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Caracterización de los pinares de *Pinus halepensis* Mill. en el sur de la Península Ibérica

Caractérisation des pinèdes de *Pinus halepensis* Mill. du sud de la Péninsule Ibérique

Characterisation of *Pinus halepensis* Mill. pine forests in southern Iberian Peninsula

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RESUMEN

Estudiamos las comunidades naturales de *Pinus halepensis* en el sur de España (Andalucía). Se recopila toda la información bibliográfica disponible que aporta datos de interés sobre su espontaneidad en toda la cuenca mediterránea, con especial referencia a la Península Ibérica. Ponemos de manifiesto el carácter edafoxerófilo de este tipo de formaciones en el área de estudio con la descripción de una nueva asociación y una comunidad vegetal : *Junipero phoeniceae-Pinetum halepensis* y comunidad de *Ephedra fragilis* y *Pinus halepensis*.

Palabras clave : *Pinus halepensis*, pinares autóctonos, carácter edafoxerófilo, sur de España

RESUME

Cette étude porte sur les communautés naturelles de *Pinus halepensis* du sud de l'Espagne (Andalusia). Toute l'information bibliographique concernant la spontanéité dans le bassin Méditerranéen, particulièrement celle de la Péninsule Ibérique, est compilée. Le caractère édapho-xérophile de ce type de formations dans l'aire d'étude est mis en évidence, et une nouvelle association est décrite : *Junipero phoeniceae-Pinetum halepensis*, ainsi qu'une communauté à *Ephedra fragilis* et *Pinus halepensis*.

Mots-clés : *Pinus halepensis*, pinèdes autochtones, caractère édapho-xérophile, sud de l'Espagne

ABSTRACT

A study on the natural communities of *Pinus halepensis* in southern Spain (Andalusia) is carried out. A compilation of the bibliographic information that contributes interesting data on their spontaneity in the Mediterranean basin is previously made, pointing out those references where the Iberian Peninsula is treated.

We emphasize the edaphoxerophilous character of this vegetation type in the study area, and we provide the description of a new phytosociological association (*Junipero phoeniceae-Pinetum halepensis*) and a new plant community (community of *Ephedra fragilis* and *Pinus halepensis*)

Key-words: *Pinus halepensis*, native pine forests, edaphoxerophilous character, southern Spain

ABRIDGED ENGLISH VERSION

A study on the natural communities of *Pinus halepensis* in the south of Spain (Andalusia) has been carried out. The bibliographic information with data of interest about its spontaneity in the whole Mediterranean basin (specially in the Iberian peninsula) has been compiled. The edaphoxerophilous character of this pine-woods in the study area has been pointed out, having described a new phytosociological association and a plant community: *Junipero phoeniceae-Pinetum halepensis* and community of *Ephedra fragilis* and *Pinus halepensis*.

The spontaneous formations of *Pinus halepensis* in the Iberian peninsula develop on basic substrata, specially in the mediterranean coastal provinces (Cataluña, Comunidad Valenciana, Murcia and Baleares), reaching interior zones of the Baetic ranges, Iberian System, Ebro valley and eastern Pirenees. They mainly appear under Mediterranean-pluviestational-oceanic, Mediterranean-xeric-oceanic and Mediterranean-pluviestational-continental bioclimates, ranging between thermomediterranean and mesomediterranean thermotypes and from semi-arid to sub-humid ombrotypes, sharing the areas occupied by shrub communities of holly-oaks (*Quercus coccifera* L.), lentiscs (*Pistacia lentiscus* L.) or savines (*Juniperus phoenicea* L.) depending on the substrata nature.

The iberian pine-woods of *P. halepensis*, take the case of the iberic southeastern have been scarcely studied, though they are one of the most characteristic elements in the plant landscape. In spite of the physiognomic importance and their widespread area, a large number of authors question the climatic role of these woods in the Mediterranean region, even stating that *P. halepensis* does not grow spontaneously in the Western Mediterranean. Though there are several bibliographic references in which a secondary and anthropic character is assigned to this pine in woods and scrubs, it has never been regarded as the main species in such communities.

There are only a few botanists that have pointed out the natural and autochthonous character of *P. halepensis* in some territories, either co-dominating with trees and shrubs or dominating the community by itself.

In our study, bearing in mind the results of fossil and subfossil registers of the last 15.000 years and the analysis and taxonomic identification of charcoals, we show interesting data about the spontaneous character of *P. halepensis* in the Baetic area (southern peninsula) where it takes part of edaphoxerophilous communities confined to the most thermic and dry zones (sunny exposures) due to the lithological, geomorphological and climatological territorial factors. The widespread calcareous-dolomitic emergences allow the existence of a sheer landscape with big rocky blocks where the permeability of the substrata reduces the effects of the real precipitations in the territory. Furthermore, the karstification processes, break and crush the rocks causing hiperxeric environments very suitable for the establishing of *P. halepensis* pine-woods.

These pine-woods can also take place on marls (even with a high content of gypsum) in extremely degraded soils that accentuate the ombroclimatic xericity. This fact is quite common in places with rains shades where the precipitations coming from the Atlantic ocean are very reduced because of the existence of high mountain boundaries.

Thus, *P. halepensis* (as other conifers) constitutes natural formations in southern Iberian peninsula, specially in the thermomediterranean and mesomediterranean belts, and at a lesser extent in the inferior suprasediterranean. In some cases, a semi-arid territory rich in Neogenous-Quaternarian deposits (marls, calcareous marls and conglomerates) with a scarce water retention is optimum for the development of *P. halepensis*. In the other hand, a rough geomorphology of calcareous-dolomitic ranges may be the determining factor for the establishing of these pine-woods, in this case under a wider range of ombrotypes (semi-arid, dry and sub-humid).

INTRODUCCIÓN

Pinus halepensis Mill. es un árbol generalmente retorcido, de unos 12-14 m de altura media, normalmente aparasolado, aunque puede llegar hasta los 22-24 m en las mejores situaciones ecológicas. Presenta una distribución básicamente circunmediterránea, formando bandas cercanas a la costa donde no suele superar los 700-800 m de altitud, a excepción de ciertas zonas de África del Norte donde puede llegar hasta los 2000 m (Quézel, 1977, 1980).

Desde el punto de vista taxonómico se trata de una especie ecológica y genéticamente muy próxima a *Pinus brutia* Ten. (Biger & Liphshitz, 1991) con el que forma un grupo bien definido (grupo *Halepenses*). Ampliamente extendido por todo el Mediterráneo occidental, es sustituido hacia el oeste por su vicariante *Pinus brutia* (Figura 1). Aunque raramente suelen coexistir ambas especies (Akman *et al.*, 1978), en el caso de hacerlo, como ocurre en algunos distritos

de Grecia, en el sureste de Anatolia y en el Líbano, suelen formar híbridos naturales (Panetsos, 1975). Las poblaciones apartadas de *Pinus halepensis* en Asia Menor y Cercano Oriente, al límite este de la Cuenca Mediterránea, plantea curiosas cuestiones a cerca del modelo de distribución en el pasado y las rutas migratorias (Barbero *et al.*, 1998).

En la Península Ibérica, las formaciones espontáneas de *Pinus halepensis* aparecen sobre sustratos básicos, principalmente en las provincias del litoral mediterráneo (Cataluña, Comunidad Valenciana, Murcia y Baleares), penetrando hacia el interior en las sierras Béticas, Sistema Ibérico, Valle del Ebro y Pirineos orientales. Se distribuye mayoritariamente en los bioclimas Mediterráneo pluviestacional-oceánico, Mediterráneo xérico-oceánico y Mediterráneo pluviestacional-continental con ciertas penetraciones en el Templado oceánico-submediterráneo (Rivas-Martínez, 1996a, 1996b). Puesto que el factor determinante para su distribución

parece ser la temperatura, especialmente las mínimas invernales (Falusi *et al.*, 1984), ocupan tan solo los termotipos termomediterráneo y mesomediterráneo con ombrotipos que oscilan entre el semiárido y el subhúmedo, donde convive sobre todo con coscojares (*Quercus coccifera* L.), lentiscas (*Pistacia lentiscus* L.) y sabinas de sabinas mora (*Juniperus phoenicea* L.), dependiendo de la naturaleza del sustrato.

Consideraciones sobre el carácter climático de *Pinus halepensis*

Los pinares ibéricos de pino carrasco, y concretamente los del sudeste ibérico, han sido objeto de escasos estudios botánicos a pesar de tratarse de uno de los elementos más característicos del paisaje vegetal de esta parte de la Península Ibérica.

En este sentido cabe mencionar las referencias que algunos botánicos clásicos hacen de dichos pinares; así, Hugué del Villar (1916, 1925) pone de manifiesto el carácter natural y autóctono de *Pinus halepensis* en algunos territorios en los que aparece, donde formaría conclímax con la encina (*Quercus ilex*). Cuatrecasas (1929) en su trabajo sobre Sierra Mágina hace referencia al carácter climático de estos pinares en las vertientes inferiores más cálidas y secas de todo el Macizo. Font Quer (1933) en sus observaciones botánicas sobre la vegetación de Los Monegros constata el papel subalterno de *Quercus coccifera* en

su *Pinetum halepensis*. Laza Palacios (1946) en sus estudios sobre la flora y vegetación de las Sierras Tejada y Almirajara describe un *Pinetum halepensis* para los pisos semiárido y templado de la clasificación fitogeográfica de Emberger donde, sin entrar a valorar la potencialidad climática del pino de Aleppo, considera de gran vitalidad el estado actual del pino carrasco. Rivas Goday (1951) al abordar el estudio de la vegetación y flora de la provincia de Granada pone de manifiesto la espontaneidad de *Pinus halepensis* sobre dolomías. Braun-Blanquet *et* Bolòs (1958) en sus estudios del Valle del Ebro al describir la asociación *Rhamno-Quercetum cocciferae* esgrimen dentro de la faciación típica una variante con *Pinus halepensis*, en ombroclima semiárido, que catalogan como una comunidad particular donde *Quercus coccifera* subsiste bajo la copa de pinares de *Pinus halepensis*. Fernández Casas (1972) en su estudio fitográfico sobre la Cuenca del Guadiana Menor vuelve a resaltar su naturalidad sobre sustratos margosos y ombrotipo semiárido. Por último, Costa (1987) al describir la vegetación del País Valenciano insiste en considerar las formaciones de *P. halepensis* como naturales, aunque con un carácter secundario (nunca ocupan una posición climática) y procedentes de la degradación de carrascales.

Más recientemente, Arrojo (1994) pone de manifiesto el carácter natural de estos pinares en la Sierra de Castril (Granada).

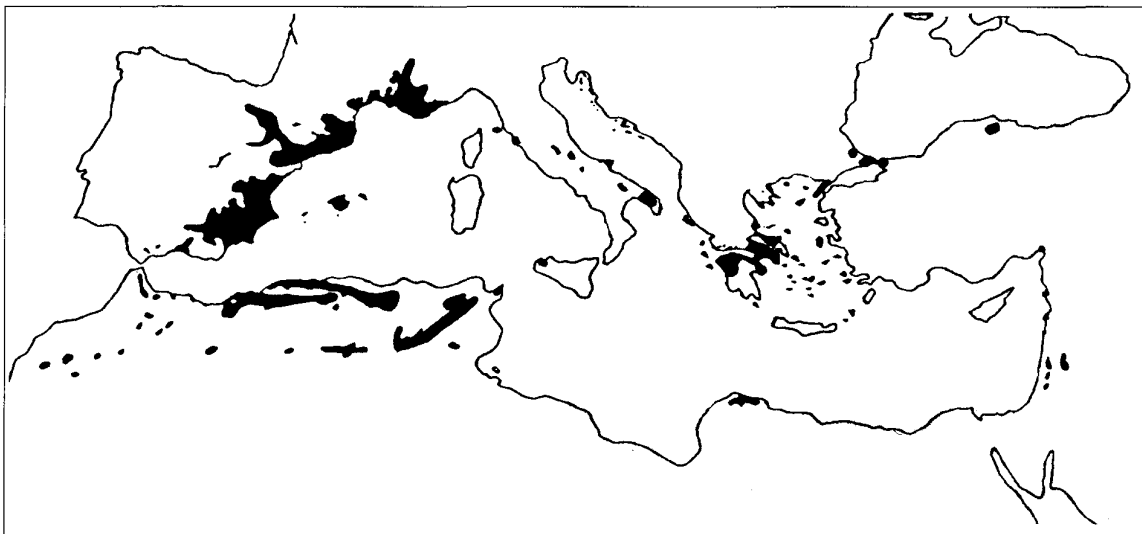


Figura 1. Distribución de *Pinus halepensis* en la Cuenca Mediterránea (modificado de Barbero *et al.*, 1998)
Figure 1. *Pinus halepensis* distribution in the Mediterranean basin (modified from Barbero *et al.*, 1998)



Figura 2. Área de estudio. Localización biogeográfica: Provincia Bética, 1 : Sector Subbético, 1a distrito Subbético-Maginense, 1b distrito Cazorlense, 1c distrito Alcaracense, 1d distrito Subbético-Murciano; 2 : Sector Guadiciano-Bacense, 2a distrito Guadiciano-Bastetano, 2b distrito Serrano-Bacense, 2c distrito Serrano-Mariense, 2d distrito Serrano-Estaciense.

Figure 2. Study area. Biogeographical location: Baetic province, 1. Sub-Baetic sector: 1a Sub-Baetic-Maginense district, 1b Cazorlense district, 1c Alcaracense district, 1d Sub-Baetic-Murciano district. 2. Guadiciano-Bacense sector: 2a Guadiciano-Bastetano district, 2b Serrano-Bacense district, 2c Serrano-Mariense district, 2d Serrano-Estaciense district.

De igual forma, Torres *et al.* (1994) en sus estudios sobre los pinares de *Pinus halepensis* en el sector Subbético consideran el carácter autóctono de estas formaciones, criterio igualmente compartido por Navarro Reyes (1995, 1997) en las sierras de Baza y Las Estancias (Granada).

De igual forma, diversos autores en otros países del entorno mediterráneo destacan el carácter espontáneo de esta especie y su papel en el dinamismo de la vegetación (Emberger, 1939; Tregubov, 1963; Loisel, 1971; Ozenda, 1975; Tomaselli, 1977; Achhal, 1986; Quézel, 1986; Quézel *et al.*, 1987; Quézel *et al.*, 1988; Fennane, 1988; Quézel & Barbero, 1992; Quézel *et al.*, 1992; Barbero *et al.*, 1998).

Pese a su importancia fisionómica y a su amplia distribución, muchos autores discuten el papel climácico de estos bosques en la región Mediterránea, llegando incluso a afirmar que no crece espontáneamente en el Mediterráneo occidental. Existen muchas referencias concretas de esta especie

que le asignan siempre un papel secundario y antrópico en diversas comunidades climácicas boscosas, o incluso de matorrales, pero en ningún caso se reconoce el papel prioritario que pueda tomar el pino carrasco en las mismas. Así, Bolòs (1962) considera la presencia de *Pinus halepensis* como un accidente en las comunidades vegetales en que aparece. Folch (1981) destaca el carácter secundario y antrópico del pino carrasco y al igual que el anterior autor alude a la falta de especies vegetales características. Bolòs (1987) en sus estudios sobre la vegetación de Cataluña y la Depresión del Ebro plantea el problema de la participación de *Pinus halepensis* en la estructura y dinamismo de la vegetación propia del dominio del *Rhamno-Quercetum cocciferae* Braun-Blanquet & Bolòs 1954, donde lo considera frecuente en la maquia climácica, aunque normalmente con una baja densidad. Ferreras *et al.* (1987) reinciden en su carácter secundario debido a la acción del hombre y los consideran como etapa serial de otras formaciones más densas y sombrías. Nuet *et al.* (1991) vuelven a

referir la falta de un cortejo florístico propio y por tanto no llegan a considerlos como una comunidad vegetal. Sánchez-Gómez *et al.* (1993) consideran al pino carrasco como especie integrante de la vegetación permanente de roquedos calizos y que puede actuar como primocolonizador de suelos degradados.

