré avec une moyenne annuelle de 400 mm de pluie et 17 °C de température. À Kasserine, situé au centre-ouest de la Tunisie et appartenant à l'étage biocli-

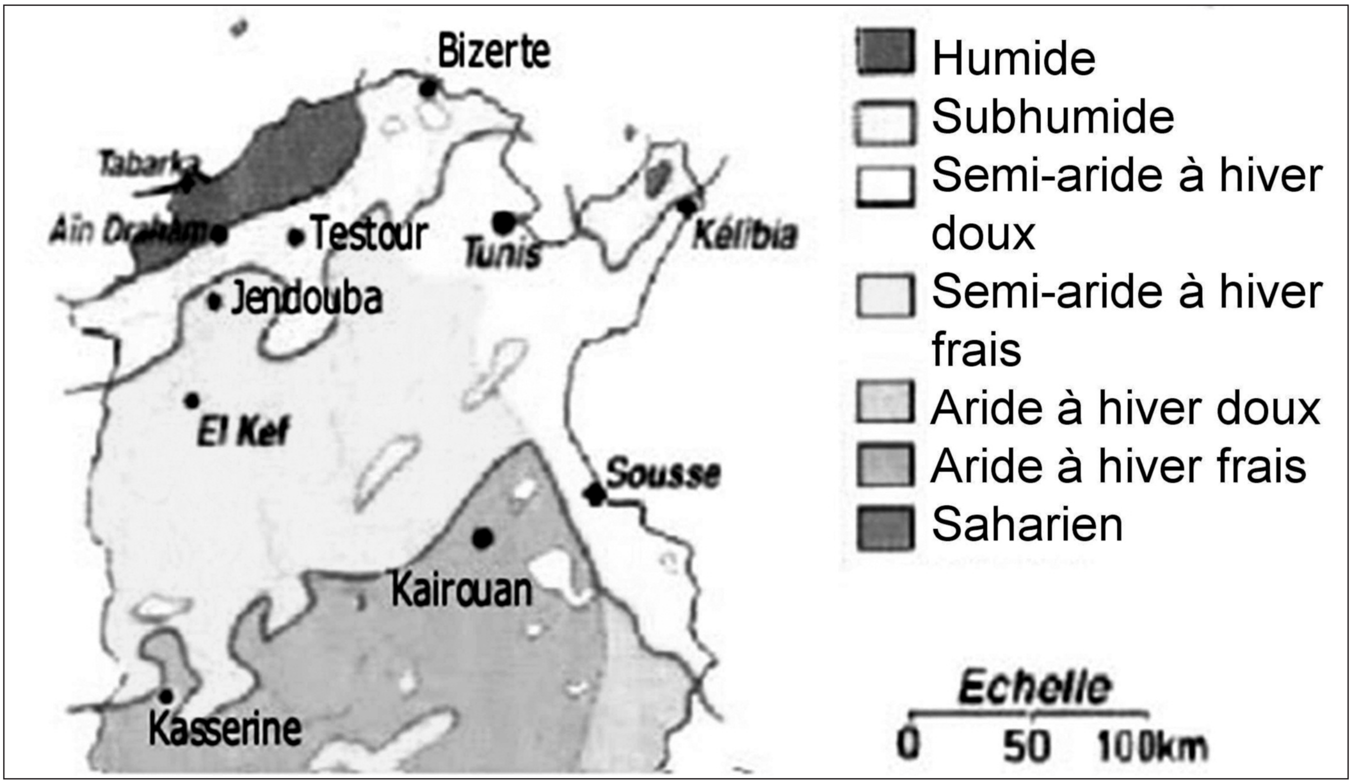

Figure 1 – Répartition des lieux d'échantillonnage en pépinières arboricoles et d'arbres à pépins en Tunisie et leurs caractéristiques climatiques.

Figure 1 – Climatic regions of Tunisia and distribution of sampling of apple tree nurseries.

matique aride supérieur, la pluviométrie annuelle moyenne est de 335 mm et la température varie de 2 à 12 °C en hiver et de 30 à 40 °C en été. À Kairouan, aride supérieur (figure 1), la température moyenne se situe entre 5 et 21 °C en hiver et entre 25 et 42 °C en été et la pluviométrie annuelle est de 250 à 400 mm. La texture du sol des pépinières de la région de Jendouba, Testour et Kairouan est argilo-limoneuse alors que celle de Kasserine est sablo-limoneuse (tableau 1).

Le pH des sols est basique (supérieur à 7,5) pour toutes les pépinières. Les sols à Jendouba et à Testour sont relativement riches en matière organique et possèdent une conductivité électrique élevée alors que les sols de Kasserine et Kairouan sont pauvres en matière organique et ont une conductivité électrique plus faible que celles des deux autres pépiniéres. Les taux de calcaire total et actif des sols sont élevés pour toutes les pépinières sauf pour celle de Kasserine (tableau 1).

Le prélèvement des échantillons de racines a été effectué en tenant compte de l'indice de vigueur des plants et de la variété de pommier (greffon). L'indice de vigueur 1 correspond à un plant dont la longueur du greffon est moins de 50 cm et le diamètre du porte-greffe est inférieur à 2 cm. L'indice de vigueur 2 est attribué aux plants dont la longueur du greffon est entre 50 cm et 90 cm et le diamètre du porte-greffe est entre 2 cm et 4 cm. Un plant

Tableau 1 – Caractéristiques physico-chimiques et texturales des sols prélevés en pépinières d'arbres à pépins.

Table 1 – Physico-chemical and textural characteristics of nursery soil samples.

	Jendouba	Kasserine	Testour	Kairouan
pH	8	8,5	7,7	8,2
Saturation (ml/cm)	48	40	52	52
Conductivité (mmho/cm)	4	1,2	3,8	2,9
Calcaire total (%)	39	7	43	37
Calcaire actif (%)	19	1,1	21	13
Matière organique (%)	1,5	0,3	1,1	0,5
Carbone (%)	0,6	0,2	0,6	0,3
Azote (%)	0,05	0,07	0,042	0,032
C/N	12	2,85	14,28	9,37
Argile (%)	27	20	25	29
Limons fins (%)	25	21	36	41
Limons grossiers (%)	13	7	8	3
Limons totaux (%)	38	28	42	44
Sables fins (%)	24	42	32	19
Sables grossiers (%)	11	10	17	7
Sables totaux (%)	35	52	49	26

de vigueur 3 a une longueur du greffon de plus de 90 cm et un diamètre du porte-greffe de plus de 4 cm. Dans la région de Bizerte, l'échantillonnage a été effectué sur des plants des trois vigueurs greffés par les variétés Golden Delicious, Starkrimson et Royal Gala. Dans la région de Jendouba, l'échantillonnage a été effectué sur des plants de vigueur 2 et 3 greffés par les variétés Starkrimson, Star Delicious, Richared et Orzac et sur des plants de vigueur 2 greffés par la variété Royal Gala. Dans la région de Testour, des échantillons de racines sont prélevés à partir des plants greffés par les variétés Golden Delicious, Starkrimson des trois vigueurs ; d'autres échantillons sont pris respectivement à partir des plants de vigueur 2 pour la variété Richared et des vigueurs 1 et 2 pour la variété Llorca. Dans la région de Kasserine, l'échantillonnage consiste à prélever des plants de la variété Golden Delicious des trois vigueurs ainsi que des plants de Richared de vigueur 1 et 3. Enfin, dans la région de Kairouan, ce sont des plants greffés par la variété Anna de vigueur 1 qui sont prélevés.

Sur des plants de la même vigueur, 50-70 g de racines sont prélevés à partir de 10-15 plants. Pour chaque variété et chaque pépinière un kg de sol est prélevé pour effectuer les analyses physico-chimiques. L'analyse physique porte sur la granulométrie des différentes particules du sol, la mesure du pH de sol et la conductivité électrique. Les analyses chimiques de sol ont porté sur le dosage du calcaire actif et total, du carbone et de l'azote.

L'extraction des nématodes est effectuée selon la technique de la double centrifugation (B'Chir, 1979). Le dénombrement des nématodes est effectué dans une coupelle quadrillée sous une loupe binoculaire en diascopie. Les individus femelles de *Pratylenchus* sont prélevés à la main par une soie de porc et fixés puis transférés dans de la glycérine (B'Chir, 1979) pour déterminer les différences morphométriques. Les nématodes fixés sont montés entre lame et lamelle et observés au microscope OLYMPUS CX40. Les caractéristiques morphométriques d'une vingtaine de femelles et de mâles des nématodes sont mesurées sous microscope à l'aide d'une caméra OLYMPUS DP25 couplée au logiciel Cell^A version 3.2. La longueur (L), la largeur (W), la longueur du stylet ($_{st}$), la longueur du bulbe médian ou métacorpus, la distance partie antérieure du nématode-vulve (L_v), la longueur du sac post-utérin (L_{pus}), et la longueur de la queue (T) sont mesurées pour chaque spécimen de femelle. Ensuite, à partir de ces valeurs, les rapports morphométriques a (L/W), c (L/T), V (L_v*100/L) et PUS (L_{pus}/W) sont calculés. Ces données relatives aux mesures et aux rapports morphométriques sont disposées en colonnes tandis que les différents individus issus des divers échantillons (régions et variétés) forment les lignes de la matrice.