Por otro lado las investigaciones paleobotánicas también contribuyen, a través de los registros fósiles o subfósiles, sobre todo los de los últimos 15.000 años, a evidenciar el carácter natural y autóctono de *Pinus halepensis*. En este sentido, los espectros polínicos (Parra, 1983; Stika, 1988; Yll, 1988; Rivera & Obón, 1991; López, 1991, 1992) y sobre todo los análisis de maderas carbonizadas con sus precisiones taxonómicas e identificación al nivel específico (Vernet *et al.*, 1983, 1987; Ros, 1988, 1992; Bernabeu & Badal, 1990, 1992; Rodríguez Ariza *et al.*, 1991; Rodríguez Ariza, 1992; Rodríguez Ariza & Vernet, 1992; Grau, 1993; Dupré, 1988; Hopf, 1991; Badal, 1991, 1995; Badal *et al.*, 1994) aportan datos interesantes sobre la presencia ancestral de pino carrasco en la Península Ibérica. Las zonas de Levante son las que presentan mayor número de datos, observándose la continuidad de pino carrasco desde el Peniglaciar (Gil Sánchez *et al.*, 1996).

Parece, pues, justificado considerar a *Pinus halepensis*, al igual que otras especies de coníferas, como una especie autóctona ampliamente distribuida por el mediterráneo Occidental, y con carácter permanente o edafoxerófilo en aquellos espacios ecológicos donde determinados factores limitantes (edáficos, litológicos, geomorfológicos y climáticos) impiden su colonización por la vegetación esclerófila potencial. En nuestra opinión muchas de las afirmaciones que discuten el carácter espontáneo de estos pinares se deben a la gran adaptabilidad ecológica de esta especie para difundirse a expensas de los bosques esclerófilos.

Los pinares de *Pinus halepensis* en el sur de la Península Ibérica : área de estudio

En el presente trabajo, se estudian las formaciones de *Pinus halepensis* en las zonas Béticas del sur peninsular. Biogeográficamente, la zona de estudio se extiende por los sectores Subbético y Guadiciano-Bacense de la provincia corológica Bética, localizados

en la zona centro-nororiental de Andalucía (España) (Figura 2).

Desde el punto de vista geológico es posible diferenciar dos grandes unidades tectónicas muy relacionadas con las tipologías de pinares que presentamos en este trabajo: por un lado, las Zonas Externas de las Cordilleras Béticas (Prebético y Subbético), de gran extensión en el territorio y eminente carácter montañoso, con alturas en algunos casos superiores a los 2000 m, donde la litología responde básicamente a formaciones calizo dolomíticas, en muchos casos incluso kakiritizadas, que proporcionan un relieve muy particular de aspecto ruiforme, donde la potencia caliza-dolomía es muy variable, llegando incluso en algunas zonas a desaparecer completamente la caliza en favor de la dolomía, como es el caso de la Sierras de Castril (Granada) y Cazorla-Segura y Las Villas (Jaén). Aunque los afloramientos rocosos ocupan una gran extensión, los suelos que aparecen son de tipo litosol, ya que se trata de zonas con fuertes pendientes que han sufrido intensos procesos de erosión.

Por otro lado, la unidad Neógeno-Cuaternaria está representada por la Depresión del Guadiana Menor en la que abundan materiales sedimentarios; aparecen margas, margo-calizas y margas yesíferas, con afloramiento en las cotas más altas de los materiales más deleznable que permiten una rápida evapotranspiración del agua y por tanto una alta xericidad edáfica. Los suelos que se desarrollan son de tipo cambisoles cálcicos y regosoles calcáreos, con pendientes que oscilan entre el 10 y el 20% con una topografía generalmente colinada.

MATERIAL Y MÉTODOS

Los datos geológicos los hemos obtenido a partir de la cartografía del Instituto Geológico y Minero de España, hojas de Villacarrillo (Virgili & Fonbote, 1987), Jaén (García Dueñas & Fonbote, 1986), Baza (Vera & Fonbote, 1982) y Granada-Málaga (Aldaya *et al.*, 1980). Para el estudio de suelos hemos seguido a Aguilar *et al.* (1987) y Pérez Pujalte & Prieto Fernández (1980). La identificación de bioclimas y pisos bioclimáticos se basan en Rivas-Martínez (1996a, 1996b). Para la distribución biogeográfica seguimos a Rivas-Martínez *et al.* (1997). Las series de vegetación han sido determinadas basándonos en la obra de Rivas-Martínez (1987) y para el muestreo de

las comunidades, hemos utilizado el método fitosociológico de la Escuela de Zurich-Montpellier (Braun-Blanquet, 1979). En la nomenclatura de los sintáxones se contemplan las normas del Código de Nomenclatura Fitosociológica (Barkman *et al.*, 1986), mientras que para la denominación y autoría de los taxones utilizamos las siguientes obras: Flora Ibérica (Castroviejo *et al.*, 1986-1998) y Flora Europea (Tutin *et al.*, 1964-1980), a excepción de *Genista cinerea* subsp. *speciosa* Rivas Goday *et* T. Losa *ex* Rivas-Martínez, T.E. Díaz, F. Prieto, Loidi *et* Penas in *Los Picos de Europa*: 268. 1984; *Leucanthemopsis spathulifolia* (Gay) Rivas-Martínez, Asensi, Molero Mesa *et* Valle in *Rivasgodaya* 6: 42. 1991.

RESULTADOS

Las comunidades espontáneas de *Pinus halepensis* en la zona de estudio constituyen formaciones edafoxerófilas, limitadas por la litología, geomorfología y climatología del territorio a las vertientes más térmicas y xerófilas del territorio, normalmente coincidentes con las exposiciones más soleadas. Los abundantes afloramientos calizo-dolomíticos definen un paisaje de escarpes, dolinas, lapiares y grandes bloques rocosos, donde la gran permeabilidad de este tipo de sustratos, amortigua las precipitaciones reales del territorio. Si a su vez sumamos los procesos de karstificación que fragmentan y triturar la roca madre, se generan medios hipérxéricos óptimos para el asentamiento de pinares de *Pinus halepensis*. De igual manera, los sustratos margosos, a veces con alto contenido en yesos y suelos extremadamente degradados, suelen acentuar la xericidad ombroclimática y soportan masas de *Pinus halepensis*, normalmente en zonas de sombra de lluvias, donde las precipitaciones procedentes del Atlántico se ven muy mermadas por los macizos montañosos del territorio.

En estos territorios hemos reconocido dos formaciones vegetales de gran importancia ecológica que describimos como nuevas para la ciencia, donde el pino de halepo o carrasco (*Pinus halepensis*) adquiere un carácter relevante en la comunidad.

Junipero phoeniceae-Pinetum halepensis ass. nova (Holotypus inv 13, Tabla 1)

Constituyen pinares abiertos de *Pinus halepensis*, de baja cobertura, normalmente aparasolados, donde

son frecuentes otras gimnospermas como *Juniperus oxycedrus* L. y *Juniperus phoenicea* L. Destaca la presencia de *Rhamnus myrtifolius* Willk. y *Rhamnus lycioides* L., ambos taxones bien adaptados a los suelos esqueléticos carbonatados y que soportan una gran desecación del suelo.

La composición florística del matorral acompañante, poco diversificada, es rica en endemismos béticos que dan matiz corológico a esta asociación; entre ellos destacan *Echinospartum boissieri* (Spach) Rothm., *Thymus orospedanus* Huguet del Villar, *Genista cinerea* subsp. *speciosa* y *Ptilostemon hispanicus* (Lam.) Greuter, junto a una cohorte de elementos propios de dolomías como son *Centaurea granatensis* Boiss., *Convolvulus boissieri* Steudel, *Centaurea boissieri* DC. subsp. *willkommii* (Schultz Bip. *ex* Willk.) Dostál, *Pterocephalus spathulatus* (Lag.) Coulter, *Fumana paradoxa* (Heywood) J. Güemes, *Scorzonera albicans* Cosson y *Leucanthemopsis spathulifolia* (Tabla 1).

La comunidad se extiende por el termotipo mesomediterráneo del sector Subbético, con irradiaciones en el sector Guadiciano-Bacense, alcanzando los 1400 m de altitud en algunas laderas soleadas del Macizo de Mágina y Sierra de Castril. Su óptimo aparece bajo ombroclima seco-subhúmedo e inviernos templados.

Se desarrolla en crestones y laderas abruptas sobre sustratos calcáreos, calizas y calizo-dolomías, con suelos poco evolucionados de tipo litosol, donde adquiere carácter de comunidad permanente. La alta xericidad del sustrato y las elevadas temperaturas del periodo estival no permiten la entrada de la serie potencial de todo el territorio, correspondiente a los encinares del *Paeonio coriaceae-Querceto rotundifoliae* sigmetum, con la que contacta catenalmente hacia los suelos más desarrollados.

Desde el punto de vista sintaxonómico guarda relación con diversas comunidades paraclimáticas donde la sabina mora (*Juniperus phoenicea*), especie extremadamente austera y de marcado carácter rupícola, está representada de forma constante (Tabla 3). La ausencia de *Pinus halepensis* en los sabinares del *Rhamno lycioidis-Juniperetum phoeniceae* Rivas-Martínez *et* G. López in G. López 1976, pone de manifiesto el claro carácter continental de esta asociación, cuyo óptimo se alcanza en los termotipos meso- y supramediterráneo de la provincia Castellano-

	NE	E	E	E	E	E	SE	S	S	SE	SE	SW	S	SE	E
Orientación															
Pendiente (%)	5	90	35	25	10	25	15	70	40	30	30	30	25	40	30
Altitud (l= 10m)	90	110	115	115	120	100	110	135	125	115	70	110	127	125	130
Area (l= 10m ²)	40	30	40	40	40	40	40	10	10	30	10	10	10	40	40
Cobertura (%)	40	40	70	60	60	40	60	40	40	60	65	65	60	40	50
Altura media (m)	4	3	3	5	3	4	5	3	4	6	4	5	5	4	5
Nº de orden	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15

Características de asociación y unidades superiores

<i>Juniperus phoenicea</i>	1	1	3	1	1	1	3	2	1	2	2	2	1	2	2
<i>Pinus halepensis</i>	2	2	3	3	3	3	2	1	2	3	3	3	3	2	3
<i>Juniperus oxycedrus</i>	1	+	.	2	3	1	.	+	.	+	1	1	+	1	+
<i>Rhamnus myrtifolius</i>	+	+	+	1	1	+	.	1	.	.	+
<i>Rhamnus lycioides</i>	+	+	+	1	1	+	1	+	.	.	1	1	+	1	.
<i>Pistacia terebinthus</i>	+	.	+	1	1	+	1	.	.	.
<i>Phillyrea angustifolia</i>	+	.	.	.	1	+
<i>Daphne gnidium</i>	+	+	.	.	+
<i>Teucrium fruticans</i>	.	.	+	+	+	+
<i>Buxus sempervirens</i>	2	.	.	1
Compañeras															
<i>Rosmarinus officinalis</i>	.	+	+	+	.	+	+	+	.	+	2	2	2	1	2
<i>Echinopartum boissieri</i>	.	1	1	1	+	.	1	.	+	2	.	.	1	.	.
<i>Bupleurum fruticosum</i>	+	1	+	.	1	.	.	.
<i>Thymus zygis</i> subsp. <i>gracilis</i>	.	+	+	+	+	+
<i>Thymus orospedanus</i>	1	+	1	1	1	1	1	1	+
<i>Teucrium capitatum</i>	.	.	.	+	+	.	.	.	+	1	+
<i>Phlomis purpurea</i>	+	.	.	+
<i>Phagnalon saxatile</i>	+	.	+	+	+
<i>Cistus albidus</i>	.	+	+	+	2	+	1	.	.	.
<i>Brachypodium retusum</i>	+	.	+	1	+	.	1	.	.	.	1	.	.	.	+
<i>Urginea maritima</i>	+	.	.	+	+	+
<i>Genista cinerea</i> subsp. <i>speciosa</i>	+	+	+	+	+
<i>Sedum sediforme</i>	+	.	.	+
<i>Stipa tenacissima</i>	.	.	+	+	+	1	.	1	+	+
<i>Lavandula latifolia</i>	+	1	.	1	.
<i>Ptilostemon hispanicum</i>	.	.	.	+	.	+	+	.	+	+
<i>Thymus mastichina</i>	.	.	.	+	+
<i>Helianthemum croceum</i>	.	.	+	1	1	+	.
<i>Bupleurum spinosum</i>	+	+
<i>Festuca scariosa</i>	+	+
<i>Helianthemum cinereum</i> subsp. <i>rubellum</i>	+	1	+
<i>Ulex parviflorus</i>	1	+
<i>Centaurea granatensis</i>	2	1
<i>Convolvulus boissieri</i>	1	1
<i>Centaurea boissieri</i> subsp. <i>willkommii</i>	+	1
<i>Pteroccephalus spathulatus</i>	+	+
<i>Fumana paradoxa</i>	+	1	.	.
<i>Scorzonera albicans</i>	+	+	.	.
<i>Leucanthemopsis spathulifolia</i>	+	1	.	.
<i>Helianthemum frigidulum</i>	+

Además : *Santolina canescens* + en 3 ; *Asphodelus albus* +, *Arbutus unedo* + en 4; *Phlomis lychnitis* + en 5; *Prunus spinosa* + en 6 ; *Aphyllantes monspeliensis* + en 8 ; *Cistus clusii* 1, *Helianthemum cinereum* + en 9 ; *Sedum dasyphyllum* 1 y *Lactuca tenerrima* + en 10 ; *Polygala rupestris* +, *Asperula hirsuta* + y *Globularia spinosa* + en 11 ; *Genista scorpius* 2, *Paronychia suffruticosa* + en 12 ; *Silene legionensis* + en 13; *Fumana ericoides* + en 14 ; *Teucrium pseudo-chamaepitys* + en 15.

Localidades: 1,2,3,4 y 5 Cerca Castillo Otiñar (Jaén); 6 Barranco El Lobo (Sierra de Jaén, Jaén); 7 Barranco Los Cortijuelos (Jaén); 8 Barranco La Cañada (Carchelejo, Jaén); 9 Cabra de Sto. Cristo (Jaén); 10 Cerro Cuello de Ventarique (Carchelejo, Jaén); 11 Arroyo Los Miradores (Los Villares, Jaén); 12 Castril-Pozo Alcón (Granada); 13 Sierra de Castril (Granada); 14 y 15 Sierra de la Cruz (Sierra de Mágina, Jaén).

Tabla 1. *Junipero phoeniceae*-Pinetum halepensis ass. nova
Table 1. *Junipero phoeniceae*-Pinetum halepensis ass. nova

	N	W	E	N	N	N	NE	SE	SWNW
Orientación	15	10	20	10	40	10	10	30	35
Pendiente (%)	60	70	60	40	48	50	52	67	70
Altitud (1 = 10m)	40	40	40	40	40	40	40	10	10
Area (1 = 10m ²)	40	35	40	60	40	50	50	60	65
Cobertura (%)	5	6	4	6	5	5	5	5	6
Altura media (m)	1	2	3	4	5	6	7	8	9
Nº de Orden									

Características de comunidad y unidades superiores

<i>Pinus halepensis</i>	2	2	2	3	2	2	2	3	3	3
<i>Ephedra fragilis</i>	1	.	.	2	2	1	2	1	1	.
<i>Juniperus oxycedrus</i>	2	+	.	3	1	1	1	2	1	1
<i>Rhamnus lycioides</i>	.	+	1	2	1	1	1	1	1	.
<i>Olea sylvestris</i>	.	+	1	+	+	+	1	.	.	.
<i>Juniperus phoenicea</i>	1	.	.	.	1	1
<i>Rhamnus alaternus</i>	1	.	.	+	.	1
<i>Phillyrea angustifolia</i>	.	+	1
<i>Asparagus acutifolius</i>	+	+	+	.	.	.