Les données sont analysées statistiquement par le logiciel SPSS® 16.0. Une analyse en composantes principales (ACP) a été effectuée dans un premier temps afin de déterminer les corrélations entre les différents caractères mesurés sur les individus des diverses populations de *Pratylenchus* (Celeux *et al.*, 1989 ; Du Toit *et al.*, 1986 ; Jolliffe, 1986). Le test de sphéricité de Bartlett, la mesure d'adéquation d'échantillonnage de Kaiser-Meyer-Olkin, le tracé des valeurs propres, les valeurs propres et l'analyse des corrélations sont utilisés en préliminaire comme test de diagnostic de l'ACP et pour sélectionner le nombre de composantes principales ou facteurs. Les valeurs propres forment un critère intéressant pour la détermination du nombre de facteurs puisqu'elles représentent le montant de la variance commune expliquée par les numéros de facteurs respectifs extraits par l'ACP. Le nombre de facteurs est déterminé par le critère de Kaiser qui ne prend en considération, pour expliquer l'ACP, que les facteurs correspondant à une valeur propre supérieure à 1 ou par la méthode empirique relative à la pente du tracé des valeurs propres. Les variables sont liées à un facteur lorsqu'elles représentent des corrélations élevées entre elles et les facteurs (ou « nouvelles variables synthétiques ») extraits par défaut ; ces corrélations sont également appelées poids factoriels. Les variables sont jugées avoir un intérêt pratique dans le cas où leur contribution au facteur serait supérieure à 0,7.

La comparaison des différentes populations sur la base des différents caractères morphométriques est effectuée grâce à une analyse discriminante puis une analyse de la variance (ANOVA) suivie d'une comparaison multiple de moyennes selon le test de Duncan à la probabilité = 0,05. Les variables quantitatives L, L_{st}, longueur du bulbe médian, a, c, v et PUS non corrélés sont associés aux variables qualitatives nombre d'anneaux (NA) et forme de la queue lisse ou crénelée (FQ) observées sur les différents spécimens femelles prélevés à partir des douze populations provenant de chaque région et associées à différentes espèces (pommier et poirier) et variétés d'arbres à pépins. Avant analyse, les données brutes des populations ont été testées pour la stabilité de la variance.

Les différentes populations sont par la suite comparées sur la base des caractères morphométriques des femelles de nos spécimens aux différentes espèces de *Pratylenchus* reconnues par Frederick et Tarjan (1989) et Handoo et Morgan Golden (1989). La moyenne des caractères mesurés, longueur du corps, longueur de stylet et les rapports a, c, v et les caractères qualitatifs tels que le nombre d'anneaux, la présence de mâle, l'importance du sac postutérin (absence, inférieur à la moitié de W, inférieur à W, supérieur à W, inférieur à 2W, supérieur à 2W et inférieur à 3W) sont placés en colonnes tandis que les différents échantillons (région et variété) ainsi que les espèces validées par les auteurs forment les lignes. *Pratylenchus clavicaudatus*, *P. goodeyi*, *P. nizamabadensis*, *P. obtusicaudatus*, *P. ranjani* et *P. typicus* n'ont pas fait l'objet d'analyses puisqu'elles présentent un nombre d'anneaux égal à 4 et seules les espèces de *Pratylenchus* dont le nombre d'anneaux est de 2 ou 3 sont prises en compte. Les variables d'origine sont de natures différentes puisque les unités de mesure sont exprimées en quantités non comparables de moyennes et de dispersions hétérogènes. Ces différentes variables sont centrées et réduites afin que l'analyse ne fasse pas surgir les effets des données brutes (unités de mesure) (Jambu, 1989). La matrice ainsi formée est soumise à l'analyse de la classification hiérarchique en utilisant deux méthodes d'agrégations (distance minimale et moyenne pondérée des groupes associés) et la méthode de mesure des distances (distance euclidienne) afin de dégager les groupes d'espèces auxquels nos populations sont associées.

Résultats

Cinq régions ont été prospectées pour étudier les *Pratylenchus* spp. en pépinières d'arbres à pépins. Une pépinière à Bizerte est indemne et seules les pépinières situées dans les régions de Testour (Béja), Jendouba, Kairouan et Kasserine sont infestées. Dans les différentes régions, le pourcentage des échantillons infestés est similaire et varie entre 72,5 % et 85 % (tableau 2). Dans la région de Jendouba, deux marcottières de MM106 sont prospectées : une est indemne et l'autre est infestée par les *Pratylenchus*. Sur les 24 échantillons de racines prélevés de cette marcottière seulement 2 ne sont pas infestés

Tableau 2 – Infestation des plants de MM106 issus de marcottière ou greffés par différentes variétés de pommiers provenant des cinq régions de Tunisie.

Table 2 – Infestation of MM106 rootstocks from stoolbeds or plants grafted with different apple varieties in nurseries from five Tunisian regions.

	Jendouba	Testour (Béja)	Kasserine	Kairouan	Bizerte
MM106 (marcottière)	1,59 ± 0,55[a] (n = 24, n′ = 2)	-	-	-	
Starkrimson	14,9 ± 15,14 (n = 10, n′ = 4)	3,47 ± 1,2 (n = 15, n′ = 2)	-	-	0 (n = 15)
Star Delicious	5,9 ± 4,13 (n = 10, n′ = 4)	-	-	-	
Richared	0,1 ± 0,20 (n = 10, n′ = 9)	0,8 ± 1,1 (n = 10, n′ = 8)	27,2 ± 13,5 (n = 10, n′ = 0)	-	
Royal Gala	8,2 ± 2,90 (n = 5, n′ = 0)	-	8 ± 2,5 (n = 5, n′ = 0)	0 (n = 15)	0 (n = 15)
Orzac	35,8 ± 21,7 (n = 10, n′ = 0)	-	-	-	
Anna	-	-	-	4,2 ± 3,5 (n = 15, n′ = 7)	
Llorca	-	21,4 ± 13,1 (n = 10, n′ = 0)	-	0 (n = 15)	
Golden Delicious	-	7,8 ± 4,8 (n = 15, n′ = 1)	13,1 ± 8,0 (n = 15, n′ = 3)	-	0 (n = 15)
Moyenne	9,7 (n = 69, n′ = 19)	8,4 (n = 50, n′ = 11)	16,1 (n = 20, n′ = 3)	1,4 (n = 30, n′ = 7)	0 (n = 45, n′ = 0)

[a] : nombre de nématodes par gramme de racine, ± : intervalle de confiance.
n est le nombre total d'échantillons de racines, n′ est le nombre d'échantillons indemnes.

par ces nématodes. En pépinières, l'infestation des marcottes de MM106 enracinées greffées par différentes variétés de pommier et provenant des quatre régions a été évaluée. Sur les 170 échantillons de racines analysés seulement 26,5 % des échantillons sont non infestés. En général, les plants greffés de la pépinière de Jendouba sont plus infestés que les marcottes (tableau 2). Les échantillons de marcottières à Jendouba et des plants greffés par Richared à Testour présentent de faibles effectifs de *Pratylenchus*. Les échantillons de plants greffés par Orzac à Jendouba, par Llorca à Testour, par Richared et Golden Delicious à Kasserine présentent des populations importantes avec une grande part des échantillons infestés. Les populations provenant des échantillons de plants greffés par Star Delicious et Royal Gala à Jendouba, par Starkrimson et Golden Delicious à Testour et par Anna à Kairouan, sont d'effectifs intermédiaires (tableau 2).

Corrélations entre les différentes variables morphologiques mesurées

L'indice d'adéquation de l'échantillonnage de Kaiser-Meyer-Olkin teste les corrélations partielles entre les variables. La mesure de cet indice pour l'ACP effectuée sur la population des nématodes, a montré une valeur égale à 0,438. Cela montre que les variables soumises à l'analyse factorielle sont utiles. Le test de Bartlett de sphéricité, défini par le test 2, a une valeur égale à 1 682 pour l'ACP effectuée. Ces valeurs sont très hautement significatives, ce qui indiquerait probablement l'existence d'une relation entre les variables. La qualité de représentation est la corrélation des carrés de la variable utilisant les facteurs comme variables explicatives et donc la part de la variabilité de chaque variable expliquée par les facteurs de l'ACP. La plupart des variables contribuent d'une façon importante à l'ACP sauf la longueur du stylet, la longueur du bulbe médian et la position de la vulve qui ne participent que pour une faible fraction (tableau 3). Quatre facteurs ayant une valeur propre supérieure à 1 sont retenus pour l'ACP sur la base du critère de Kaiser. Le tracé des valeurs propres montre qu'au-delà de trois facteurs la pente du tracé des valeurs propres change et les valeurs semblent s'équilibrer à droite du tracé ne présentant que des « éboulis factoriels ». Le tracé des valeurs propres semble confirmer le choix de 4 facteurs principaux pour définir l'ACP. L'ACP effectuée explique respectivement 76,87 % de la variabilité totale. Le premier axe factoriel explique 26,19 % de la variabilité totale, le deuxième axe extrait par l'ACP explique seulement 21,85 %, le troisième par contre ne contribue que pour 14,81 % de la dispersion et le dernier pour seulement 14,01 % du nuage de points. Le facteur 1 extrait par l'ACP est lié à L et L_v, le facteur 2 est associé à L_{pus} et PUS, le troisième axe factoriel est négativement corrélé à T et positivement lié au rapport c et le quatrième axe est expliqué par W et le rapport a (tableau 3).

Tableau 3 – Contribution des différentes variables soumises et coordonnées des variables mesurées dans le repère défini par les différents facteurs retenus par l'ACP.

Table 3 – Variable contribution and their coordinates on factors extracted by principal component analysis (PCA).

Caractère	Contribution	Facteur 1	Facteur 2	Facteur 3	Facteur 4
L (µm)	0,875	0,929[z]	0,056	– 0,084	– 0,030
W	0,987	0,561	0,208	– 0,265	– 0,748
T	0,938	0,000	0,584	– 0,713	0,298
L_v	0,968	0,965	– 0,084	– 0,146	0,090
L_{st}	0,268	0,313	0,411	– 0,037	0,006
Long. bulbe médian	0,365	0,404	0,341	0,225	0,184
L_{PUS}	0,907	0,136	0,848	0,388	– 0,140
a	0,885	0,382	– 0,177	0,235	0,808
c	0,959	0,390	– 0,527	0,669	– 0,284
v	0,388	0,431	– 0,313	– 0,173	0,272
PUS	0,915	– 0,079	0,773	0,536	0,158

[z] : les coordonnées des différentes variables sur l'axe factoriel sont comprises entre – 1,00 et 1,00. La contribution de la variable à un facteur est mesurée par les valeurs relatives des coefficients de cette variable sur les différents facteurs.

Effet régional et de la plante hôte sur les caractères morphologiques des *Pratylenchus*

L'analyse discriminante (AD) effectuée sur les caractères morphométriques (L, L_{st}, longueur du bulbe médian, PUS, a, c, v) et morphologiques (NA et FQ) des nématodes afin de dégager un effet régional et le rapport entre les populations de *Pratylenchus* et la plante hôte ont permis d'extraire deux axes qui expliquent une variabilité globale de 63,6 %. Le premier axe explique 35,1 % de la variation totale contre seulement 28,5 % pour le second. Le premier axe, défini par l'importance du sac postutérin par rapport à l'épaisseur du corps (tableau 4), sépare clairement les populations des nématodes des sites de Kasserine et celles des sites de Jendouba et Testour (figure 2). Cet axe sépare les populations de nématodes sur la base de texture du sol. En effet, les sols des pépinières de la région de Jendouba et Testour sont de nature argilo-limoneuse alors que le sol de Kasserine est sablo-limoneux. Le deuxième axe canonique de l'AD expliqué par la longueur du stylet et la longueur du corps (tableau 4) sépare les greffons des variétés précoces Starkrimson et Royal Gala des variétés tardives (figure 2).

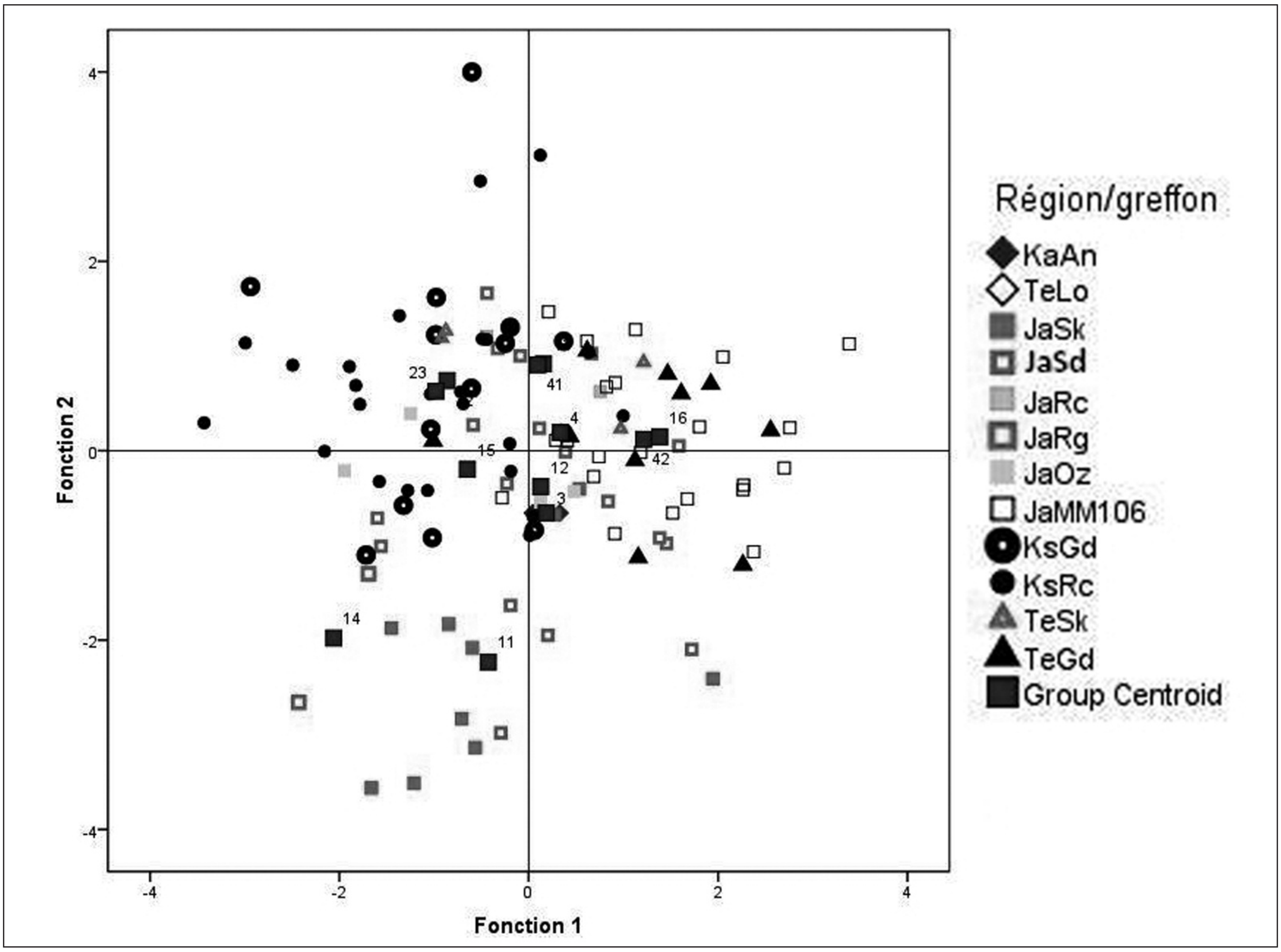

Figure 2 – Distribution des nuages de points relatifs aux observations effectuées sur les populations de nématodes, provenant des différentes régions et des divers plants issus des marcottières ou greffés en pépinières par différentes variétés, en prenant en considération les différentes variables déterminées sur les femelles de *Pratylenchus* dans le plan extrait par l'analyse discriminante. Populations de nématodes 3 (KaAn), 11 (JaSk), 14 (JaRg), 4 (TeLo), 41 (TeSk), 12 (JaSd), 13 (JaRc), 15 (JaOz), 22 (KsGd),16 (JaMM106), 23 (KsRc), 42 (TeGd). Ka = Kairouan, Te = Testour, Ja = Jendouba, Ks = Kasserine, Rg = Royal Gala, Sd = Star Delicious, Sk = Starkrimson, An = Anna, Rc = Richared, Oz = Orzac, Lo = Llorca, Gd = Golden Delicious, MM106 = porte-greffe en marcottière.

Figure 2 – Discriminant analysis of characteristics female nematode populations collected in different regions and from stoolbeds or grafted plants in nurseries. Nematode populations 3 (KaAn), 11 (JaSk), 14 (JaRg), 4 (TeLo), 41 (TeSk), 12 (JaSd), 13 (JaRc), 15 (JaOz), 22 (KsGd), 16 (JaMM106), 23 (ksRc), 42 (TeGd). Ka = Kairouan, Te = Testour, Ja = Jendouba, Ks = Kasserine, Rg = Royal Gala, Sd = Star Delicious, Sk = Starkrimson, An = Anna, Rc = Richared, Oz = Orzac, Lo = Llorca, Gd = Golden Delicious, MM106 = rootstocks in stool bed.

Tableau 4 – Corrélations entre les différentes variables et les fonctions canoniques standardisées définies par l'analyse discriminante.
Table 4 – Correlations between variables and standardized canonical factors extracted by discriminant analysis.