Compañeras

<i>Rosmarinus officinalis</i>	.	1	1	+	.	.	+	2	1	.
<i>Phlomis purpurea</i>	.	1	1
<i>Chronanthus biflorus</i>	.	1	+	+	1	.
<i>Ulex parviflorus</i>	+	.	1	+	+	+	+	.	1	.
<i>Cistus albidus</i>	.	1	1	1	+	+	1	.	1	.
<i>Thymus gracilis</i>	1	.	.	+	+	+	.	1	2	.
<i>Brachypodium retusum</i>	+	1	1	+	+	1	1	.	1	.
<i>Stipa tenacissima</i>	.	+	.	2	+	+	+	1	2	+
<i>Cistus clusii</i>	.	+	1	.
<i>Dactylis hispanica</i>	.	+	1

Además : *Echinopartum boissieri* y *Linum suffruticosum* + en 1 ; *Daphne gnidium* +, *Phagnalon saxatile* +, *Stachelina dubia* + en 2 ; *Phillyrea latifolia*, *Lonicera hispanica* + en 3 ; *Bupleurum frutescens* + en 10.

Localidades : 1 Cortijo de Herrera (Pegalajar, Jaén) ; 2 Cerca Castillo de Otiñar (Jaén) ; 3 Finca de Otiñar (Jaén) ; 4 Puente Nuevo (Pegalajar, Jaén) ; 5,6 y 7 Cerro del Prior (Pegalajar, Jaén) ; 8 Cerca de Guadahortuna (Granada) ; 9 Cabra de Sto. Cristo (Jaén) ; 10 Peñón de Alhamedilla (Granada).

Tabla 2. Comunidad de *Ephedra fragilis* y *Pinus halepensis*
Table 2. *Ephedra fragilis*-*Pinus halepensis* community

Maestrazgo-Manchega (sectores Manchego y Maestrazgo), aunque en algunos enclaves supramediterráneos de este último sector y del sector Celtibérico-Alcarreño llega a enriquecerse en especies montanas como *Juniperus communis* L. *hemisphaerica* (K. Presl) Nyman y *Pinus nigra* Arnold subsp. *salzmannii* (Dunal) Franco. En las sierras Béticas sus relaciones se establecen tanto con el *Rhamno myrtifolii*-*Juniperetum phoeniceae* Molero Mesa et Pérez Raya 1987 de distribución Malacitano-Almijareense y Rondense occidental (Pérez Raya et al., 1990), como con el *Junipero phoeniceae*-*Pinetum salzmannii* Valle, Mota et Gómez-Mercado 1988 de areal Subbético, Guadiciano-Bacense y Malacitano-Almijareense (Valle et al., 1989). En ambos casos las diferencias florísticas de nuestra comunidad con ellas son muy significativas a nivel de las comunidades seriales y en el estrato arbóreo las diferentes especies

del género *Pinus* matizan los distintos sintaxones (Tabla 3). En la tabla 1, presentamos distintos inventarios de esta comunidad, donde recogemos una variante más húmeda por la presencia de *Buxus sempervirens* L., localizado en topografías menos accidentadas, y mayor humedad ambiental.

Recientemente, Pérez Latorre et al. (1998) describen la asociación *Pino halepensis*-*Juniperetum phoeniceae* Pérez Latorre et Cabezudo 1998 para caracterizar los pinares-sabinares edafoxerófilos dolomíticos termomediterráneos que sustituirían al *Chamaeropo*-*Juniperetum phoeniceae* Rivas-Martínez in Alcaraz, T.E. Díaz, Rivas-Martínez & Sánchez-Gómez 1989 en el sector Rondeño, aunque sin aportar diferencias ecológicas y florísticas con respecto a este último. Por nuestra parte consideramos que deben de sinonimizarse prevaleciendo la asociación de mayor antigüedad, en este caso *Chamaeropo*-*Juniperetum*

phoeniceae (art. 25, C.P.N.), donde ya en su tipo nomenclatural (Rivas-Martínez *ex* Alcaraz *in* Cantó, Laorga & Belmonte, inv. 3, tabla 34, *Opusc. Bot. Pharm. Complutensis*, 3: 65, 1986) *Pinus halepensis* participa en la comunidad.

En todo caso presenta marcadas diferencias con nuestra comunidad, sobre todo por la ausencia de especies de claro carácter termófilo y de óptimo termomediterráneo como *Ceratonia siliqua* L., *Rhamnus lycioides* L. subsp. *velutinus* (Boiss.) Nyman, *Chamaerops humilis* L., *Aristolochia baetica* L.

Comunidad de *Ephedra fragilis* y *Pinus halepensis* (Tabla 2)

Constituyen también formaciones abiertas de *Pinus halepensis* de porte más moderado que en el caso anterior que ocupan sustratos blandos, principalmente margas, margas yesíferas y conglomerados con escasa capacidad de retención de agua. En su composición florística es frecuente la presencia de *Ephedra fragilis* Desf., *Juniperus oxycedrus* y *Rhamnus lycioides*, a veces acompañados de *Olea europaea* L. var. *sylvestris* Brot. y en ocasiones *Juniperus phoenicea*.

Aparece en el piso bioclimático mesomediterráneo inferior semiárido del sector Guadiciano-Bacense (distrito Guadiciano-Bastetano), donde ocupa aquellos relieves y posiciones más complejas, como cárcavas, taludes de cierta pendiente y ramblas sometidos a elevada xericidad, con claro carácter topográfico. Hacia las zonas más favorables, con mayor compensación hídrica y edáfica es reemplazado por las comunidades climáticas del territorio, coscojares y lentiscares del *Rhamno lycioidis-Quercion cocciferae* Rivas Goday *ex* Rivas-Martínez 1975. Suele irradiar hacia las zonas basales de ombrotipo seco del sector Subbético donde la continuidad de estos sustratos margosos, sumado al efecto de sombras de lluvias que producen la accidentada orografía de toda la unidad biogeográfica permiten la presencia local del ombroclima semiárido.

La alteración que presenta el territorio por el uso del hombre a lo largo de la historia aconseja, por ahora, su tratamiento como comunidad a la espera de estudios posteriores más exhaustivos.

CONCLUSIONES

Pinus halepensis, al igual que otras coníferas, constituye formaciones naturales en todo el sur de la Península Ibérica, ampliamente distribuidas por los termotipos termo- y mesomediterráneo, y en menor medida en el supramediterráneo inferior.

En unos casos, la presencia de ambientes semiáridos ricos en materiales de depósitos neógeno-cuaternarios (margas, margocalizas y conglomerados) con escasa capacidad de retención de agua, constituyen medios óptimos para el desarrollo de *Pinus halepensis*. En otros, la abrupta geomorfología del territorio, rica en sustratos calizo-domíticos de difícil edafización, actúa como factor determinante en la instalación de comunidades permanentes de *Pinus halepensis*, en este caso, con una gran amplitud ombroclimática (semiárido-seco-subhúmedo).

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Asociación	Bioclimatología Corología	Composición florística Sintaxonomía	Complejos teselares Contactos catenales
<i>Rhamno lycioidis- Juniperetum phoeniceae</i>	Mesomediterráneo superior Supramediterráneo inferior Seco-subhúmedo	<i>Juniperus phoenicea</i> <i>Rhamnus lycioides</i>	Matorrales: <i>Sideritido-Salvion lavandulifoliae</i> Espartales: <i>Arrhenathero-Stipetum tenacissimae</i>
	Provincias Castellano-Maestrazgo- Manchega y Aragonesa Irradicaciones setabenses (Catalano- Valenciano-Provenzal) y subbético- murcianas (sector Subbético, Provincia Bética)	<i>Rhamno-Quercion cocciferae</i>	<i>Quercetum rotundifoliae</i>
<i>Junipero phoeniceae- Pinetum halepensis</i>	Mesomediterráneo Seco-subhúmedo	<i>Pinus halepensis</i> <i>Juniperus phoenicea</i> <i>Rhamnus lycioides</i>	Matorrales: <i>Lavandulo-Genistion boissieri</i> ; <i>Thymo- Cistetum clusii</i> Espartales: <i>Thymo-Stipetum tenacissimae</i>
	Provincia Bética: sectores Subbético y Guadiciano-Bacense	<i>Rhamno-Quercion cocciferae</i>	<i>Paeonio-Quercetum rotundifoliae</i>
<i>Rhamno myrtifoli- Juniperetum phoeniceae</i>	Termomediterráneo, Mesomediterráneo Seco-subhúmedo	<i>Pinus pinaster</i> <i>Rhamnus myrtifolius</i> <i>Juniperus phoenicea</i> <i>Rhamnus lycioides</i> subsp. <i>velutinus</i>	Matorrales: <i>Lavandulo-Genistion boissieri</i> ; <i>Centaureo-Lavanduletum lanatae</i> , <i>Helianthemo-Anthyllidetum argyrophyllae</i> Pastizales: <i>Helictotricho-Brachypodietum boissieri</i> , <i>Brachypodio-Trisetetum velutini</i>
	Provincia Bética: sectores Malacitano- Almijarense y Rondense occidental	<i>Asparago-Rhamnion oleoidis</i>	<i>Paeonio-Quercetum rotundifoliae</i>
<i>Junipero phoeniceae- Pinetum salzmannii</i>	Supramediterráneo Subhúmedo-húmedo	<i>Pinus nigra</i> subsp. <i>salzmannii</i> <i>Juniperus phoenicea</i> , <i>Juniperus hemisphaerica</i>	Matorrales: <i>Lavandulo-Genistion boissieri</i> ; <i>Saturejo- Velletum spinosae</i> , <i>Siderito-Genistetum longipedis</i> Pastizales: <i>Seselido-Festucetum hystricis</i>
	Provincia Bética: sectores Subbético, Guadiciano-Bacense, Malacitano- Almijarense	<i>Pino-Juniperion sabiniae</i>	<i>Berberido-Quercetum rotundifoliae</i> <i>Daphno-Aceretum granatensis</i>
<i>Chamaeropo humilis- Juniperetum phoeniceae</i>	Termomediterráneo Semiárido-húmedo	<i>Juniperus phoenicea</i> <i>Chamaerops humilis</i> <i>Osyris quadripartita</i> <i>Pinus halepensis</i>	Matorrales: <i>Eryngio-Ulicion erinacei</i> <i>Anthyllidetalia terniflorae</i>
	Península Ibérica	<i>Asparago-Rhamnion oleoidis</i>	<i>Quercococciferae-Lentiscetum</i> <i>Chamaeropo-Rhamnetum lycioidis</i> <i>Bupleuro-Pistacietum lentisci</i> <i>Asparago-Rhamnetum oleoidis</i>

Tabla 3. Cuadro resumen de las principales diferencias entre los sintaxones afines a la asociación propuesta (*Junipero phoeniceae-Pinetum halepensis*)

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Selective herbivory of thyme chemotypes by a mollusk and a grasshopper

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ABSTRACT

The common thyme (*Thymus vulgaris*, Labiatae) is biochemically variable, and in southern France individual plants belong to one of six chemotypes defined by the presence of specific monoterpenes. These chemotypes were exposed to herbivory by *Deroceras reticulatum* (Limacidae, Mollusca) and *Leptophyes punctatissima* (Tettigoniidae, Orthoptera). Members of both animal species were given the opportunity to select among all six chemotypes in individual arenas. Both species showed preferences for specific chemotypes. The chemotypes selected by *Deroceras* were very different from those selected by *Leptophyes*. Such species-specific feeding selection is found in a number of thyme herbivores, and can contribute to the maintenance of the biochemical polymorphism common to this and other species of the genus *Thymus*.

Key-words: Herbivory, monoterpenes, *Thymus vulgaris*, genetic polymorphism, chemical polymorphism

RESUME

Le thym commun (*Thymus vulgaris*, Labiatae) est biochimiquement variable ; en France méridionale, les individus appartiennent à l'un des six chémotypes définis par la présence de monoterpènes spécifiques. Ces chémotypes ont été soumis à la prédation de *Deroceras reticulatum* (Limacidae, Mollusque) et *Leptophyes punctatissima* (Tettigoniidae, Orthoptère). Des individus de ces deux espèces animales, placés dans des cages individuelles, ont eu l'opportunité de choisir parmi les six chémotypes. Les deux espèces ont montré des préférences pour des chémotypes spécifiques. Les chémotypes choisis par *Deroceras* étaient très différents de ceux choisis par *Leptophyes*. Une telle alimentation espèce-dépendante a été observée chez un certain nombre de prédateurs du thym, et peut contribuer au maintien du polymorphisme biochimique commun à cette espèce de thym et à d'autres du genre *Thymus*.

Mots-clés : Herbivorie, monoterpènes, *Thymus vulgaris*, polymorphisme génétique, polymorphisme chimique

INTRODUCTION

Many Mediterranean ecosystems are characterised by a limited availability of nutrients and water. For plants, this means that costs of leaf construction are high, and leaves must be well protected against the herbivores that are found in these challenging habitats (Ross & Sombrero, 1991). This need for protection has led to the synthesis by many Mediterranean plants of a large diversity of secondary compounds, many of which are aromatic. These plant species have characteristic smells and tastes, which are often so specific that plants can be identified simply by these features, without recourse to other botanical characteristics such as floral features or leaf morphology. Rosemary (*Rosmarinus*), sage (*Salvia*), myrtle (*Myrtus*), bay (*Laurus*), junipers (*Juniperus*) and scores of other species evoke specific odours and tastes. Many plants also show a significant amount of genetically-based intra-specific variability (Gleizes, 1976; Langenheim, 1994). Foremost among them are species of the genus *Thymus* (Labiatae) which often have a diversity of smells and tastes, associated with the presence of several monoterpenes (Adzet *et al.*, 1977; Thompson, in press and refs. therein). Such intra-specific variability always elicits attention and questions about its origin and maintenance. This has been true for various *Thymus* species and especially for *T. vulgaris*, a common component of dry garrigue-like or matorral ecosystems of southern France and Spain. In *T. vulgaris*, individual plants are characterised by the predominance of a specific monoterpene (chemotype) in the essential oil sequestered in the epidermal glands that cover its leaves and stems. As a result, a given plant will have a characteristic odour and flavour. The six monoterpenes present in southern France are geraniol (G), linalol (L), alpha terpineol (A), thuyanol (U), carvacrol (C) and thymol (T). Structurally, the first two are straight chains, the next two are cyclic and the last two are cyclic and phenolic. The synthesis of all six is under the control of a series of independently assorting epistatic loci. The details of its biochemistry and genetics are described in many publications (e.g. Passet, 1971; Vernet *et al.*, 1977; Thompson *et al.*, 1998; Linhart & Thompson, 1999). Many populations of thyme contain two or more chemotypes and the association between chemotypes and various botanical and geographic features is also well described, especially in southern

France (e.g. Gouyon *et al.*, 1986b; Thompson, in press).

The question we wish to address in this study has to do with the influences of this variability upon herbivory of *T. vulgaris* by two of its consumer species, the grasshopper *Leptophyes punctatissimum* (Tettigoniidae, Orthoptera) and the slug *Deroceras reticulatum* (Limacidae, Mollusca).

MATERIALS AND METHODS

Framework

The primary issues we addressed were i) whether the two herbivores exhibited repeatable patterns of selectivity among chemotypes by feeding on some chemotypes more than on others, and ii) whether the two species fed preferentially on the same chemotypes.

Plant material

Thyme plants offered to the herbivores were clonally produced from mother plants, with at least 10 mother plants per chemotype (A, C, G, L, T, U).

Artificial diets for slugs

Gelatine cakes were produced following the methods of Whelan (1982) and Linhart and Thompson (1995), and contained measured weights of chopped thyme leaves.