	Fonction								
	1	2	3	4	5	6	7	8	9
PUS	**0,583**^{z}	– 0,093	0,156	0,152	0,210	– 0,093	0,471	0,472	– 0,327
L (µm)	– 0,070	**0,713**^{z}	– 0,331	0,015	– 0,399	0,049	0,411	– 0,044	– 0,210
L_{st}	0,350	**0,542**^{z}	0,204	– 0,241	0,376	– 0,357	0,034	– 0,422	0,190
Nombre d'anneaux	– 0,356	– 0,028	**0,660**^{z}	0,222	0,201	0,155	0,567	0,037	– 0,009
v	– 0,012	– 0,017	**– 0,595**^{z}	0,195	0,246	0,470	0,243	– 0,344	0,384
Long. bulbe médian	0,132	0,149	– 0,147	**0,656**^{z}	0,053	– 0,611	0,282	– 0,217	0,080
a	– 0,288	0,350	– 0,329	0,085	**0,569**^{z}	– 0,032	0,225	0,293	– 0,467
c	– 0,003	0,434	– 0,081	0,477	– 0,102	0,396	**– 0,541**^{z}	0,344	0,004
FQ	– 0,045	0,110	– 0,026	– 0,238	0,051	– 0,303	0,067	0,540	**0,734**^{z}

^{z} : large corrélation absolue entre la variable et les différentes fonctions discriminantes.

Tableau 5 – Caractéristiques morphologiques des femelles de différentes populations de *Pratylenchus* en pépinières.
Table 5 – Female morphological characteristics of different* Pratylenchus *populations from nurseries.

Population	N	Nombre d'anneaux	L (µm)	Diamètre du corps	Longueur stylet	Longueur bulbe médian	Longueur queue	Longueur sac postutérin	PUS	a	c	v
16 (JaMM106)	22	2	567,86 bc (442-707)	18,32abc (15-22)	14,55c (13-16)	13,41a (7-18)	25,18a (11-38)	48,45c (23-92)	2,6602c (1,10-4,38)	30,73abc (23-37)	24,09ab (15-48)	79,14a (63-87)
42 (TeGd)	10	2	559,70 b (510-609)	17,60abc (13-24)	14,00c (11-17)	14,24a (9-21)	19,60ab (10-25)	45,60c (21-65)	2,6126bc (1,31-4,06)	31,80abc (27-36)	30,50c (19-55)	81,00a (78-83)
11 (JaSk)	10	2	464,1a (344-656)	15,50a (12-20)	11,80a (10-14)	10,90a (8-14)	27,20b (19-34)	27,40ab (20-55)	1,7932a (1,05-3,33)	29,40a (26-33)	17,10a (10-24)	81,60a (70-94)
3 (KaAn)	2	2	539 (535-543)	18,50 (18-19)	13,00 (13-13)	9,35 (9-10)	21,50 (20-23)	32,50 (32-33)	1,7573 (1,74-1,78)	29,00 (28-30)	24,50 (23-26)	82,00 (81-83)
14 (JaRg)	2	3	373,50 (367-380)	13,00 (13-13)	12,50 (11-14)	12,00 (12-12)	23,50 (22-25)	26,00 (26-26)	2,0000 (2,00-2,00)	28,50 (28-29)	15,50 (14-17)	68,00 (63-73)
41 (TeSk)	4	2	645,00 c (617-677)	19,25c (17-22)	14,25c (14-15)	12,00a (11-14)	26,75ab (19-33)	39,50bc (25-56)	1,9963abc (1,47-2,55)	33,50abc (29-39)	24,75ab (19-33)	79,25a (74-83)
12 (JaSd)	19	2-3	555,63 b (344-736)	16,36b (10-23)	13,32bc (12-16)	12,79a (8-20)	23,18ab (10-30)	35,95abc (16-81)	2,2628abc (1,14-5,79)	34,21abc (27-50)	24,74ab (18-52)	83,53a (72-104)
15 (JaOz)	4	2	620,50 bc (567-646)	17,75abc (13-21)	12,50ab (11-14)	18,00b (11-27)	21,75ab (18-27)	30,75ab (14-42)	1,8411ab (0,74-3,23)	35,25bc (29-43)	29,25c (21-35)	85,00a (78-89)
22 (KsGd)	13	2-3	629,00 bc (518-878)	18,69abc (13-25)	13,31bc (10-16)	13,00a (8-23)	21,92ab (11-36)	28,46ab (16-49)	1,5901a (0,84-3,27)	33,92abc (27-52)	31,77c (16-54)	81,00a (66-91)
23 (KsRc)	25	2-3	602,36 bc (494-727)	16,44abc (13-19)	13,88c (12-18)	12,30a (8-21)	24,72ab (13-40)	25,08a (14-48)	1,5204a (0,83-3,00)	36,52c (29-49)	26,52ab (15-48)	80,96a (56-100)
4 (TeLo)	2	2	531 (531-531)	14,00 (14-14)	14,00 (14-14)	16,00 (16-16)	15,00 (15-15)	30,00 (30-30)	2,1429 (2,14-2,14)	37,00 (37-37)	35,00 (35-35)	87,00 (87-87)
13 (JaRc)	2	2	586,0 (559-613)	19,00 (18-20)	14,00 (13-15)	12,00 (12-12)	16,50 (14-19)	32,50 (30-35)	1,7222 (1,50-1,94)	30,50 (27-34)	36,00 (29-43)	73,50 (66-81)

N = nombre de spécimens mesurés, PUS = longueur du sac post-vulvaire/épaisseur du corps, a = longueur du corps/épaisseur du corps, c = Longueur du corps/longueur de la queue et v = longueur entre la partie antérieure et la vulve*100/longueur du corps. Ka = Kairouan, Te = Testour, Ja = Jendouba, Ks = Kasserine, Rg = Royal Gala, Sd = Star delicious, Sk = Starkrimson, An = Anna, Rc = Richared, Oz = Orzac, Lo = Llorca, Gd = Golden Delicious, MM106 = porte-greffe en marcottière. Les chiffres entre parenthèses correspondent aux valeurs minimales et maximales, les valeurs de la même colonne suivies par les mêmes lettres (a,b,c…) ne sont pas statistiquement différentes selon le test de Duncan au seuil de 5 %.

La comparaison des différents individus prélevés des échantillons et des espèces de *Pratylenchus* décrites par Frederick et Tarjan 1989, Handoo et Morgan Golden 1989 et ayant deux à trois anneaux sur la base de la classification hiérarchique ascendante montre qu'il est possible de séparer trois groupes (figure 3).

Le premier groupe renferme les individus prélevés à partir des échantillons de marcottières de Jendouba et qui s'apparentent aux espèces *P. neglectus*, *P. brachyurus*, *P. sefaensis* et *P. thornei*. Néanmoins, les individus femelles examinés de ces échantillons ont seulement deux anneaux, ce qui les rapproche de *P. neglectus* et *P. brachyurus*, avec des valeurs