Feeding trials

Eight grasshoppers and nine slugs were used in individual cages. Each animal was presented with two replicates of all six chemotypes simultaneously. This methodology, while less tidy than the often used binary choice trials involving only two items at a time, is more realistic, as it reflects more accurately the complexities of garrigue vegetation which can contain several thyme chemotypes in addition to other monoterpene-containing species such as *Juniperus* spp., *Rosmarinus*, and others. Individual plants were 4-6 cm tall and had 6 leaves. Artificial diets for slugs consisted in food disks measuring 8 mm in diameter, and weighing 0.2 g. Each disk contained the leaf equivalent to about eight fresh leaves. For grasshop-

pers, no artificial diet was available, so that this type of experiment could not be carried out.

Containers for individual animals consisted of: i) circular, soil-filled glass dishes 15 cm in diameter for the mollusks, covered with damp muslin, and ii) rectangular planting trays 20x30 cm in size covered with metal mesh cages about 5 cm in height for the grasshoppers.

All experiments that followed the protocols described here were carried out once. In the case of slugs, different animals were used in the two experiments, to prevent the possibility that learning in the first trial with the living plants, might influence slug behaviour in the second experiment. Some further trials were run, usually with fewer animals, and lasting longer periods of time. Because of these differences, they were not directly comparable to the experiments reported here, and were not analysed statistically. However, all observations germane to the results reported here are also noted.

RESULTS

Deroceras

The slugs ate primarily plants of the G and A chemotypes, and ate little of the U, C, and T chemotypes (Table 1) of the nine individuals tested, five ate mostly G, three ate more A than G and one ate mostly A and L. In subsequent tests with fewer animals, G was also the chemotype most eaten.

Tests with gel cakes showed that animals ate more of G than the other chemotypes with L also selected,

and C the least eaten. Once again, there were differences among individuals, with 4/10 individuals preferring G, two a combination of G and L, one feeding mostly on L, one on U, and two showing no clear preference.

Leptophyes

The grasshoppers ate all chemotypes, but ate most of chemotype T (Table 1). There was marked heterogeneity among individuals. In additional runs (data not shown) of 8 individuals exposed to 6 chemotypes, three showed a strong preference for T while the others were less selective in their feeding.

DISCUSSION

Both herbivores ate a diversity of thyme chemotypes but concentrated their feeding on some chemotypes and were deterred by others. There was a general consensus about the most and least eaten chemotypes for each species, although there was also some heterogeneity among individuals. This heterogeneity reflects phenotypic variation among individuals, observed in most studies of this type, and underscores the need to carry out such tests with adequate numbers of animals. The two species differed dramatically in their preferences, with *Leptophyes* feeding more on thymol (T), while *Deroceras* fed very little on that chemotype, eating primarily plants of geraniol (G) and terpineol (A) chemotypes.

Species	Chemotype						P (3)
	G	L	A	U	C	T	
SLUG							
Plants (1)	4.1±0.6	2.7±0.5	3.9±0.6	1.0±0.2	0.9±0.2	1.0±0.3	<0.01
Gels (2)	51.9±9.5	4.2±9.5	15.6±5.7	19.9±6.9	1.3±0.9	5.4±1.8	<0.001
GRASSHOPPER							
Plants (1)	2.3±0.5	1.9±0.3	2.3±0.5	2.2±0.4	2.5±0.5	3.1±0.6	<0.05

- (1) "plants" consisted of cuttings, all with six leaves. The amount eaten represents \bar{x} i.e. leaves ± S.E. per animal;
- (2) "gels" consisted of dried, ground leaves mixed with gelatine (see text for details). The amount eaten represents \bar{x} percent eaten ± S.E. per animal;
- (3) the significance of differences among chemotypes was tested using the heterogeneity G-test (Sokal & Rohlf, 1981).

Table 1. Comparison of amounts of thyme material of six chemotypes eaten by the slug *Deroceras reticulatum* and the grasshopper *Leptophyes punctatissimum*

At first contact, the primary detectable differences among thyme plants are those associated with the monoterpene contents of their glands. But there are also other, more subtle differences among them: these include for example pubescence, leaf size, thickness, toughness and disposition, and all may affect the plants' palatability to various herbivores (Strong *et al.*, 1984). For this reason, an artificial diet which reduces these differences among food items is an important confirmation of the specific role of terpenes in herbivore choice. We were only able to use artificial diets using ground leaves for the slugs as no artificial diets were available for the grasshoppers.

The slugs ate somewhat larger amounts of geraniol containing cakes, just as they ate more plants of the G chemotype than the others. This observation provides support for the role of the specific monoterpenes synthesised by the plants as determinants of level of herbivory. This role was further supported in other experiments which involved the snail *Helix aspersa* (Linhart & Thompson, 1995) goats (*Capra hircus*) and sheep (*Ovis aries*) (Linhart & Thompson, 1999). In all three cases, patterns of relative preference of live plants characterised by specific chemotypes were the same as choices made when feeding on synthetic diets supplemented with pure distilled monoterpenes (Linhart & Thompson 1995, 1999).

The difference in patterns of preference between slugs and grasshoppers is notable as it shows that the two animals react very differently to the smell and/or the taste of the two molecules. These interspecific differences are also interesting in combination with another comparison made between patterns of herbivory by the grasshopper *Omocestus viridulus*, and the mollusk *Deroceras reticulatum* feeding upon mixtures of the graminoid *Dactylis glomerata* and the legume *Trifolium repens*. The two animals behaved very differently, with the grasshopper feeding disproportionately on the common species, with a periodic preference for the grass, while the slug fed disproportionately on the rarer species, with a consistent preference for the legume (Cottam, 1985). Such results further document the existence of important interspecific differences in herbivore behaviour, and suggest that the presence of multiple species of herbivores can contribute to small-scale heterogeneity of botanical and biochemical composition within plant communities.

The patterns of herbivory shown by the slugs in our experiment differ markedly from those of Gouyon *et al.* (1986a) who found the animals in their experiments showed preference patterns of A=C>T>U. We presume the differences are associated with the fact that their slugs had no experience feeding on thyme, and also were not exposed to G or L. In any case, the differences illustrate how animal origin and experimental design can influence the outcome of a feeding trial.

The inter-specific differences we saw are consistent with other patterns of herbivory of *T. vulgaris*. For example *Helix aspersa* and the Chrysomelid beetle *Arima marginata* preferred the L chemotype, while sheep (*Ovis aries*) preferred U, while goats although less specific in their choices, clearly preferred A, L or C to the other three chemotypes either in the form of whole plants or in synthetic diets (Linhart & Thompson, 1999). Other plants that show genetically-based intra-species variability in chemical defenses have also been studied experimentally by exposing diverse chemical phenotypes to various herbivores and parasites. In the great majority of cases, the herbivores show species-specific host selection; that is, there are consistent, inter-specific differences in the chemical phenotypes they select as food or host plants. This is not surprising, as one may well expect that these differences reflect the interspecific differences in physiology, metabolism and behaviour that are to be expected among organisms as different as molluscs, insects, fungi, birds, fish and mammals. These patterns have been observed repeatedly in many plant species as diverse as Labiatae, Leguminosae, Graminae, Fucoidae, Compositae, and various conifers (Simms, 1990; Linhart, 1991; Linhart & Thompson, 1999; Iwao & Rausher, 1997; Van Der Meijden, 1996; Snyder & Linhart, 1998). The consistent nature of these observations implies that such species-specific herbivory and parasitism can contribute to the maintenance of genetic variability in host defenses via complex patterns of selection. The results also indicate that for a given plant species, no one molecule can be counted on as a dependable defense against diverse herbivores.

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Patterns and correlates of exotic and endemic plant taxa in the Balearic islands

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ABSTRACT

We analysed the taxonomy and biogeography of endemic and exotic plants in the Balearic Islands (Spain), one of the "hot-spots" of the Mediterranean Basin. Richness, diversity and density (number of taxa/ \log_{10} area) of exotic taxa (species and subspecies) is higher than that of endemic taxa. Mallorca is the island with the highest number of endemic and exotic taxa. On average, exotic and endemic taxa are little abundant or rare and represent 8.4% and 6% of the total flora, respectively. The taxonomic distribution of both exotic and endemic species is not random: Solanaceae, Amaranthaceae, Iridaceae and Euphorbiaceae are over-represented families within the exotic taxa. Plumbaginaceae, Labiatae and Rubiaceae are over-represented among endemics. While most exotic taxa are therophytes, chamaephytes are the dominant life-form among endemics. Exotics are mainly found in cultivated areas, in disturbed and ruderal communities, while most endemics are located in rocky habitats. Coastal communities display a great proportion of endemic taxa (35.94 %), and are little represented by exotic taxa (5.94 %). It is in this habitat where most effort should be addressed in order to preserve both endemic and non-endemic native vegetation.

Key words: commonness, conservation of islands, endemism, Mallorca, Pithyusic Islands, rarity

RESUME

Nous avons analysé la taxonomie et la biogéographie des plantes endémiques et exotiques des îles Baléares (Espagne), l'un des "hot-spots" du bassin méditerranéen. La richesse, la diversité et la densité (nombre de taxa/ \log_{10} zones) des taxa exotiques (espèces et sous-espèces) sont plus élevées que celles des taxa endémiques. Majorque est l'île ayant le plus grand nombre de taxa endémiques et exotiques. En moyenne, les taxa exotiques et endémiques sont peu abondants ou rares, et représentent respectivement 8,4% et 6% de la flore totale. La répartition taxonomique des espèces exotiques et endémiques n'est pas aléatoire : les Solanaceae, Amaranthaceae, Iridaceae et Euphorbiaceae sont les familles sur-représentées parmi les exotiques. Les Plumbaginaceae, Labiatae et Rubiaceae sont sur-représentées parmi les endémiques. Tandis que la plupart des taxa exotiques sont des thérophytes, les chamaephytes constituent la forme de vie dominante parmi les endémiques. Les espèces exotiques se rencontrent principalement dans les zones cultivées et les communautés perturbées et rudérales, alors que la plupart des endémiques s'observent dans les habitats rocheux. Les communautés côtières affichent une grande proportion de taxa endémiques (35,94 %), mais peu de taxa exotiques (5,94 %). Ce sont dans ces biotopes littoraux que la plupart des efforts devraient être entrepris afin de préserver la végétation indigène, endémique et non-endémique.

Mots-clés : fréquence, conservation des îles, endémisme, Majorque, îles Pithyuses, rareté

INTRODUCTION

There is a great interest in understanding the processes that shape the ecology of endemic and introduced species (e.g. Gaston, 1994; Drake *et al.*, 1989, respectively). This concern requests a strong previous knowledge of the diversity and abundance patterns of these taxa (McIntyre, 1992; Schwartz, 1993; Cowling & Samways, 1995). On the other hand, preservation of endemic species and control of introduced species are two main goals of conservation programmes world-wide that often are simultaneously carried out (Usher, 1986; Houston & Scheiner, 1995; Schierenbeck, 1995). Thus research on the distribution patterns of endemics and exotics at the regional level and taxonomic, biological and ecological affinities of both groups of taxa is imperative to highlight hypothesis to be experimentally tested, and also to advance on basic knowledge for conservation practices.

Islands have high levels of plant endemism. The best examples are found in big isolated islands such as Madagascar with 12.000 species 80 % of which are endemic or New Zealand with 82 % endemic species. Endemics are also common in small islands: Canary Islands (612 endemics), Mauricio Island (280 endemics), Madeira Islands (129 endemics) (Lean & Hinrichsen, 1990). In the Mediterranean Basin, the Tyrrhenian Islands are one of the 10 "hot-spots" of species diversity and have almost 20 % of endemic plant taxa (Médail & Quézel, 1997).

Endemic plant species are especially vulnerable in islands (Eliasson, 1995). For example, more than 90 % of endemic plants in Sta. Elena, Ascension Island and Lord Howe island are endangered (Lean & Hinrichsen, 1990). Intrinsic causes of vulnerability are related to the characteristics of insular species such as biological simplicity and reduced dispersal (Carlquist, 1965; Eliasson, 1995; Cody & McCovert 1996; Schiffman 1997). However, the main causes of such vulnerability are overexploitation, deforestation, habitat destruction, alteration of regional hydrological cycles, water pollution and species introductions.

Islands are very vulnerable to biological invasions (Loope & Mueller-Dombois, 1989; Atkinson & Cameron, 1993; McDonald & Cooper, 1995). The percentage of exotic plant species is very high in islands, i.e. Hawaii (44 %), New Zealand (40 %), British Islands (43 %), Ascension Island (83 %) (Vitousek *et al.*, 1997). This high fraction of exotic species may be re-

lated to higher invasibility of islands due to higher number of releases and propagules per unit area, a lack of biotic mechanisms controlling invasion, the existence of unsaturated communities, high disturbance regimes, higher susceptibility to the effects of invaders than similar mainland areas (D'Antonio & Dudley, 1995) and also to a large perimeter-area ratio than that for continents (Lonsdale, 1999).

The Balearic Islands have a high species diversity (Simon, 1994) and are rich in endemic taxa (Gómez-Campo *et al.*, 1984). Endemic plants have been studied with regard to evolutionary origin based on cytogenetics analysis (Cardona & Contandriopoulos, 1979; Contandriopoulos & Cardona, 1984). However, the diversity and distribution of endemic taxa has not been quantified and compared to that of the exotic component. In this study we analyse several aspects of the diversity and distribution of both the endemic and the exotic component of the Balearic flora. The questions are: 1) Are endemic and exotic taxa similarly abundant? 2) Are there taxonomic and life-history similarities between endemic and exotic taxa? 3) In which communities are endemic and exotic taxa located? The biogeographic origin of exotics is also commented. We base our study on a bibliographic survey.

METHODS

Area of study

The Balearic Islands are the most eastern islands of the Mediterranean Basin and belong together with Corsica, Sardinia and Sicily to the Tyrrhenian Islands. They originated after the geologic drift and posterior rotation of 30° of the Cyno-Sardinian plate at the end of the Oligocene and early Miocene from the adjacent coast of Provence, Languedoc and NE Catalonia. Materials are calcareous from the Triassic to the tertiary except in Menorca, where the geology is more heterogeneous and contains silicic esquistes. The flora is typically Mediterranean dominated by evergreen sclerophyllous shrubs and forests. The Balearic Islands form two different groups in terms of their geology and endemism. The eastern Balearic Islands or Gymnesias Islands (Mallorca and Menorca) that have Tyrrhenian affinities, and the western Balearic Islands or Pithyusic Islands (Eivissa and Formentera) that have an Iberian and North African affinity.

Bibliographic survey

A data base with species and subspecies (taxa hereafter) was created with all endemic and exotic taxa of the Balearic Islands according to "Flora Manual del Paísos Catalans" (Bolòs *et al.*, 1993). We chose this flora because it is the most complete and modern of this region. Screening a single flora guarantees homogeneity in nomenclature and homogeneous taxonomic treatment between endemics and exotics. Furthermore, using this flora instead of detailed taxonomic monographies minimises author's effects in subdividing genera into more or fewer species according to the taxonomic approach. It is for this reason that we did not use the following references: Bonafé (1977-1980), Contandriopoulos & Cardona (1984), Pla *et al.* (1992) or Romo (1994).

Endemic taxa were easily identified, although taxa listed as endemic may not be exclusively endemic to the Balearic Islands but also endemic in adjacent NE continental regions (Catalonia or Valencia) and Corsica or Sardinia Islands.

Exotic taxa were those considered in the flora as spontaneous, adventitious, introduced or naturalised. Species listed as "cultivated" or "planted" were excluded, as well as those that were rarely found as spontaneous or their naturalisation status was uncertain. Thus our list is not over-represented in exotics. The following information for each taxon was gathered: family, life-form (Raunkiaer, 1934), habitat and origin if exotic.

Bolòs *et al.* (1993) considers three biogeographic regions: Mallorca, Menorca and Pityusic Islands. For each biogeographic region and for the Balearic Islands in general, we calculated: 1) richness of endemic and exotic taxa as the absolute number of endemic and exotic taxa respectively, 2) percentage of exotic and endemic taxa from the total, 3) density of endemic and exotic taxa as the ratio of endemic and exotic taxa to \log_{10} area (Rejmánek & Randall, 1994) and 4) family diversity of endemic and exotic taxa calculated by the Shannon index: $S = -\sum p_i \times \log_e p_i$ where p_i is the number of endemic or exotic taxa in family i divided by the total number of endemic or exotic taxa, respectively (Solbrig, 1994). The number of taxa per family

was compared by a t-test after ln transformation of data and evenness expressed by the CV.

To test whether endemics were taxonomically random assemblages, over-representation of main endemic families was assessed by comparing the ratio $p_{en} = (\text{endemic taxa within a family} / \text{total number of endemic taxa})$ with the ratio $p_{nn} = (\text{native non-endemic taxa within a family} / \text{total number of native non-endemic taxa})$ performing a X^2 test (Cowling & Hilton-Taylor, 1997). Likewise, over-representation of main exotic families was assessed by comparing the ratio $p_{ex} = (\text{exotic taxa within a family} / \text{total number of exotic taxa})$ with the ratio $p_n = (\text{native taxa within a family} / \text{total number of native taxa})$.

For each biogeographic region and for the Balearic Islands in general we calculated an abundance index for endemic and exotic taxa by assigning the following values to the abundance nomenclature used by Bolòs *et al.* (1993): 1 = RRR (very rare), 2 = RR (rare), 3 = R (not abundant), 4 = C (relatively common), 5 = CC (common) and 6 = CCC (very common). This abundance index is an estimation of the geographic range of the taxa within the Balearic Islands.

RESULTS

Diversity of endemic taxa

In the Balearic Islands there are 89 endemic taxa distributed in 29 families that represent 6 % of the total number of taxa. One species is a Pteridophyte, 5 monocotyledons and 23 dicotyledons. Density of endemics is 24 taxa per 10 km² and family diversity is 2.92 (Table 1).

Families with endemics have in average 3 taxa per family (Figure 1). The families with more endemic taxa are Plumbaginaceae (14), Fabaceae (12), Compositae (9), Labiatae (7), Umbelliferae (6), Scrophulariaceae (4) and Rubiaceae (4). Plumbaginaceae, Labiatae and Rubiaceae are over-represented among native taxa (Table 2).

Most endemic taxa are chamaephytes (44.94 %) followed by hemicryptophytes (26.97 %), nanophanerophytes (13.48 %), geophytes (7.87 %) and therophytes (5.62 %). Macrophanerophytes (1.12 %) is the less represented life-form (Table 3).

Region	Area (km ²)	No. endemics (%)	No. endemics/log ₁₀ area	Family diversity ^a	Abundance ^b
Balearic Islands	5014	89 (6)	24	2.9	2.2
Mallorca	3655.9	70 (5.8)	19.6	2.6	2.3
Menorca	701.8	39 (4.4)	13.7	2.5	2.6
Pithyusic Islands	623.3	26 (2.3)	9.3	2.9	2.4

Pithyusic Islands = Eivissa and Formentera.

^aCalculated as the Shannon index = $-E p_i \times \ln p_i$ where p_i is the number of endemic taxa in family i divided by the total number of endemic taxa.

^b Median value of 1 = RRR (very rare), 2 = RR (rare), 3 = R (not abundant), 4 = C (relatively common), 5 = CC (common) and 6 = CCC (very common) according to Bolòs et al (1993) nomenclature.

Table 1. Numbers of endemic taxa of the Balearic Islands

Family	No. endemic taxa (%) ¹	No. native non-endemic taxa (%) ¹	χ^2
Plumbaginaceae	14 (15.7)	18 (1.3)	627.7 *
Fabaceae	12 (13.5)	132 (9.7)	1.5 ns
Asteraceae	9 (10.1)	151 (11.1)	0.0 ns
Labiatae	7 (7.8)	46 (3.4)	6.5 *
Umbelliferae	6 (6.7)	52 (3.8)	2.5 ns
Scrophulariaceae	4 (4.5)	46 (3.4)	0.3 ns
Rubiaceae	4 (4.5)	24 (1.8)	4.2 *
Caryophyllaceae	3 (3.4)	59 (4.3)	0.3 ns
Euphorbiaceae	3 (3.4)	26 (1.9)	1.0 ns
Ranunculaceae	3 (3.4)	29 (2.1)	0.65 ns

¹ number of taxa in the family/total number of taxa of the respective group

* $p < 0.05$, ns = not significant. χ^2 compares the no. endemic taxa (%) with the no. native non-endemic taxa (%). If significant, the family is over-represented.

Table 2. The ten largest families of endemic taxa in the Balearic Islands

Lifeform	% endemics	% exotics
Therophytes	5.6	37.9
Hemicryptophytes	27.0	17.7
Nanophanerophytes	13.5	5.6
Macrophanerophytes	1.1	11.3
Phanerophytes	-	5.6
Chamaephytes	44.9	12.1
Geophytes	7.9	9.7

Table 3. Percentage of lifeforms of endemic and exotic taxa in the Balearic Islands

Distribution and abundance of the endemic taxa

Of the 89 endemic taxa, 5 are also endemic in other north-eastern regions of Spain: *Medicago arborea* subsp. *citrina* (Papilionaceae) also endemic to Columbretes islands (Valencia), *Asplenium petrarachae* subsp. *majoricum* (Polypodiaceae), *Asperula cynanchica* subsp. *pau* (Rubiaceae) and *Saxifraga corsica* subsp. *cossoniana* (Saxifragaceae) are also present in Valencia and *Limonium gobertii* (Plumbaginaceae) is also endemic to Catalonia.

Mallorca is the island with most endemic taxa, and with the highest density and family diversity of endemic taxa. Endemic taxa have low abundance (R) or are rare (RR) in all islands (Table 1).

Most endemic plants occur on rocky habitats (64 %) in the mountaintops mainly in non coastal sites (39.36 %). Coastal communities also display a great proportion of endemic plants (35.11 %). Only 7 taxa are located in ruderal communities. There are 10 endemic taxa in shrublands and only two in forests (Table 4).

Diversity and origin of the exotic taxa

The Balearic Islands display 124 exotic taxa distributed in 46 families that represent 8.4% of the total flora. Only one exotic species is a gymnosperm, 17 are monocotyledons and 106 are dicotyledons. Density and family diversity for exotics are 33.5 and 3.31 respectively (Table 5).

Habitat	No. endemic taxa (%)	No. exotic taxa (%)
Non-littoral rocks	37 (39.4)	6 (4.9)
Coastal	33 (35.1)	6 (4.9)
Shrublands	10 (10.6)	2 (2.0)
Ruderal	7 (7.4)	52 (51.5)
Grasslands	3 (3.2)	3 (3.0)
Forests	2 (2.1)	2 (2.0)
Ponds, riparian	2 (2.1)	11 (10.9)
Crops, fallows	-	19 (18.8)

Table 4. Habitat classification of endemic and exotic taxa from the Balearic Islands

Region	Area (km ²)	No. exotics (%)	No. exotics/log ₁₀ area	Family diversity ^a	Abundance ^b
Balearic Islands	5014	124 (8.4)	33.5	3.3	2.6
Mallorca	3655.9	117 (8.8)	32.8	3.3	2.6
Menorca	701.8	62 (6.6)	21.8	3.1	3.1
Pithyusic Islands	623.3	65 (5.3)	23.2	3.2	3.1

Pithyusic Islands = Eivissa and Formentera.

^a Calculated as the Shannon index = $-E p_i \times \ln p_i$ where p_i is the number of exotic taxa in family i divided by the total number of exotic taxa.

^b Median value of 1 = RRR (very rare), 2 = RR (rare), 3 = R (not abundant), 4 = C (relatively common), 5 = CC (common) and 6 = CCC (very common) according to Boldòs et al (1993) nomenclature.

Table 5. Numbers of exotic taxa of the Balearic Islands

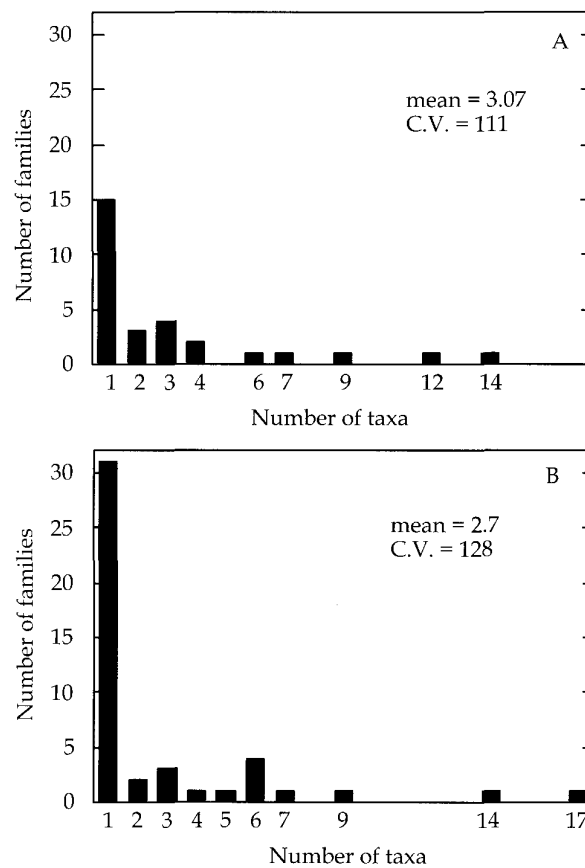


Figure 1. Frequency distribution of the number of endemic (A) and exotic (B) taxa (species and subspecies) per family

As for endemics, distribution of taxa among families is strongly skewed with most families having only one taxon (Figure 1). The number of taxa per family was not significantly different between endemics and exotics (t -value = 0.831, p = 0.409, data ln transformed). The families with more exotic taxa are: Asteraceae (17), Fabaceae (14), Solanaceae (9), Poaceae (7), Amaranthaceae (6), Brassicaceae (6), Euphorbiaceae (6), Iridaceae (6), Labiatae (5); Solanaceae, Amaranthaceae, Iridaceae and Euphorbiaceae are over-represented exotic families (Table 6).

Most exotic taxa are therophytes (37.90 %), followed by hemicryptophytes (17.74 %), chamaephytes (12.10 %) and macrophanerophytes (11.29 %). Geophytes (9.68 %), nanophanerophytes (5.65 %) and phanerophytes (5.65 %) are the least represented life-forms (Table 3).

Most exotics have an American (32.83 %) or Mediterranean (19.40 %) origin. Asia is also well represented. Unfortunately, almost 15 % of taxa have an unknown origin (Table 7).

Distribution and abundance of the exotic taxa

Within the archipelago, more than 90 % of exotic taxa are found in Mallorca. Only two exotic taxa are exclusively found in Menorca (*Lepidium spinosum* and *Hedysarum coronarium*) and five in Pithyusic Islands are not present in Mallorca. Menorca is the island with the lowest number of exotic taxa. Density and family diversity follow the same pattern (Table 5).

Exotic taxa in the Balearic Islands have low abundance (R) or are rare (RR), especially in Mallorca. Exotics are significantly less rare than endemics (t -value = 2.096, p = 0.037). In Menorca and Pithyusic Islands exotic taxa are mostly little abundant (R) but relatively common (C). The 7 most abundant exotic taxa in the Balearic Islands are: *Amaranthus retroflexus* subsp. *retroflexus* (Amaranthaceae), *Aster squamatus*, *Conyza bonariensis*, *C. sumatrensis* (Asteraceae), *Arundo donax* (Poaceae), *Oxalis pes-caprae* (Oxalidaceae) and *Ulmus minor* (Ulmaceae).

Most exotic plants are found in ruderal communities (51.48 %) such as old fields, wasting areas, dumps and roadsides. Cultivated fields are also very invaded by exotic taxa (18.81 %). Fifty eight percent of the taxa that invade cultivated areas are also found in ruderal communities. Exotic taxa are also well repre-

sented in coastal communities (5.94 %), mainly in dunes and salt marshes (Table 4).

DISCUSSION

Although mediterranean climate regions occupy only 2 % of the world surface, they have high family diversity which conservation status needs to be explored (Cody, 1986; Cowling *et al.*, 1996). This study is the first attempt as far as we know to combine patterns of diversity and abundance of endemic and exotic taxa at the regional level. We found that richness, density and family diversity of exotic taxa is higher than for endemic taxa.

Density of endemic taxa is similar to that of adjacent islands: Corsica (32.98 sp/log₁₀ area) and Sardinia (24.19) (Médail & Verlaque, 1997). Density of exotic taxa is also similar than in other Mediterranean islands. For example, in Corsica there are 473 exotic taxa which represent a 17% of the total flora. Most of these species set up in the last 20 years (Jeanmonod, 1998). Weber (1997) found that the Flora Europea (1964-1980) listed only 71 exotic species, a value which is less than half of the total number of exotics presented in the present study. Thus, immigration rates of exotic species are extremely high in these islands.

Mallorca is the Balearic island with the highest number of endemic and exotic taxa. The richness of exotic taxa may be related to island area, thus being higher in Mallorca and lower in Menorca. Instead, endemic taxa richness is more related to the geological and evolutionary formation of islands (Contandriopoulos & Cardona, 1984). Mallorca and Menorca with the highest number of taxa have a different origin than Pithyusic Islands.

Our regional survey is consistent with the general assessment that the endemic (Prance & Elias, 1977; Cowling & Hilton-Taylor, 1997) and the exotic (Pysek, 1998; Daehler, 1998) components of a flora are not randomly assemblages of taxa. However, causes underlying these taxonomical patterns are different for both flora components. Endemism of the Balearic Islands is the result of the geologic and insular origin of the islands (Contandriopoulos & Cardona, 1984). In contrast, the exotic component depends on their geographic origin and the equilibrium between propagule pressure and extinction rate (Lonsdale, 1999).

Family	No. exotic taxa (%) ¹	No. native taxa (%) ¹	X ²
Asteraceae	17 (13.7)	160 (10.8)	1.2 ns
Fabaceae	14 (11.3)	144 (9.9)	0.3 ns
Solanaceae	9 (7.2)	16 (1.1)	99.0 ***
Poaceae	7 (5.6)	160 (10.8)	2.8 ns
Amaranthaceae	6 (4.8)	9 (0.6)	78.6 ***
Brassicaceae	6 (4.8)	59 (4)	0.3 ns
Euphorbiaceae	6 (4.8)	29 (2.2)	5.0 *
Iridaceae	6 (4.8)	11 (0.7)	60.7 ***
Labiatae	5 (4)	53 (3.4)	0.1 ns
Chenopodiaceae	4 (3.2)	30 (2.0)	0.9 ns

¹ number of taxa in the family/total number of taxa of the respective group

*** p < 0.001, * p < 0.05, ns = not significant. X² compares the no. exotic taxa (%) with the no. native taxa (%). If significant, the family is over-represented.

Table 6. The ten largest families of exotic taxa in the Balearic Islands

Region	No. taxa	% taxa
Non tropical America	26	19.4
Tropical America	18	13.4
Mediterranean region	26	19.4
Africa	13	9.7
Asia	10	7.5
Middle East	10	7.5
Submediterranean region	5	3.7
Tropical	4	3.0
Oceania	2	1.5
Macaronesia	1	0.7
Unknown	19	14.2

Table 7. Biogeographic origin of exotic taxa of the Balearic Islands

In the Balearic Islands, the most represented exotics have an American origin like for other Mediterranean Basin regions (Di Castri, 1989; Groves & Di Castri, 1991), and the families with the largest number of exotic taxa belong also to the largest families world-wide i.e. Asteraceae, Fabaceae, Poaceae (Weber, 1997; Daehler, 1998; Pysek, 1998). However, some families were over-represented. This may partly be explained by deliberate and reiterated introductions of certain taxa and by specific features of these taxa, making them more invasive. It may also reflect the identity of naturalised plants, e.g. the Amaranthaceae contain many weeds in agroecosystems.