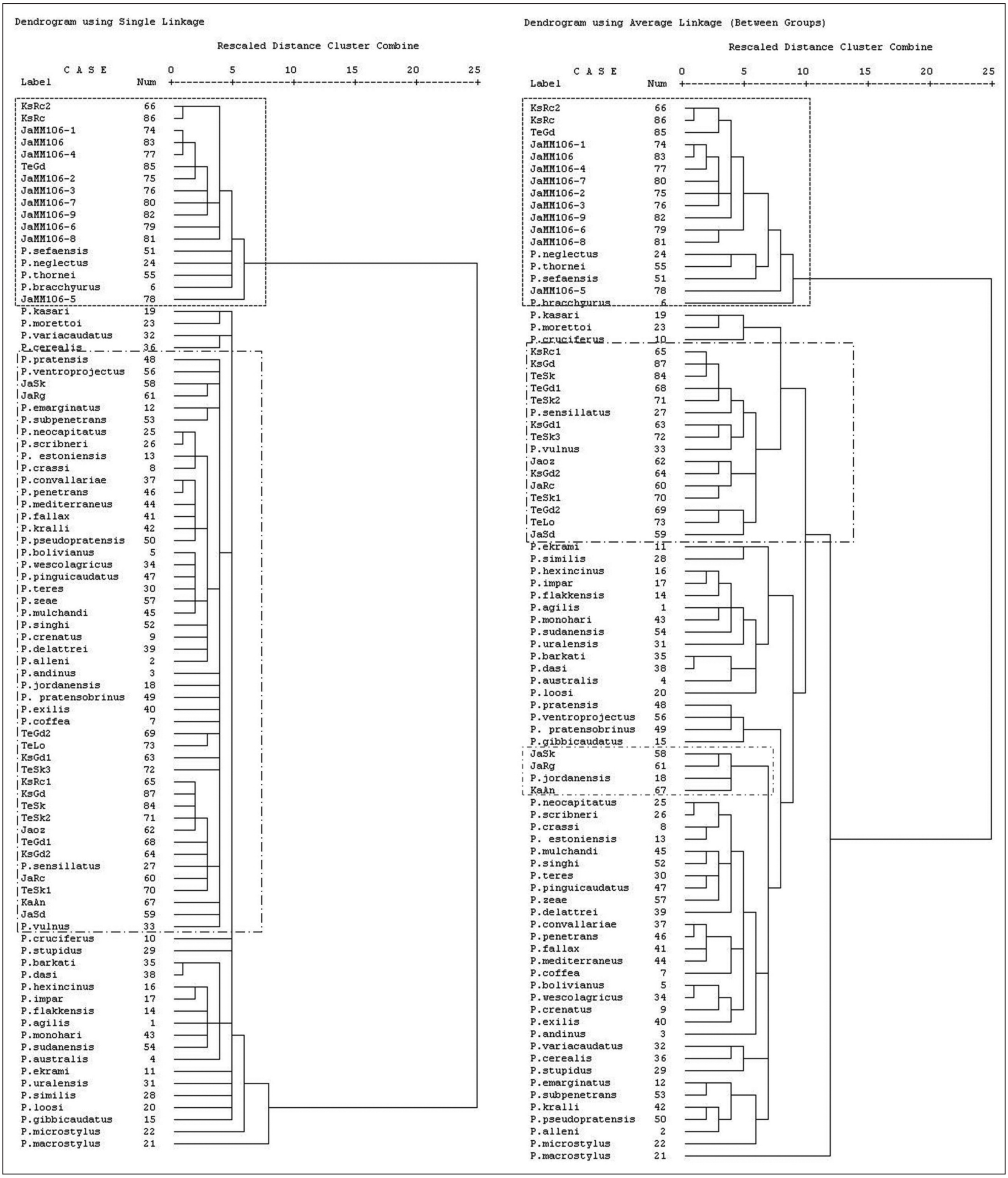

Figure 3 – Dendrogramme de la classification hiérarchique ascendante des différentes populations des espèces de *Pratylenchus* ayant deux ou trois anneaux labiaux en utilisant la distance euclidienne comme méthode de mesure des distances et la distance minimum (A) et la moyenne pondérée des groupes associés (B) comme méthodes d'agrégation.
Ka = Kairouan, Te = Testour, Ja = Jendouba, Ks = Kasserine, Rg = Royal Gala, Sd = Star Delicious, Sk = Starkrimson, An = Anna, Rc = Richared, Oz = Orzac, Lo = Llorca, Gd = Golden Delicious, MM106 = porte-greffe en marcottière.

Figure 3 – Ascending hierarchical classification dendrogram of different* Pratylenchus *species populations having two or three lip rings using the Euclidean distance as a method of measuring distances and single linkage (A) and Weighted Pair-Group Method using Arithmetic averages (B) as method aggregations.
Ka = Kairouan, Te = Testour, Ja = Jendouba, Ks = Kasserine, Rg = Royal Gala, Sd = Star Delicious, Sk = Starkrimson, An = Anna, Rc = Richared, Oz = Orzac, Lo = Llorca, Gd = Golden Delicious, MM106 = rootstocks in stool bed.

du rapport a plus élevées et la longueur du stylet et l'épaisseur du corps plus faibles que *P. brachyurus*. Les individus examinés ont un sac postutérin largement plus grand que l'épaisseur du corps alors que les deux espèces associées ont des valeurs inférieures à l'épaisseur du corps. Les populations prélevées des sites de Testour sur Golden Delicious ressemblent à celles observées dans la région de Jendouba sur marcottière avec un coefficient significativement plus faible (tableau 5). En ce qui concerne les mesures morphométriques sur les deux échantillons de *Pratylenchus* provenant de Kasserine sur des plants de Richared aucune différence significative n'a été observée sur la plupart des caractères morphométriques à l'exception du coefficient c, ce qui permet de conclure qu'ils appartiennent à une même population. Néanmoins, au niveau de l'échantillon KsRc1, les mâles n'ont pas été observés. La population KsRc renferme des femelles qui présentent trois anneaux et les individus présentent un sac postutérin statistiquement plus petit que les populations JaMM106 et TeGd (tableau 5).

Le deuxième groupe de nématodes se distingue du premier par un coefficient c statistiquement plus faible (tableau 5). Les individus des échantillons de Jendouba sur pommier Starkrimson et Royal Gala et de Kairouan sur pommier Anna s'apparentent avec *Pratylenchus jordanensis* (figure 3). Ces femelles présentent un stylet < 18 µm et la population de Jendouba sur Royal Gala présenterait une position de la vulve nettement antérieure.

Enfin le troisième groupe qui renferme treize échantillons s'apparente à *P. sensillatus* et *P. vulnus* (figure 3). Mais ces populations appartiennent vraisemblablement à *P. vulnus* car elles portaient les caractéristiques majeures de cette espèce qui est d'avoir des femelles avec une spermathèque et des mâles fréquents. Les femelles sont significativement plus longues que celles des autres groupes ; elles présentent un métacorpus ovale plus long et un sac postutérin supérieur à deux fois la largeur du corps à la vulve (tableau 5). Néanmoins, la population isolée à Testour sur Starkrimson et celle de Kasserine sur Golden Delicious ont le diamètre du corps le plus élevé. La population de Jendouba sur Orzac a la longueur de stylet la plus faible et le métacorpus le plus long (tableau 5).

Discussion

Plusieurs espèces de *Pratylenchus* sont répertoriées comme inféodées aux porte-greffes de pommier : ce sont *P. vulnus* (Fernandez *et al.* 1992), *P. brachyurus* et *P. coffeae* (Mai et Abawi 1981). *Pratylenchus penetrans* (Vrain & Rousselle 1980), *P. pseudofallax* (Café Filho et Huang 1989), *P. crenatus* (Vrain & Rousselle 1980), *P. neglectus* (Sögüt & Devran 2011), *P. thornei* (Fortuner 1977), *P. manaliensis* (Khan et Sharma 1991) et *P. jordanensis* (Stirling *et al.* 1995) sont répertoriées comme associées aux arbres à pépins. *Pratylenchus jordanensis* serait une espèce synonyme de *P. zeae* (Inserra *et al.* 2005). *Pratylenchus vulnus* et *P. penetrans* ont une aire de répartition très vaste ; elles sont les plus répandues sur les racines des arbres fruitiers à pépins, tant en pépinières qu'en vergers (Scotto La Massèse 1989). *Pratylenchus penetrans*, présent essentiellement dans les zones tempérées froides, parasite la plupart des rosacées fruitières et ornementales ; cette espèce infeste principalement le pommier et le poirier (Esmenjaud *et al.* 1994a). *Pratylenchus vulnus* est considéré comme l'espèce la plus dangereuse pour les cultures pérennes du bassin méditerranéen. Son spectre d'hôte très large lui permet de survivre sur plusieurs plantes cultivées ou spontanées, annuelles ou pérennes (Esmenjaud *et al.* 1994b). Au cours de notre étude trois espèces sont identifiées : *P. jordanensis*, *P. vulnus* et *P. neglectus*.

Cette étude montre qu'en pépinières de pommier, *Pratylenchus vulnus* est l'espèce de nématode dominante en Tunisie. *P. jordanensis* (= *P. Zeae*) est une espèce secondaire et *P. neglectus* est une espèce mineure. Ces résultats concordent avec les travaux de Scotto La Massèse (1975) en France et Pinochet *et al.* (1993) en Espagne qui montrent que *P. vulnus* est la principale espèce de *Pratylenchus* sur pommier en Europe du Sud.

Pratylenchus vulnus préfère les sols légers (sableux) et chauds (Scotto La Massèse 1989). Il peut alors les coloniser jusqu'à un mètre de profondeur (Esmenjaud *et al.* 1994a). La faible humidité du sol peut diminuer leur densité, et à l'inverse peut favoriser leur dissémination lorsqu'elle est élevée. Mais l'influence de l'humidité du sol sur l'expression des symptômes n'est pas confirmée (Jaffee *et al.* 1979). Le buttage avec de sable de carrière ou d'oued dans les marcottières permet la multiplication de ces nématodes sur les jeunes racines initiées sur les plants issus de la plante-mère. En effet, La température affecte la dissémination dans le sol, le taux de croissance, la reproduction et la détermination du sexe de ces nématodes. La population de *Pratylenchus* croît avec la température jusqu'à 29 °C (température optimale de pénétration) alors que les températures optimales de colonisation et de développement sont respectivement de 20 °C et 25 °C (Acosta & Malek 1979). Selon Scotto La Massèse (1989), ce ne sont pas uniquement les exigences thermiques qui régissent la répartition de *P. vulnus* et *P. penetrans,* mais aussi les besoins hydriques qui sont particulièrement élevés pour cette dernière espèce.