There is not a strong overlap of habitats occupied by endemic and exotic taxa. While endemic taxa are located in more isolated pristine habitats, exotic taxa are located in most disturbed habitats, except for coastal communities where an important proportion of both taxa co-occur. These habitats, are the ones where endemics will be most threatened by invasion by exotics. For example, invasion of *Carpobrotus edulis* is very high in the Mallorcan coast and is threatening several endemic *Limonium* spp. (PANDION, 1997). Moreover, in coastal habitats the human influence is

the strongest, and this increases the rate of species introduction and threat to endemics.

Isolated edaphic systems appear to be major endemic centres (Gómez-Campo *et al.*, 1984). Besides crop fields, most exotic taxa were found in anthropogenic habitats (dumps, roadsides). Water courses are especially prone to invasion by exotic plants because they act as effective corridors providing a route for the dispersal of water-borne propagules (de Waal *et al.*, 1994). Very few exotics succeed in closed forest and shrublands. Low disturbance levels may prevent invasion of closed forest and shrublands (Hobbs & Huenneke, 1992).

Often the term rarity is confused with that of endangered taxa but they are not synonyms (Kruckeberg & Rabinowitz, 1985). It is important to notice that in average both endemic and exotic taxa are rare. However, putative mechanisms of rarefaction are different in both group of taxa and their fate may also discourse in opposite directions. At the human scale, we have witnessed changes from common to rare in native taxa and from rare to common in exotic taxa (Kruckeberg & Rabinowitz, 1985). The rarity status of exotic taxa does not prevent their invasion status either. Because

rarity depends on geographical range, habitat specificity and population size, one exotic taxa can be restricted to a small geographical area but be very abundant or vice-versa, have widespread small populations. In both cases its presence may be considered invasive and may have an impact on the native biota and ecosystem functioning (Rabinowitz *et al.*, 1986).

Endemics and exotics are two faces of the same coin because management of both taxa have strong conservation implications. Five percent of the overall flora of the Balearic Islands is seriously endangered (Mus & Mayol, 1993). In addition, new introduced species are becoming naturalised (Fraga & Pallicer, 1998). Because low-altitude areas are both fairly rich in threatened endemic taxa and exotic taxa there is a need to tackle conservation priorities in these habitats and to reduce main threats which are from more to less important: tourism, fire, overgrazing, urbanisation and cropping (Médail & Quézel, 1997).

Conservation priorities should be strongly enforced to those taxa that are evolutionary unique (Williams *et al.*, 1994). In the Balearic Islands, relict taxa (paleoendemics) should be conserved because they are those that have gone through major disturbances and environmental changes. Paleoendemics include species represented by monospecific genera (*Naufraga balearica*), morphologically isolated species (*Pimpinella bicknellii*, *Daphne rodriguezii*), and those without clear affinities (*Helichrysum ambiguum*, *Hypericum balearicum*, *Paeonia cambessedesii*) some of which are located in coastal habitats also invaded by exotic species.

More studies like this one should be conducted at other regions in order to have a global assessment of the diversity and distribution of endemic and exotic taxa. Next research step should focus on the experimental study of the ecological mechanisms that control the establishment of plants of conservation interest (Mack, 1996), such as the studies undertaken with *Cyclamen balearicum* (Affre *et al.*, 1995) or the ones currently analysed by Traveset *et al.* (unp. data) on endemics, in order to have ecological bases for conservation efforts as for example the *Ligusticum huteri* Porta reintroduction program (Vicens, 1998).

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Changements édaphiques le long d'un gradient d'intensité de pâturage dans une steppe d'Algérie

Edaphic changes along a gradient of grazing intensity in a steppe of Algeria

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RESUME

Un ensemble de caractères édaphiques est analysé dans une steppe aride en voie de désertification, le long d'un transect comportant trois niveaux d'intensité de pâturage. Le système préexistant correspond à une steppe d'alfa qui caractérisait l'ensemble de la région il y a une vingtaine d'années, avec des conditions homogènes de milieu. Les résultats montrent que dans la steppe non pâturée les caractères du sol sont restés proches de ceux mesurés dans le système préexistant. Dans les parcours pastoraux, exploités librement, marqués par le surpâturage, les changements les plus significatifs sont une baisse globale de 38 % du taux de matière organique et une diminution du taux des argiles et limons fins de 43 %. Ces changements sont hautement significatifs mais plus importants dans la couche de surface. A l'échelle stationnelle, les changements concernent aussi bien le sol sous-jacent à la touffe que le sol interstitiel. Le dépérissement des touffes d'alfa a entraîné la perte de ses fonctions édaphiques par la désstructuration du sol. Ces changements confirment ceux observés sur la végétation et confortent l'hypothèse d'un changement irréversible des attributs vitaux fondamentaux du système.

Mots-clés : désertification, dynamique, zone aride, surpâturage, *Stipa tenacissima* L., alfa, sol

ABSTRACT

A set of soil characters are analysed, in an arid steppe subject to desertification, along a transect that presents three levels of grazing intensity. The pre-existing system had been, about twenty years ago, a pure steppe dominated by alfa-grass that was the typical landscape of the whole region under relatively homogeneous environmental features. Results show a relative stability in the non-grazed area where soil characters remain similar to those of the pre-existing system. In the open rangelands, freely used and marked by over-grazing, the more significant changes are declining rates of organic matter (38%) and of clay and fine silt (43%). These changes are highly significant but are more important at the surface layer. At a local scale, changes concern both soil underneath the tussock and the interstitial one. The destruction of the alfa-grass tussocks has led to the loss of its edaphic functions by breaking down the soil structure. Our results confirm those obtained on vegetation and strengthen the hypothesis of irreversible changes of main vital attributes of the system.

Key-words: desertification, dynamics, arid zone, overgrazing, *Stipa tenacissima* L., alfa, soil

ABRIDGED ENGLISH VERSION

The aim of the present paper is to emphasise the effects of overgrazing on soil through a set of characters. The study was conducted in an arid steppe (mean annual rainfall : 260 mm). The study area is located in the western part of the steppic high-plains of Algeria. This region has been subject to land degradation due to overgrazing which is one of the main causes of desertification in arid rangelands. During the two last decades, vegetation has been marked by important changes that have been pointed out through a long-term monitoring of phytomass, primary net productivity and specific composition.

Steppic landscape is dominated by pediment surfaces gently sloped (<2%) subject to erosion by wind. Soils are shallow over a limestone crust at 15 to 30 cm depth. The study was undertaken using a grazing gradient method. The chosen transect includes three levels of grazing intensity : (1) a non-grazed enclosure P0 of the pristine system that had been, 20 years ago, a typical steppe with an alfa-grass pure stand under homogeneous environmental conditions; (2) a field P1 of about 500 ha under controlled grazing with 0.25 unit/ha stocking rate; (3) the rest of the steppic open rangelands P3 in which the stocking rate has rapidly increased reaching 0.50-0.75 unit/ha in 1990. Perennial plant cover, sand cover, soil organic matter and texture are the main indicators used to assess soil degradation. The main results are the following:

(1) at the transect scale:
- soil features within the non-grazed enclosure (P0) remain similar to those of the pre-existing system. The dominant

perennial *Stipa tenacissima* covers $36 \pm 5\%$, the sand layer is almost completely lacking, soil organic matter rate is $1.7 \pm 0.3\%$ and clay and fine-silt rate is $29 \pm 5\%$;

- on heavily grazed area (P2), the difference with P0 is highly significant ($p < 0.001$) for perennial cover which is $15.5 \pm 2.7\%$, sand layer ($50 \pm 7\%$) with 8 ± 1 cm deep, soil organic matter and clay-silt have lost respectively 38% and 43%. These later soil changes are significant at any level but are more important within the surface layer.

(2) at the local scale, degradation has affected both the soil underneath the tussock and the interstitial one. In the pre-existing system, the *S. tenacissima* tussock ensures a set of properties and especially the protection of the entire system against wind erosion. Destruction of the tussock by overgrazing and trampling has led to the loss of its edaphic functions and has broken down the pre-existing highly patterned system.

The desertification by overgrazing corresponds to a set of step-wise changes. Early effects had been a rapid reduction of perennial biomass. The removal of perennial plants is the original key process of desertification. Soil alteration is considered as the last step of degradation and thus an indubitable threshold of irreversibility.

The results seem to be in concordance with those of specific composition and vegetation structure along the gradient. They show irreversible changes that make restoration (s.s.) of the pre-existing system nearly impossible. However, according to soil and vegetation features, it seems that a rehabilitation remains possible in a grazing land-use context.

INTRODUCTION

La désertification peut être définie comme une dégradation des terres sous climat aride (s.l.). Cette définition simple, adoptée par la Conférence des Nations Unies pour l'Environnement et le Développement en 1992, cache en fait une grande complexité qui se reflète à travers le débat actuel autour de ce concept (Hellden, 1988 ; Thomas & Middleton, 1993 ; Dodd, 1994 ; Hutchinson, 1996 ; Thomas, 1997). Dans ce débat, le caractère réversible ou irréversible des changements demeure une question centrale (Mainguet, 1994, 1998). Un indicateur incontestable d'irréversibilité, considéré comme ultime changement, est la dégradation du sol (Friedel, 1992 ; Floret *et al.*, 1992 ; Mainguet, 1994 ; Milton *et al.*, 1994). Les sols sous climat aride sont pauvres en matière organique (Evenari, 1985) ce qui confère au système une faible résilience vis-à-vis des changements naturels ou induits par l'homme (Albaladejo *et al.*, 1998). Aussi, les dommages causés dans ces milieux sont-ils difficiles à réparer (Milton *et al.*, 1994).

Sous climat aride, la désertification agit par stades successifs (Milton *et al.*, 1994). L'un des premiers

correspond, le plus souvent, à la réduction du couvert des espèces pérennes (Verstraet & Schwartz, 1991 ; Le Houérou, 1992) dont une des causes prépondérantes, en Afrique, serait le surpâturage (UNEP, 1992). La destruction de la végétation pérenne fragilise le sol (Rognon, 1993 ; Le Houérou, 1995) et l'expose à l'érosion, plus particulièrement à l'érosion éolienne qui caractérise les milieux arides (Bullock & Le Houérou, 1996). L'action du vent devient nettement plus efficiente pour un couvert végétal inférieur à un seuil qui serait d'environ 40% d'après l'évaluation de Fryrear (1990). Le rôle protecteur de la végétation pérenne contre l'érosion a été particulièrement bien établi dans le cas de l'alfa (Puigdefábregas & Sánchez, 1996 ; Cerda, 1997) dont le peuplement typique, est structuré en touffes individualisées formant de véritables îlots de fertilité.

Durant les deux dernières décennies, une dégradation rapide et intense a marqué les steppes d'alfa de plaine en Algérie (Le Houérou, 1986 ; Aidoud & Aidoud-Lounis, 1992) mais peu d'études diachroniques ont été réalisées. Le présent travail s'appuie sur un suivi d'une vingtaine d'années dans le site permanent de Rogassa (Sud-Oranais). Les travaux dans ce site,

homogène au départ, ont montré une dynamique directionnelle régressive de la végétation, dont la cause principale est le surpâturage par les ovins (Aidoud, 1989, 1994). Des changements ont été mis en évidence, le long d'un transect d'intensité de pâturage, par la baisse de la biomasse de l'espèce pérenne dominante (Aidoud & Touffet, 1996) et par des changements de composition spécifique de la végétation ainsi que des caractères de surface du sol (Aidoud, 1994 ; Slimani, 1998). Le transect utilisé représente un gradient comportant trois états de pâturage : nul, contrôlé et libre. Il constitue une situation expérimentale *in natura* permettant d'approcher des changements dans le temps par la transposition de variations analysées dans l'espace (Pickup, 1992).

Le présent travail, qui s'intègre à cette approche, a pour objectif de vérifier, le long de ce même transect, en se basant sur les principaux caractères du sol sous climat aride, l'hypothèse d'un changement édaphique significatif.

CADRE D'ETUDE ET METHODOLOGIE

Le plateau de Rogassa, couvrant près de 30 000 ha, est situé à une trentaine de km au nord de la ville d'El Bayadh. Les principales caractéristiques écologiques sont données dans le tableau 1. Les données météorologiques placent le site dans l'étage méditerranéen aride moyen à hiver froid au sens d'Emberger. Jusqu'au début des années 1980, le paysage végétal était une nappe alfatière de plaine considérée parmi les plus denses et les plus homogènes d'Algérie et où *Stipa tenacissima* L. assurait près de 95% du couvert végétal global. La végétation du plateau de Rogassa a été intégrée aux groupements d'alfa purs selon l'analyse réalisée dans le bassin du Chott Chergui du Sud-Oranais (Aidoud-Lounis, 1989). Exploitée en pâturage collectif et libre, cette steppe supportait, dans son état préexistant, une charge pastorale moyenne de 0,25 unité ovine par hectare. La charge a augmenté très rapidement atteignant 0,5 à 0,75 uo/ha en 1990 (Aidoud & Touffet, 1996).

Le terme « plateau » est attribué au site étudié en raison de la topographie homogène qu'imprime le glacis d'érosion sub-horizontale ou légèrement ondulé (versant-glacis) du quaternaire ancien (Pouget, 1980). Située à une profondeur de 20 à 30 cm, la croûte calcaire zonale, feuilletée et très dure en surface, est caractéristique de ce type de glacis (Ruellan, 1971). A la

surface du sol, dominant les éléments grossiers (graviers) et la pellicule de glaçage. Le sol montre un profil calcaire bien différencié avec en particulier des taux de 1,9 % pour la matière organique et de 28 % pour la fraction fine regroupant les argiles et les limons fins. Ces caractéristiques édaphiques sont indicatrices d'un état relativement bien conservé par rapport aux autres formations steppiques considérées comme issues de la dégradation de nappes alfatières (Aidoud-Lounis, 1997).

Le dispositif d'échantillonnage est un transect long de 4500 m traversant trois niveaux de pâturages P0, P1 et P2 :

- P0 est une parcelle clôturée de 12 ha, non soumise au pâturage depuis l'été 1975 ;

- P1 est un terrain englobant P0, d'environ 500 ha, pâturé sous surveillance (depuis l'été 1975) avec une charge moyenne d'environ 0,25 unité ovine par hectare ;

- P2 correspond au reste de la steppe du plateau de Rogassa, pâturée librement avec une charge pouvant atteindre voire dépasser 0,75 unité ovine par hectare.

Le long du transect, 25 stations espacées de 200 m ont été échantillonnées. A chaque station, deux fosses ont été creusées, l'une sous la touffe d'alfa et l'autre dans l'espace interstitiel, jusqu'à la croûte calcaire située à une profondeur variant respectivement de 15 à 35 cm et de 10 à 25 cm. Dans chaque fosse, sont échantillonnées deux couches : celle en surface est de 6 ± 1 cm d'épaisseur ; celle, sous-jacente est de 14 ± 2 cm d'épaisseur.

La granulométrie est pratiquée sur la terre fine (moins de 2 mm de diamètre), après dispersion des particules, par tamisage puis par prélèvement à la pipette de Robinson. La texture est exprimée par la fraction fine comprenant les argiles et les limons fins selon la définition de Pouget (1980). Quant à la fraction grossière, elle est formée majoritairement par du sable (90 % en moyenne).

Le taux de matière organique TMO est évalué par la formule : $TMO = TCO \times 1.724$ (Baize, 1988). Le taux de carbone organique TCO est dosé selon la méthode d'Anne (Bonneau & Souchier, 1979).

Les éléments de la surface du sol comprennent les fréquences en % du couvert végétal, de la litière, des éléments grossiers, de la pellicule de glaçage et du sable dont l'épaisseur a été également mesurée (moyenne de 10 mesures par station).