Une fois les jeunes plants séparés de la plante porte-greffe mère, puis transférés et greffés en pépinières, les nématodes continuent à se multiplier sur les racines nourricières. Les mesures morphométriques des femelles de *Pratylenchu*s prélevées sur les différents échantillons montrent une variabilité élevée et plus importante que celle qui a servi à déterminer les espèces. Cette variabilité paraît liée à la région de production et à la variété de pommier greffée. D'autres chercheurs ont pu observer une variabilité morphométrique liée à l'origine géographique et à la plante hôte sur *P. vulnus* (Doucet *et al.* 1996), *P. penetrans* (Tarte et Mai 1976) et d'autres genres de nématodes tels que *Rotylenchulus* (Agudelo *et al.*, 2005) et *Xiphinema* (Georgi 1988).

Les céréales sont cultivées dans le cadre d'une jachère avant l'installation de la marcottière dans toutes les pépinières étudiées, ce qui pourrait contribuer à l'infestation des jeunes plants de MM106 et par la suite des plants greffés. En effet, Niang (1985) a montré que les céréales en Tunisie sont attaquées par *P. neglectus* et *P. thornei*, espèces également retrouvées sur les plants de MM106.

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Résumés de thèses

Anna GUITTONNY-PHILIPPE 2014

Phytoépuration de mélanges de polluants organiques et métalliques pour la préservation des zones humides méditerranéennes. Approche exploratoire vers la mise au point d'outils d'ingénierie écologique

Thèse de doctorat en écologie soutenue le 23 juin 2014 à l'université d'Aix-Marseille, laboratoire : IMBE et entreprise ECO-MED, France.

Jury – Jean-Louis MOREL (P^{r}, de l'université de Lorraine), Jacques HAURY (P^{r}, agrocampus de Rennes), rapporteurs. Jean-Luc BOUDENNE (P^{r}, université d'Aix-Marseille), Isabelle COMBROUX (MCF de l'université de Strasbourg), examinateurs. Isabelle LAFFONT-SCHWOB (MCF, université d'Aix-Marseille), Véronique MASOTTI (MCF, université d'Aix-Marseille), directrices. Julien VIGLIONE (PDG d'ECO-MED).

Mots clés : phytoépuration, bioindication, hélophytes natives, multi-pollution.

L'objectif de la thèse était de développer un système de phytoépuration par marais artificiel permettant le traitement simultané de micropolluants organiques (MPO) et d'éléments traces métalliques et métalloïdes (ETMM) en milieu méditerranéen, en vue de traiter les rejets chroniques et accidentels émis par un bassin versant industrialisé, et favoriser ainsi la résilience d'une zone humide protégée. Une étude en serre, dans des microcosmes avec un substrat de pouzzolane, a été conduite sur cinq hélophytes (*Alisma lanceolatum* With., *Carex cuprina* (Sandor ex Heuff.) Nendtv. ex A. Kern., *Epilobium hirsutum* L., *Iris pseudacorus* L. et *Juncus inflexus* L.) natives du marais des Paluns (Marignane, 13). La croissance et le développement des plantes ont été suivis pendant 113 jours d'exposition à des mélanges de MPO (HCT, PHE, PYR, et LAS) et/ou d'ETMM (Al, As, Cd, Cr, Cu, Fe, Mn, Ni, Pb, Sn et Zn), à des concentrations maximales dix fois plus élevées que les seuils de rejets réglementaires. Les concentrations en ETMM dans les parties souterraines et aériennes des plantes ainsi que les communautés bactériennes de la rhizosphère ont été analysées à la fin de l'étude. Les résultats ont confirmé l'efficacité épuratoire du système (taux d'épuration supérieurs à 88 % pour tous les contaminants), et ont permis de mieux comprendre les interactions entre plantes, substrat, polluants et microorganismes, et d'évaluer leurs effets sur les processus épuratoires. Les résultats encouragent l'utilisation de *C. cuprina* pour la phytoaccumulation des ETMM et la phytostimulation, et d'*E. hirsutum* pour la bioindication dans les marais artificiels. Par ailleurs, un outil de bioindication (indice de développement des hélophytes, IDH) a été mis au point pour faciliter l'intégration du marais artificiel au sein du territoire industrialisé, en complément d'une approche sociologique. La thèse a abouti à la mise en place de trois éco-filtres expérimentaux pour le traitement d'effluents industriels et d'eaux de ruissellement routières, en amont du marais des Paluns, afin de tester en conditions réelles les outils développés et de constituer un site pilote pour le bassin méditerranéen.

Keywords: Phytoremediation, bioindication, native helophytes, mixed-pollution.

The thesis aimed at developing a constructed wetland for simultaneous phytoremediation of organic micropollutants (OPM) and trace metals and metalloids (MM) in Mediterranean environment, for treating chronical and accidental releases from an industrialized catchment, and enhancing the resilience of a protected wetland. A greenhouse study was conducted in microcosms with pozzolan substrate, with five native helophytes (*Alisma lanceolatum* With., *Carex cuprina* (Sandor ex Heuff.) Nendtv. ex A. Kern., *Epilobium hirsutum* L., *Iris pseudacorus* L. and *Juncus inflexus* L.) from the "Les Paluns" wetland (Marignane, 13). Plant growth and development parameters were monitored during 113 days of exposure to mixtures of OPM (THC, PHE, PYR, and LAS) and/or MM (Al, As, Cd, Cr, Cu, Fe, Mn, Ni, Pb, Sn, and Zn) with the maximum concentrations ten times over the limits of European quality standards. MM concentrations in belowground and aboveground plant parts and rhizosphere bacterial communities were analyzed at the end of the study. Results confirmed the system depurative efficiency (removal rates superior to 88% for all contaminants) and provided an insight into the interactions between plants, substrate, pollutants and microorganisms, and an assessment of their effects on phytoremediation processes. Results encourage the use of *C. cuprina* for MM phytoaccumulation and for phytostimulation, and of *E. hirsutum* as a bioindicator in constructed wetlands. Finally, a bioindication tool (the Helophyte Development Index, HDI) was created to assist the constructed wetland integration in the industrialized territory,

as a complement of a sociological approach. The thesis led to the implementation of three experimental eco-filters for the treatment of industrial effluents and road runoffs, upstream from the Les Paluns wetland, in order to test in natura the tools developed and to have a pilote site for the Mediterranean basin.

Anne-Cyrielle GENARD-ZIELINSKI 2014

Impact du stress hydrique sur les émissions d'isoprène de Quercus pubescens *Willd*

Thèse de doctorat en écologie et chimie atmosphérique soutenue le 23 juin 2014 à l'université d'Aix-Marseille, laboratoires : Lsce et Imbe.

Jury – Joan Llusià Benet (chercheur à Universitat Autònoma de Barcelona, Espagne), Valérie Simon (maître de conférences Hdr, université de Toulouse), rapporteurs. Mattias Beekmann (directeur de recherche, Lisa Umr Cnrs), Henri Wortham (P^{r}, université d'Aix-Marseille), examinateurs. Catherine Fernandez (P^{r}, université d'Aix-Marseille), Christophe Boissard (maître de conférences, université Diderot, Paris 7), directeurs. Laurence Galsomiès (Ademe), membre invité.

Mots clés : composés organiques volatils biogènes (Covb), isoprène, stress hydrique, sécheresse, croissance, paramétrisation, réseau de neurones artificiels (Rna), algorithme.

Les composés organiques volatils biogènes (Covb) sont des molécules issues du métabolisme secondaire des végétaux, dont l'émission peut être modulée (en intensité et en termes de diversité de molécules) par les conditions environnementales. Parmi ces composés, l'isoprène a été particulièrement étudié du fait des flux d'émission importants, et de sa forte implication dans la photochimie troposphérique. Cependant, tous les mécanismes d'action des contraintes (en particulier environnementales) sont encore mal connus, et notamment l'impact du stress hydrique reste encore contradictoire. Dans un contexte de changements climatiques, les modèles climatiques prévoient que ce type de stress va particulièrement impacter la région méditerranéenne d'ici 2100.

Dans cette étude, nous nous sommes donc intéressés à l'impact du stress hydrique sur les émissions d'isoprène de *Quercus pubescens* Willd. Cette espèce, largement représentée en région méditerranéenne, est également fortement émettrice d'isoprène puisque l'on estime qu'il s'agit de la seconde source biogénique en Europe.

Pour répondre à cette question nous avons menée deux études.

La première, effectuée en pépinière sur de jeunes chênes pubescents, a consisté à appliquer un stress hydrique modéré et sévère tout au long de la période de végétation des chênes (avril à octobre). Elle a permis de mettre en évidence une augmentation significative des émissions d'isoprène des arbres modérément stressés alors qu'aucune modification des émissions n'a été observée pour les arbres stressés.

La seconde expérimentation a consisté à faire un suivi saisonnier *in situ* du stress hydrique au sein d'une chênaie pubescente (O3HP) habituée à subir de longues périodes de stress. Un stress hydrique amplifié a été appliqué au moyen d'un système d'exclusion de pluie (toit déroulant au-dessus de la canopée), permettant de recréer une diminution de la quantité de pluie de 30 %. Lors de cette expérimentation, nous avons mis en évidence que le stress hydrique amplifié engendrait une augmentation significative des facteurs d'émission d'isoprène des arbres.

La base de données expérimentale ainsi constituée a permis le développement, par réseau de neurones artificiels (Rna), d'un algorithme d'émission d'isoprène réduisant significativement les incertitudes des autres paramétrisations disponibles. Nous avons ainsi mis en évidence l'impact prédominant du contenu en eau du sol sur les variations d'émission d'isoprène.

Keywords: Biogenic Volatile Organic Compounds (BVOC), isoprene, water stress, drought, growth, parameterization, Artificial Neural Network (ANN), algorithm.

Biogenic Volatile Organic Compounds (BVOC) are plants secondary-metabolism-molecules. Their emissions are modulated (in terms of intensity and molecules' diversity) by environmental conditions. Among these compounds, isoprene has been particularly studied due to its intense emission fluxes as well as its major contribution to tropospheric photochemistry. However, the impacts of environmental constraints on isoprene emission are still not yet well known. In particular, water stress impact is still a contradictory issue. In a world facing multiple climatic changes, climatic models expect this kind of stress to hit Mediterranean area by 2100.

This work focused on the impact of water stress on Quercus pubescens Willd. isoprene emissions. This species, widely spread in the Mediterranean area, is also a huge isoprene emitter – in fact the second largest over Europe.

Two types of study were used.

First, during an experimental carried out in a nursery, young *Q. pubescens* saplings were grown under a moderate and severe water stress during oak growth period (April to October). This experimentation highlighted a significant increase of isoprene emissions for mid-stressed trees, while no emission changes were observed for the highly stressed trees.

Secondly, an *in situ* experimentation was conducted at the O3HP on a pubescent oak forest with trees acclimated to long lasting stress periods. We followed, during a whole season, the impact, on isoprene emissions, of a water stress created by artificially reducing 30% of the rains by means of a specific deploying roof. Isoprene emission factors were observed to significantly increase under water stress.

The experimental emission database thus obtained was used in an Artificial Neural Network (ANN) to develop an appropriate isoprene emission algorithm, which managed to significantly reduce uncertainties of the other available parameterizations. We underlined the predominant impact of soil water content on isoprene emission variations.

Imen SMIDA **2014**

Recherche des capacités antibactériennes et antioxydantes des Ludwigia *spp, hydrophytes invasives*

Thèse de doctorat des universités de Tunis El Manar et d'Aix-Marseille, soutenue le 5 mai 2014, laboratoire : IMBE.

Jury – Riadh KSOURI (chercheur au CBBC, Tunisie), Jean-Michel SAVOIE (directeur de recherche, INRA Bordeaux), rapporteurs. Hassen AMRI (P^{r}, université Tunis El Manar, Tunisie), Alain LE COUSTUMIER (D^{r}, Hôpital Cahors), examinateurs. Samira ASCHI-SMITI (P^{r}, université Tunis El Manar, Tunisie), Claude CHARPY-ROUBAUD (chargée de recherche IRD, Aix-Marseille), directrices.

Mots clés : *Ludwigia grandiflora*, *Ludwigia peploides*, hydrophytes invasives, capacités antibactériennes, capacités anti-oxydantes.

Introduite depuis l'Amérique du Sud au début du XIX^{e} siècle à Montpellier, les *Ludwigia*, hydrophytes amphibies, ont depuis envahi toute la France. L'objectif de nos recherches a été d'étudier les possibilités de valoriser les tonnes annuelles de biomasse polluante de leurs herbiers. Ainsi, notre étude s'est centrée sur la mise en évidence des capacités biologiques (antibactériennes et antioxydantes) de *L. grandiflora* (durant deux cycles de développement) et de *L. peploides* (durant une période de floraison) d'herbiers du sud de la France. Il s'est avéré que les extraits bruts de leurs différents organes se sont montrés actifs contre 14 souches de bactéries Gram + ou Gram –, potentiellement pathogènes. L'importance de l'inhibition est cependant apparue liée à l'organe et au stade de développement de la plante. Ainsi, les meilleurs résultats ont été obtenus avec les extraits des organes des plantes en période de floraison. En règle générale, les capacités antibactériennes de *L. grandiflora* sont apparues supérieures à celles de *L. peploides*. De même, les extraits des fleurs et des feuilles ont été les plus inhibiteurs. Certains d'entre eux se sont montrés plus actifs que six antibiotiques communs, dont certains très puissants, contre les 14 souches testées et en particulier contre *S. aureus* et *S. enterica*. L'activité antioxydante totale a également été mise en évidence et suivie durant le cycle de développement des deux *Ludwigia*. Elle a été confirmée par le test anti-DPPH. Les EC50 sont même très basses, et parfois concurrentielles de celle obtenue avec le Trolox, le témoin utilisé. En ce qui concerne la composition chimique des organes des *Ludwigia*, les teneurs en composés polyphénoliques analysées durant leur cycle de développement ont pu être reliées aux pouvoirs antioxydants. Au vu des résultats, notre recherche a tenté de s'élargir à celle de la détermination des molécules actives. Les fractionnements bioguidés effectués au cours de cette étude préliminaire ont permis d'isoler des fractions plus actives que l'extrait brut. Toutefois, les analyses par spectrométrie de masse (SM) et de spectroscopie (RMN 1D, IR) n'ont pas permis de pouvoir à ce stade en déterminer les molécules actives. Nos travaux, novateurs, ouvrent cependant des perspectives de valorisation dans les domaines de la pharmaceutique, de la cosmétique et de l'alimentation et, également, pour les recherches en phytochimie et en écologie.

Keywords: *Ludwigia grandiflora*, *Ludwigia peploides*, hydrophytes invasive, antibacterial capacities, antioxidant capacities.

Introduced from South America in the early nineteenth century in Montpellier, *Ludwigia*, amphibious hydrophytes have since invaded the whole of France. The objective of our research was to study the possibilities to enhance the annual tons of biomass clean their beds. Thus, our study focused on the identification of biological capacities (antibacterial and antioxidant) of *L. grandiflora* (during two development cycles) and of *L. peploides* (during a period of flowering) in herbarium southern France. It was found that crude extracts of the different organs are shown active against 14 strains of Gram + and Gram – potentially pathogenic bacteria. However, the extent of inhibition appeared linked to the organ and stage of plant development. So, the best results were obtained with extracts of plant organs during flowering. In general, the antibacterial capacities of *L. grandiflora* appeared superior to those of *L. peploides*. Extracts of flowers and leaves were the most inhibitors. Some of them were more active than six common antibiotics, some very powerful, against the 14 strains tested, particularly against *S. aureus* and *S. enterica*. The total antioxidant activity was also highlighted and followed during the development cycle of both *Ludwigia*. It was confirmed by the anti- DPPH test. The EC50 is even very low, and sometimes competing that obtained with the control used Trolox. As regards the chemical composition of the organs of *Ludwigia*, the analyzed contents of polyphenolic compounds during their development cycle could be related to their antioxidant powers. Given the results, our research attempted to extend to the determination of active

molecules. The guided biosplits made during this preliminary study led to the isolation of the most active fractions as the crude extract. However, mass spectrometry (MS) and spectroscopy (1D NMR, IR) analyses did not allow this time to be able to determine the active molecules. Our innovative study yet provides opportunities for enhancement in the areas of Pharmaceutical, Cosmetics and alimentation, and also for research in phytochemistry and ecology.

Laure MALAGNOUX 2014

Évaluation des impacts environnementaux liés aux pratiques phytosanitaires en vergers de pommiers. Approches écotoxicologique et écologique utilisant un auxiliaire des cultures, le forficule

Thèse de doctorat en écotoxicologie le 6 juin 2014 à l'université d'Avignon et des Pays de Vaucluse, France, laboratoire : Institut méditerranéen de biodiversité et d'écologie, équipe biomarqueurs et bioindicateurs environnementaux

Jury – Éric PINELLI (Pr, ENSAT Toulouse), Annette DE VAUFLEURY (maître de conférences HDR de l'université de Besançon), rapporteurs. Rita TRIEBSKORN (Pr, université de Tübingen, Allemagne), David LEJON (IR au pôle Ecotox Rovaltain), examinateurs. Magali RAULT (maître de conférences, IMBE UMR CNRS, université d'Avignon et des Pays de Vaucluse), Yvan CAPOWIEZ (chargé de recherche, INRA d'Avignon), Mohamed EL MAÂTAOUI (Pr, université d'Avignon et des Pays de Vaucluse), directeurs.