Altitude (m)	1130 ± 25
Pluviométrie moyenne (mm/an)	260 ± 6
Température moyenne annuelle	15,5 °C
Moyenne des minimums du mois le plus froid	-0,9 °C
Moyenne des maximums du mois le plus chaud	35 °C
Couvert végétal global (avec 51% pour <i>S. tenacissima</i>)	54 ± 6 %
Surface du sol sans végétation :	
Litière	17 ± 3 %
Éléments grossiers	16 ± 5 %
Sable	1 ± 1 %
Pellicule de glaçage	12 ± 4 %
Caractères du sol * (20-30 cm) :	
Granulométrie : Argiles	13 ± 1 %
Limons	21 ± 2 %
Sables	66 ± 4 %
(Argiles + limons fins)	28 ± 2 %
Taux de matière organique :	1.88 ± 0.36 %

* Les données du sol ont été mesurées dans l'espace entre les touffes en considérant toute l'épaisseur du sol au dessus de la croûte calcaire.

Les moyennes sont calculées sur la base de 11 stations échantillonnées entre 1975 et 76 (Aidoud-Lounis, 1989).

Tableau 1. Caractéristiques écologiques du plateau de Rogassa

Table 1. Ecological characteristics of the Rogassa plateau

		P0	P1	P2	Var %	F	p	
Surface du sol								
Végétation (fréquences en %)	Couvert des pérennes	36,2 ± 4,9	25,0 ± 4,2	15,5 ± 2,7	-57	10.73	<0.001	
	Couvert global	57,0 ± 8,4	46,2 ± 8,2	35,1 ± 4,6	-38	3.80	=0.038	
Sol nu (fréquences en %)	litière	20,0 ± 3,2	19,4 ± 5,1	4,5 ± 1,1	-77	14.57	<0.001	
	pellicule de glaçage	18,2 ± 4,9	21,8 ± 6,4	6,7 ± 4,1	-63	3.24	=0.058	
	éléments grossiers	4,8 ± 1,7	6,2 ± 0,5	3,3 ± 1,4	-31	1.37	=0.270	
	voile sableux	0	6,4 ± 2,6	50,3 ± 6,7	-	34.39	<0.001	
	épaisseur du sable (cm)	0	3,6 ± 1,3	7,6 ± 1,3	-	13.65	<0.001	
Sol								
Argiles + limons fins (%)	Prélèvement global*	28,9 ± 5,3	20,0 ± 3,2	16,4 ± 2,5	-43	11.97	<0.001	
	dans la touffe							
	1ère couche	19,0 ± 2,1	14,4 ± 1,5	3,0 ± 0,3	-84	72.7	<0.001	
	idem	2ème couche	27,0 ± 2,8	19,4 ± 2,2	14,3 ± 2,3	-47	8,90	=0.002
	entre les touffes	1ère couche	29,4 ± 1,1	17,2 ± 3,7	3,7 ± 0,7	-87	43,9	<0.001
idem	2ème couche	35,7 ± 5,6	26,2 ± 1,8	25,5 ± 2,3	-28	3,43	=0.050	
Matière organique (%)	Prélèvement global*	1,7 ± 0,3	1,4 ± 0,3	1,0 ± 0,1	-38	11,98	<0.001	
	dans la touffe							
	1ère couche	2,0 ± 0,1	1,3 ± 0,1	0,8 ± 0,1	-63	44,73	<0.001	
	idem	2ème couche	1,6 ± 0,3	1,3 ± 0,3	1,2 ± 0,1	-23	1,31	=0.291
	entre les touffes	1ère couche	1,5 ± 0,2	1,1 ± 0,2	0,6 ± 0,2	-59	6,24	=0.007
idem	2ème couche	1,7 ± 0,2	1,6 ± 0,3	1,0 ± 0,2	-39	3,98	=0.034	

* la moyenne par relevé est calculée après pondération par rapport à l'épaisseur des couches.

P0 : parcelle mise en défens ; P1 : pâturage contrôlé ; P2 : pâturage libre.

Var % : différence entre P0 et P2

F : valeur critique de la loi de Fisher-Snedecor de l'analyse de variance à une voie permettant de tester la signification des changements le long du transect. Les changements sont significatifs pour 0.05 > p > 0.01, très significatifs pour 0.01 > p > 0.001 et hautement significatifs pour p < 0.001

Tableau 2. Caractéristiques du couvert végétal et du sol le long du transect

Table 2. Characteristics of vegetation cover and soil along the transect

	Différence entre 1 ^{ère} et 2 ^{ème} couches			Différence entre touffes et inter-touffes			
	P0	P1	P2	P0	P1	P2	
MO T	ns	ns	***	MO 1	*	ns	ns
MO I	ns	ns	**	MO 2	ns	ns	ns
ALF T	*	ns	***	ALF 1	**	ns	ns
ALF I	ns	*	***	ALF 2	ns	ns	***

P0 : parcelle mise en défens ; P1 : pâturage contrôlé ; P2 : pâturage libre ; MO : taux de matière organique (%) ;

ALF = taux d'argiles et limons fins.

1 : couche superficielle ; 2 : couche profonde ; T : sous la touffe d'alfa ; I : entre les touffes d'alfa.

Différence des moyennes : ns : non significative ; * : 0.01 < p < 0.05 ; ** : 0.001 < p < 0.01 ; *** : p < 0.001

Tableau 3. Comparaison des moyennes des caractères du sol selon la localisation du prélèvement le long du transect

Table 3. Comparison of soil characters means according to the sampling location along the transect

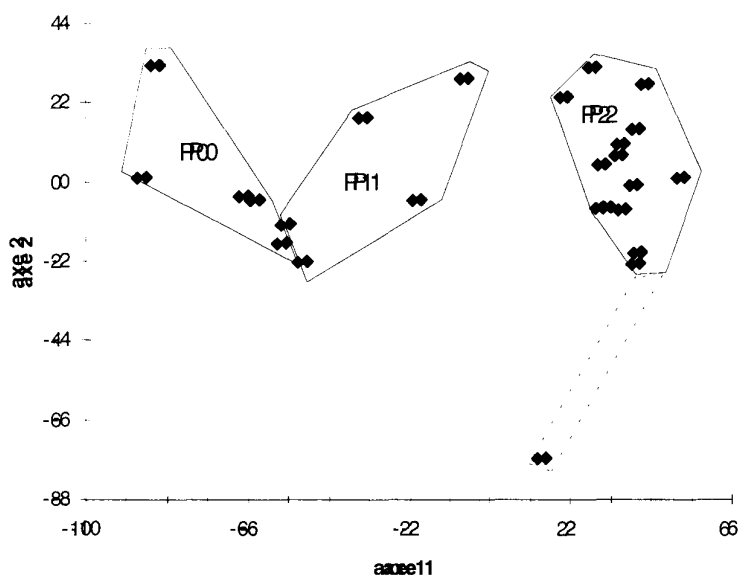


Figure 1. Analyse en composantes principales (système d'axes 1 - 2) montrant la répartition des stations échantillonnées le long du gradient de pâturage

Figure 1. Principal component analysis (axis system 1 - 2) showing the distribution of sampled stations along the grazing gradient

La fréquence de chaque élément a été évaluée à partir d'un relevé de points quadrat (200 points de lecture le long d'une ligne de 20 m) selon la technique de Daget & Poissonet (1971).

Les traitements statistiques ont été réalisés à l'aide du logiciel Statistix (ver. 2.0) pour les comparaisons de moyennes et l'analyse de variance et de Statgraphics-plus pour l'analyse en composantes principales (ACP). L'ACP a été effectuée sur les conditions stationnelles (éléments de surface et données pédologiques).

RESULTATS

Les résultats sont présentés de façon à différencier deux échelles de variations : celle du transect et celle stationnelle qui distingue le sol sous la touffe par rapport au sol interstitiel.

L'ACP (Figure 1) montre un regroupement des stations selon les trois zones P0, P1 ou P2 et leur ordination par rapport à l'axe 1 qui extrait une grande part de l'information, avec un taux d'inertie de 42,45 % et une valeur propre de 18,25 (respectivement de 9,82 %

et 4,22 pour l'axe 2). Cette ordination, conforme au gradient de pâturage, souligne l'importance de ce facteur sur les caractères traités.

Le relevé situé à l'extrémité négative de l'axe 2 se détache nettement du groupe P2. Les données de ce relevé, non représentatif car localisé dans une dépression (daya), n'ont pas été intégrées aux analyses ci-après.

Les caractères du couvert végétal et du sol, le long du transect, sont résumés dans le tableau 2. Les caractères de surface qui varient le plus significativement sont le couvert végétal et le voile sableux. Le couvert des plantes pérennes diminue de 36 à 16 %, soit plus de la moitié, entre la parcelle mise en défens (P0) et le terrain surpâturé (P2). La diminution du couvert végétal global est de 40 % mais a cependant une valeur indicatrice moindre en raison de la plus grande fluctuation des espèces annuelles. Dans l'espace interstitiel ou sol nu, le voile sableux, pratiquement absent dans P0, atteint, dans P2, un taux de couverture de près de 50 % et une épaisseur de près de 8 cm en moyenne.

Ces changements édaphiques le long du transect se traduisent, corrélativement et très nettement, par une baisse des argiles et limons fins et du taux de matière organique. Les variations des caractères édaphiques, mesurées sous la touffe et dans le sol interstitiel, sont significatives. La variation est cependant nettement plus importante en considérant la couche de surface.

La baisse globale du taux d'argiles et limons fins est de 43 % entre P0 et P1. Elle est de 87 % dans la couche superficielle du sol sous la touffe et de 84 % entre les touffes. La diminution, moindre dans la deuxième couche (47 et 28 %), reste cependant significative. Exprimée selon les classes définies par Pouget (1980), la texture passe de « grossière » à « très grossière » sous la touffe et de « moyenne » à « très grossière » dans l'espace entre les touffes.

Les valeurs obtenues dans P1 (sous pâturage contrôlé) sont à la fois intermédiaires et significativement différentes de celles correspondant à P0 et P2. Elles demeurent cependant, comme illustré par la figure 1, plus proches de la situation de mise en défens.

La baisse de matière organique dans le sol est globalement de 38%. Elle suit à peu près la même évolution que celle des argiles et limons fins, mais dans des proportions légèrement inférieures. Cette diminution est, respectivement pour le sol sous la touffe et le sol

interstitiel, de 63 et 59 % pour la couche supérieure et de 25 et 35 % en profondeur.

A l'échelle stationnelle, c'est dans la zone surpâturée que les différences sont hautement significatives ($p < 0.01$) entre couche superficielle et couche profonde (Tableau 3). La différence entre sol sous la touffe et sol interstitiel est significative, pour la fraction fine, de la première couche dans la parcelle mise en défens et de la seconde couche dans la zone surpâturée.

DISCUSSION

A l'échelle du gradient, le principal résultat concernant le sol est l'augmentation du taux de la fraction sableuse qui peut être attribuée soit au départ de la fraction texturale fine, suite à une déstructuration du sol, soit à un apport éolien. La variation granulométrique significative le long du transect, quel que soit le niveau de prélèvement, suggère en fait l'existence des deux phénomènes (ablation et dépôt) dont l'importance respective est variable dans le temps et dans l'espace (Aidoud & Touffet, 1996). La diminution du taux de matière organique est nettement corrélée à celle des limons fins et à celle des argiles qui sont connues pour assurer une meilleure conservation de la matière organique (Pouget, 1980). La comparaison des résultats obtenus en 1975 et en 1993 (Tableau 1), implique une baisse du taux de matière organique de l'ordre de 40 % pour tout le profil. Un changement d'une telle ampleur est considéré comme une réelle catastrophe écologique (Bullock & Le Houérou, 1996). Il est l'expression d'une baisse du niveau trophique du sol mais également l'indicateur de la destruction de nombreuses propriétés du sol comme la structure, la capacité d'échange et la capacité hydrique, ce qui augmente la sensibilité à l'érosion éolienne (Middleton, 1985 ; Bullock & Le Houérou, 1996).

Le long du transect, le taux de matière organique est toujours plus élevé dans la deuxième couche avec une différence qui devient plus nette dans la zone P2. Il semble donc que cela puisse s'expliquer par la dégradation des horizons superficiels, phénomène déjà constaté par Pouget (1980) dans des formations arides algériennes mais à l'échelle plus large d'un gradient climatique. Le taux plus élevé en profondeur ne peut pas être entièrement attribué à une incorporation profonde de la matière organique par décomposition de la biomasse souterraine. Comme discuté par Bottner

(1982), l'isohumisme qui est souvent reconnu dans ce type de sol ne serait qu'apparent. En effet, la décomposition relativement active de la litière dans cette steppe (Bessah, 1998), suggère un apport organique essentiellement lié aux parties aériennes de l'alfa. La faible contribution à la biomasse totale des organes souterrains (Aidoud, 1989), en accord avec la synthèse dressée par Barbour (1981) pour les zones arides en général, peut conforter cette hypothèse. Ceci doit cependant être relativisé, car les processus fonctionnels en cause doivent être considérés plus en terme de turnover de la matière organique qu'en terme de biomasse.

Les changements édaphiques observés le long du gradient peuvent s'expliquer par la réduction du couvert de l'alfa. La détérioration d'attributs vitaux édaphiques (Aronson *et al.*, 1995) du système, tels que la texture ou la matière organique, a pu être évaluée ainsi après une période relativement courte de moins de dix ans. Cette rapidité est confirmée en Espagne, par Albaladejo *et al.* (1998) qui montrent qu'après environ 5 ans la réduction de la couverture végétale peut se répercuter significativement sur les caractéristiques du sol par la baisse de la matière organique et la détérioration des propriétés physiques.

A l'échelle stationnelle, la végétation steppique est constituée de touffes séparées par un espace interstitiel à couverture végétale très faible. Dans la parcelle protégée P0, les résultats montrent une différence significative entre touffe et espace interstitiel pour les caractères édaphiques, en particulier ceux de la couche de surface. Ils confirment ceux obtenus notamment par Puigdefàbregas & Sanchez (1996), Cerda (1997) et Domingo *et al.* (1998), montrant le rôle que la touffe d'alfa joue, dans le système, par ses aptitudes à intercepter et à retenir l'eau et les sédiments. La relation entre la baisse de vigueur des touffes d'alfa et la sensibilité à l'érosion a été montrée par simulation (Sanchez & Puigdefàbregas, 1994). Ajoutées à ses capacités adaptatives à l'aridité (Nedjraoui, 1990 ; Aidoud, 1992 ; Pugnaire & Haase, 1996), ces propriétés font de l'alfa une « espèce clef de voûte » du système, au sens de Aronson *et al.* (1995). A l'opposé, dans la zone surpâturée P2, le dépérissement des touffes entraîne la destruction de leurs propriétés édaphiques et en particulier du rôle protecteur contre l'érosion. La différence plus faible entre la touffe et l'espace interstitiel dans la zone P2 reflète la destruction de la structure du système, tendance qui semble se refléter à travers la composition de la végétation (Aidoud, 1994).

Dans le Sud-Oranais, cet état correspond à celui de l'ensemble des anciennes steppes d'alfa de plaine. Le niveau de dégradation atteint constitue un stade irréversible qui peut indiquer d'un point de vue édaphique, un seuil fondamental entre pâturage et surpâturage. Notons que l'« irréversibilité » est employée ici dans la sens où la restauration *s.s.* (Aronson *et al.*, 1995) du système préexistant est devenue très peu probable, voire impossible. Dans la logique pastorale actuelle, la zone P1 sous pâturage contrôlé, malgré les changements édaphiques observés, constitue le système de référence présentant les normes à atteindre par réhabilitation (Aronson *et al.*, 1995).