Mots clés : *Forficula auricularia*, approche multiscalaire, biomarqueurs, pesticides, lutte intégrée, *Forficula pubescens*

Dans le contexte européen actuel visant la réduction des risques et de l'utilisation des pesticides, le développement d'outils permettant d'évaluer les impacts environnementaux est un objectif majeur. Cette thèse recouvre approche écotoxicologique et approche écologique sous forme d'études de l'échelle tissulaire à l'échelle des populations. L'espèce modèle est un prédateur généraliste, le forficule, et le site d'étude les vergers de pommiers du sud-est de la France. Les effets des pesticides ont été testés aussi bien en conditions de laboratoire qu'en conditions réelles (en vergers). Les études en laboratoire nous ont permis de caractériser et d'étudier la localisation tissulaire des B-estérases (AChE et CbE) et d'évaluer la capacité prédatrice chez *Forficula auricularia* après exposition, sur le puceron *Dysaphis plantaginea*. Les CbE sont plus sensibles que l'AChE chez F. auricularia et les B-estérases des mâles sont toujours plus sensibles aux insecticides organophosphorés que celles des femelles. Ces résultats nous permettent de valider l'utilisation des B-estérases comme biomarqueurs biochimiques chez *F. auricularia*. La capacité prédatrice de *F. auricularia* est diminuée par certains insecticides avec les mâles plus impactés que les femelles. Les mesures d'activité des B-estérases ont corroboré les résultats validant le comportement de prédation comme un nouveau biomarqueur. À l'échelle de l'organisme, la reproduction et le développement des premiers stades larvaires ont été suivis grâce à un élevage mis en place à partir d'insectes prélevés dans des vergers soumis à différentes pratiques phytosanitaires (agriculture biologique, raisonnée et conventionnelle). Le nombre d'œufs par ponte est réduit et la date de ponte retardée pour les forficules provenant des vergers à agriculture « conventionnelle ». Pour évaluer l'effet des pesticides à l'échelle des populations, l'abondance et la diversité du forficule (*F. auricularia* et *F. pubescens*) ont été suivies en vergers en prenant également en compte des caractéristiques paysagères. L'impact des pratiques phytosanitaires est plus important que celui des caractéristiques paysagères. L'espèce *F. pubescens* est plus sensible que F. auricularia, avec la même différence de sensibilité entre sexes chez les deux espèces (mâles plus sensibles). Le forficule devient alors une espèce bioindicatrice pertinente de l'utilisation des pesticides en vergers de pommiers. Cette étude soulève le besoin de biomarqueurs complémentaires capables de mettre en évidence les modifications physiologiques et comportementales qui influencent les populations d'auxiliaires et la régulation naturelle des ravageurs.

Comptes rendus d'ouvrages
Books reviews

Écologie et conservation d'une steppe méditerranéenne. La plaine de Crau

Book editors: Laurent Tatin, Axel Wolff, Jean Boutin, Étienne Colliot et Thierry Dutoit

Publisher: Éditions Quae

Link: http://www.quae.com/fr/r3190-ecologie-et-conservation-dune-steppe-mediterraneenne.html

Reviewers: Manuel B. Morales and Juan Traba, Departamento de Ecología, Universidad Autónoma de Madrid, c/ Darwin 2, 28049. Madrid, Spain.

As unique, fragile and mistreated ecosystems, steppes have received much scientific attention, being the subject of a whole plethora of treatises and monographs. However, very few have so far treated all the most relevant aspects of a particular steppe ecosystem's ecology and management. Such is the case of *Écologie et conservation d'une steppe méditerranéenne. La plaine de Crau* (Éditions Quae, Paris, 2013) edited by Laurent Tatin, Axel Wolff, Jean Boutin, Étienne Colliot and Thierry Dutoit. But the interest of this complete work comes primarily from the fact that it focuses on the only remain of natural Mediterranean grass steppe that can be found north of the Pyrenees. Once much more extended, the steppe of Crau, located in the French Department of Bouches-du-Rhône in the Provence-Alpes-Côte d'Azur region, and formed on the ancient delta of the river Durance, on the east shore of the Rhône, expands nowadays over about 10,000 ha. This is the surface still covered by the *coussoul*, its most characteristic vegetation type, which makes up the unique phyto-sociological association *Asphodelletum fistulosii*, found nowhere else in Europe and dominated by the ramose false-brome *Brachypodium retusum* and the common thyme *Thymus vulgaris*. The *coussoul* of Crau is the result of at least 4,000 years of interaction between livestock grazing and the natural climate, geological and soil conditions of the area and most of its former domains have been transformed into agricultural land over the last few centuries.

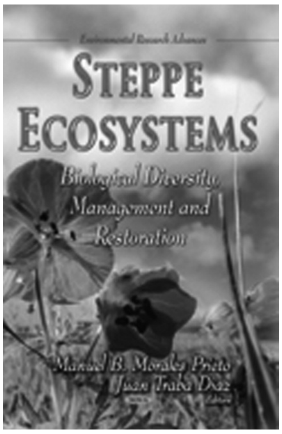
Through its 21 chapters authorized by different experts from management and research public institutions of France, the reviewed volume comprise the main issues regarding the ecology, conservation, restoration and management of Crau's ecosystem, from the description of its biological communities (including plants, invertebrates, birds and lizards) to the social implications of its conservation, especially centred in the success of the co-management. It thus provides a complete synthesis of this fragile and human-pressured ecosystem's origin, functioning, history of human use, and future perspective, based on solid scientific knowledge and compromise for its maintenance. This work should undoubtedly serve as a useful guide in the ever-demanding effort to spread the existing knowledge on Crau's ecosystem and preserve this steppe corner of Mediterranean France.

Steppe Ecosystems: Biological Diversity, Management and Restoration

Book editors: Manuel B. Morales Prieto and Juan Traba Diaz

Publisher: NOVA Publishers

Link: https://www.novapublishers.com/catalog/product_info.php?products_id=43444&osCsid=5623fa8a359634a03977ef96d9718b3b



Steppe environments impose strong constraints on organisms due to limiting climate and soil conditions. Biotic factors also exert important selection pressures on steppe organisms, which display a whole array of remarkable adaptations. However, steppes are also among the most fragile and human-impacted ecosystems of the world. As a consequence of these ecological and conservation characteristics, steppe ecosystems and organisms have always drawn the attention of ecologists and conservation biologists.

Through the contribution of steppe ecologists from world regions, Steppe Ecosystems: Biological Diversity, Management and Restoration (NOVA Publishers, New York, 2013) edited by Manuel B. Morales and Juan Traba, addresses hot issues in steppe ecology and conservation such as how did present-day steppe ecosystems arise? Is the steppe a perfectly identifiable and homogeneous biome, or are there different types of steppes? If the latter is true, what are the abiotic and biotic factors that define steppe ecosystems? Do they function differently? In other words, what is a steppe? Can we identify clearly steppe-specific taxa? Are their functional traits homogeneous across steppe ecosystems? How are their main biodiversity patterns?

Through its 361 pages, this book gives answers to these questions, starting with an extensive overview of steppes across the world, and providing a definition of steppe for the consensus. The initial series of 7 chapters is dedicated to describe patterns and processes in steppe ecosystems, relating steppe diversity with both biotic and abiotic factors, and using examples from different parts of the world.

This volume also results from the current concern about the fate of the world's steppes, threatened by increasing land-use intensification, highlighting the need for their sustainable management on the basis of adequate scientific knowledge. A second part of the volume with another 7 chapters is therefore dedicated to describe examples of conservation and restoration all around the world. Precisely, this is another interest of this book: its broad view of steppe diversity and conservation in many different countries, from Argentina to Mongolia, passing by Spain, China, Hungary, Russia, France, Algeria or Tibet, covering almost all the steppe biomes of the world.

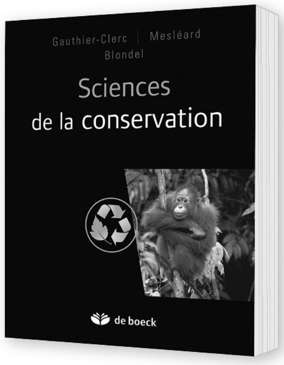
In summary, the chapters comprising this work not only contribute to disseminate up-to-date scientific knowledge on steppe ecosystems, which is always a major aim, but provide cues and tools to assess their state and to scientifically inform and help their management. Hopefully, these messages will reach the right ears.

Sciences de la conservation

Auteurs : Michel Gauthier-Clerc, François Mesléard, Jacques Blondel

Éditeur : de boeck

Site : http://superieur.deboeck.com/titres/131006_/sciences-de-la-conservation.html



Les sciences de la conservation prennent une importance grandissante et répondent à une forte demande sociétale. Il était devenu urgent de réaliser à l'intention des lecteurs francophones un manuel de référence dans ce domaine. Ce livre comble cette lacune en étant édité sous forme d'un manuel, qui puisse servir de support à l'enseignement de cette discipline et également constituer un portail d'entrée pour un large public (gestionnaires, politiques, professionnels de l'environnement, etc.).

Ce livre se situe à l'interface d'un champ très large de disciplines, abordant entre autres les causes et les mécanismes de la perte de biodiversité, les aspects historiques et les concepts philosophiques de la conservation, les politiques publiques, les décisions partagées et la gestion des conflits ou encore les valeurs économiques de la biodiversité. Les connaissances scientifiques de base sont illustrées par un grand nombre d'encarts, illustrant des exemples concrets et des cas pratiques.

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