CONCLUSION

Les changements édaphiques, analysés à travers le taux de matière organique et la texture dans les steppes d'alfa de plaine, sont significatifs. Ils montrent l'importance des phénomènes de désertification dans ce type de steppes qui semblent les plus affectées en Algérie. Les résultats obtenus soulignent tout l'intérêt de l'approche utilisant le gradient d'intensité de pâturage, partant d'une situation de steppe soustraite au pâturage durant une vingtaine d'années, à celle où la steppe d'origine a pratiquement disparu par surpâturage. La disparition des principales fonctions édaphiques des touffes d'alfa suite à leur dépérissement confirment les changements observés sur la biomasse (Aidoud & Touffet, 1996) ainsi que sur la diversité et la composition floristique (Aidoud, 1994 ; Slimani, 1998). Les changements édaphiques restent cependant moins importants en profondeur qu'en surface, traduisant ainsi une certaine inertie du système. Malgré l'intensité de dégradation, les attributs édaphiques, dans le pire des cas, n'ont pas atteint les niveaux observés dans un désert et une réhabilitation demeure donc possible. Celle-ci reste cependant tributaire de l'efficacité et de la rapidité des mesures de gestion durable des pâturages qui doivent être prises à différents niveaux de décision.

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Soil variables affecting the vegetation of inland western desert of Egypt

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ABSTRACT

The present study provides a quantitative estimate of soil, vegetation structure and species distribution in 144 stands along two transects in two extreme desert zones of western Egypt. This area is of a biogeographic importance due to its transitional character where the Nubian Desert and the Northern Mediterranean vegetation meet. Six soil variables were estimated: salinity, pH, calcium carbonate, moisture, organic matter and texture. A total of 59 angiospermic species and a gymnospermic (*Ephedra alata*) were recorded. The sampled stands were classified into eight groups according to TWINSpan techniques. Detrended correspondence analysis (DCA) showed that these groups separated along the first two axes, could also be effectively interpreted with canonical correspondence analysis (CCA). Based on a forward regression, salinity, fine sediments (silt and clay), organic matter and soil moisture content related closely to the first three canonical axes, and accounted for 84.1% of the species-environment relation among the stands. Both classification and ordination resulted in a clear demonstration of the vegetation pattern in the study area.

Key-words: Egypt, plant distribution, classification, accidental vegetation, gradient analysis, soil characteristics

RESUME

Cette étude a pour objectif de dresser une estimation quantitative du sol, de la structure de la végétation, et de la distribution des espèces de 144 stations le long de deux transects, dans deux zones désertiques d'Égypte occidentale. Cette région est biogéographiquement importante à cause de son caractère transitoire entre la végétation du désert de Nubie et celle du nord de la Méditerranée. Six variables de sol ont été estimées : salinité, pH, carbonate de calcium, humidité, matière organique et texture. Cinquante neuf espèces d'angiospermes et une espèce de gymnosperme (*Ephedra alata*) ont été recensées. Les stations échantillonnées ont été classées en huit groupes selon les techniques de TWINSpan. L'analyse des correspondances détendancée (DCA) a montré que ces groupes, séparés sur les deux premiers axes, pourraient également être interprétés par une analyse canonique des correspondances (CCA). À partir d'une régression au pas à pas, il apparaît que la salinité, les sédiments fins (vase et argile), la matière organique et la teneur en humidité du sol sont fortement corrélés aux trois premiers axes canoniques, et participent pour 84,1% de la relation espèce-environnement au sein des stations. La classification et l'ordination ont toutes deux montré clairement l'organisation des patrons de végétation au sein de la zone d'étude.

Mot- clés : Égypte, distribution de végétation, classification, végétation accidentelle, analyse de gradient, caractéristiques de sol

INTRODUCTION

Desert vegetation in Egypt is by far the most important and characteristic type of the natural plant life. It covers vast areas and is formed mainly of xerophytic shrubs and subshrubs. Monod (1954) recognised two types of desert vegetation, namely contracted and diffuse. Both types refer to permanent vegetation which can be accompanied by ephemeral (or annual) plant growth depending on the amount of precipitation in a given year. Kassas (1966, 1971) added a third type "accidental vegetation" where precipitation is so low and falls so irregularly that no permanent vegetation exists. It occurs mainly as contracted patches in runnels, shallow depressions, hollows, wadis and on old dunes with coarse sand. Accidental vegetation consists of species which are able to perform an annual life cycle: potential annuals (*sensu* Haines, 1951), or potential perennials (*sensu* Bornkamm, 1987), but can likewise continue growing as long as water persists in the soil. Thomas (1988) identified these plants as those with episodic growth strategies linked to immediate water availability. Recently, Springuel (1997) classified the accidental vegetation in south eastern Egypt into three groups: run-off dependent vegetation in the main wadi channels, run-on dependent vegetation of playa formation, and rain dependent vegetation on levelled plains of sand sheets.

In a survey of the vegetation units in the Western Desert of Egypt, outside the Oases, Bornkamm and Kehl (1990) distinguished five desert zones along a precipitation gradient. Besides the well known semidesert and full desert zones in the very north, three zones of extreme desert show a significant differentiation (Figure 1). Both extreme desert zones III and IV support the growth of accidental vegetation, where the precipitation in the former amounts to 5-10 (20) mm year⁻¹ whereas in the latter is 1-5 mm year⁻¹. On the other hand, extreme desert V in the very south is practically void of vegetation where precipitation is proposed to be less than 1 mm year⁻¹. Typical accidental vegetation types in the Western Desert of Egypt are: *Zygophyllum coccineum* with *Salsola imbricata* subsp. *imbricata*, *Stipagrostis acutiflora* with *Zilla spinosa* as well as stands of *Salsola imbricata* subsp. *imbricata* with *Fagonia arabica*. However, ground-water-dependent vegetation in all the three extreme desert zones exists too: Zahran (1972) and Abd El-

Ghani (1981, 1985) in large oases (Siwa, Bahariya and Farafra), and in small oases and depressions (Bir Safsaf, Bir El-Shab, Bir Tarfawi and Qara): El-Hadidi (1980b), Bornkamm (1986), Abd El-Ghani (1992).

Although our knowledge of the growth of accidental vegetation in Egypt has considerably increased during the last two decades (Alaily *et al.*, 1987; Bornkamm, 1987; Springuel *et al.*, 1990), much less is known about this vegetation in quantitative terms. The present study aims at describing the floristic composition of the accidental type of vegetation growing in parts of the Western Desert of Egypt and analysing the distribution of species in relation to certain environmental factors by applying the multivariate analysis techniques.

STUDY AREA

The present study has been conducted in two consecutive extreme desert zones (*sensu* Bornkamm & Kehl, 1990), where the accidental type of vegetation exists. Data is from two transects: the northern one extends for a distance of about 150 km; half-way along Siwa Oasis-Mersa Matruh road, and represents the extreme desert zone III (Figure 1). This transect is principally located in the inland part of the Middle Miocene plateau that rises to about 100 m above the depression floor (reaches 20 m below sea level). The southern transect extends for a distance of about 140 km, along the Dakhla-Farafra road and represents the extreme desert zone IV. It is located in the middle limestone plateau (500 m above sea level). The northern transect lies in the Libyan Desert while the southern one in the Nubian Desert (El-Hadidi, 1980a). In general, the landscape of the northern transect is a part of the Central Sahara, whereas the southern transect is a part of the Southern Sahara (Schiffers, 1971).

According to Walter and Breckle (1984) the study area lies in the zone of subtropical arid deserts. The temperature regime is characterised by mild winters and very hot summers. Whereas average January temperature remains rather constant between 12°C and 14°C, the July mean rises to approximately 31°C. The absolute maxima of the southern region of the study area may reach 49°C. Precipitation is erratic, variable and unpredictable with frequent long dry periods. Zahran and Willis (1992) reported that the mean annual rainfall ranges from 9.6 mm year⁻¹ in Siwa Oasis (the nearest station to the northern transect) to nearly 1 mm

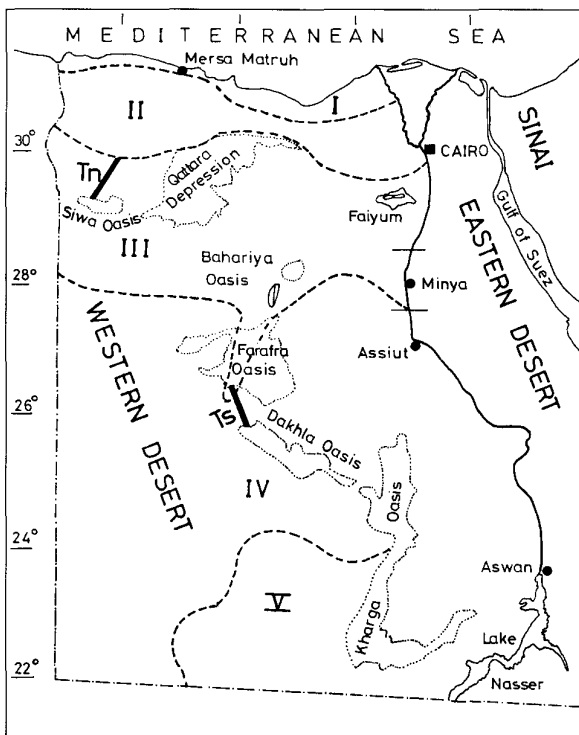


Figure 1. Map showing the five vegetation zones of the Western Desert of Egypt (after Bornkamm & Kehl, 1990), indicating the position of the two studied transects: T_n = Northern transect, T_s = Southern transect

year⁻¹ in Dakhla Oasis (the nearest to the southern transect). The climatic gradient along the N-S direction in the study area is obvious (Table 1). The Pluviothermic Quotient (Emberger, 1955) for Siwa Oasis is about 1.43, while that of Dakhla Oasis is nearly zero indicating extreme aridity.

METHODS

The phytosociological survey of the study area was carried out during several visits in 1986-88 and 1995-96. Stands were randomly chosen at locations where either dense vegetation or change in species composition was encountered. A total of 144 stands (each of a size of 25 x 25 m) were sampled: 83 in the northern transect and 61 in the southern one. In each stand, density (individuals/100 m²) and frequency (occurrences/100 quadrats) of the present species were estimated using fifty 1 x 2 m² randomly located quadrats. Plant cover (m/100 m) was determined by the line-intercept method (Canfield, 1941), using five parallel lines distributed randomly across the stand. Relative importance value (IV) for each species in each stand

was calculated by the sum of its relative density, frequency and cover (it has a maximum value out of 300). Voucher specimens of each species were collected, identified and deposited in the Herbarium of Cairo University (CAI). Taxonomic nomenclature is according to Täckholm (1974), and updated following Boulos (1995, 1999).

For each sampled stand, four soil samples were collected from profiles of 0-50 cm and pooled together to form one composite sample. Soil texture was determined with the hydrometer method and CaCO₃ by Collin's calcimeter. Organic matter content and soil moisture were estimated by drying and then ignition at 600°C for 3 hours. Soil-water extracts (1: 2.5) were prepared for the determination of electric conductivity and pH using conductivity-meter and pH-meter, respectively.

Stand-species data matrix was classified using the importance values of perennial species by Two-way indicator species analysis (TWINSPAN; Hill, 1979) (Table 2). Due to the relative paucity of most stands (generally between 5 and 14 species), classification by TWINSPAN was stopped at the third level so that the size of stands would demonstrate ecological meaning though their floristic structure. All the default settings were used for TWINSPAN, except the pseudo-species cut levels were altered to 0, 2, 5, 10, 20, 40, 50, 60 and 80, and the number of indicator species was four per class.

Canonical correspondence analysis (CANOCO: ter Braak, 1988 & 1990) was used for the same set of data. Rare species were downweighted to reduce distortion of the analysis. Detrended Correspondence Analysis (DCA: Hill & Gauch, 1980) was applied to check the magnitude of change in species composition along the first ordination axis (i.e. gradient length in standard deviation units). Direct gradient analysis, Canonical Correspondence Analysis (CCA) were used in order to examine the relationships between the floristic composition of the sampled stands and the estimated soil variables. An exploratory CCA was performed using all studied edaphic variables, followed by a CCA with forward selection. The CCA with forward selection was evaluated by examining the canonical coefficients (significance assessed by approximate *t*-tests) and the intraset correlations (ter Braak, 1986).

Station	Temperature (°C)		Relative Humidity (%)		Rainfall (mm annual ⁻¹)	Evaporation (mm day ⁻¹)
	Mean Min	Mean Max	Mean Min	Mean Max		
Mersa Matruh	12.4	24.7	51	67	144.0	8.3
Siwa	4.1	38.0	42	61	9.6	11.5
Dakhla	5.8	39.3	19	42	0.7	18.4

Table 1. Climatic characteristics (average 1931-1978) of three stations distributed in the study area (after Zahran, 1972; Zahran & Willis, 1992)

TWINSPAN group	I	II	III	IV	V	VI	VII	VIII
Group size	7	16	45	19	5	23	24	5
<i>Prosopis farcta</i> (P fr)	121	2	1	-	-	-	-	-
<i>Phoenix dactylifera</i> (P df)	15	9	5	-	-	-	-	-
<i>Calotropis procera</i> (C pr)	1	12	1	-	-	-	-	-
<i>Tamarix nilotica</i> (T ni)	30	109	19	4	23	6	1	-
<i>Stipagrostis plumosa</i> (S pl)	-	2	6	3	6	-	1	9
<i>Pulicaria incisa</i> (P cr)	-	1	1	1	12	4	8	5
<i>Heliotropium digynum</i> (H dg)	-	5	1	-	7	3	2	4
<i>Alhagi graecorum</i> (A gr)	-	77	22	-	-	2	3	2
<i>Citrullus colocynthis</i> (C cl)	-	1	2	-	2	1	-	-
<i>Fagonia bruguieri</i> (F br)	-	1	9	3	-	-	-	-
<i>Zygophyllum album</i> (Z al)	-	12	-	4	-	-	-	-
<i>Traganum nudatum</i> (T nd)	-	1	2	-	-	-	-	-
<i>Imperata cylindrica</i> (I cy)	-	5	1	-	-	-	-	-
<i>Nitraria retusa</i> (N rt)	-	11	1	-	-	-	-	-
<i>Launaea nudicaulis</i> (L nu)	-	5	2	-	-	-	-	-
<i>Hyoscyamus muticus</i> (H mu)	-	1	1	-	-	-	-	-
<i>Zygophyllum coccineum</i> (Z co)	-	8	69	14	5	4	5	-
<i>Salsola imbricata subsp. imbricata</i> (S im)	-	18	62	10	-	-	-	-
<i>Cornulaca monacantha</i> (C mo)	-	1	15	142	-	5	-	-
<i>Fagonia arabica</i> (F ar)	-	1	1	71	5	6	1	-
<i>Pulicaria crispa</i> (P cr)	-	-	36	4	-	2	5	-
<i>Monsonia nivea</i> (M nv)	-	-	2	1	3	2	1	-
<i>Fagonia indica</i> (F in)	-	-	4	-	-	-	-	-
<i>Sarcocornia fruticosa</i> (S fr)	-	-	1	-	-	-	-	-
<i>Calligonum polygonoides subsp. comosum</i> (Ccm)	-	-	1	3	-	1	-	-
<i>Zilla spinosa subsp. spinosa</i> (Z sp)	-	-	10	2	9	4	2	1
<i>Acacia tortilis subsp. raddiana</i> (A rd)	-	-	1	19	-	6	2	-
<i>Astragalus trigonus</i> (A tr)	-	-	3	2	3	2	2	-
<i>Anabasis articulata</i> (A ar)	-	-	3	13	-	14	1	15
<i>Atriplex leucoclada</i> (A lu)	-	-	-	-	109	4	2	-
<i>Herniaria hemistemon</i> (H he)	-	-	-	-	-	1	-	1
<i>Deverra tortuosa</i> (D tr)	-	-	-	-	14	39	86	-
<i>Randonia africana</i> (R af)	-	-	-	-	-	107	26	19
<i>Carduncellus mareoticus</i> (C mr)	-	-	-	-	-	2	14	-
<i>Farsetia aegyptia</i> (F ag)	-	-	-	-	-	3	1	-
<i>Capparis spinosa var. aegyptia</i> (C sp)	-	-	-	-	-	12	96	75
<i>Zilla spinosa subsp. biparmata</i> (Z bi)	-	-	-	-	-	3	7	33
<i>Helianthemum lippii</i> (H lp)	-	-	-	-	-	1	1	6
<i>Salsola villosa</i> (S vr)	-	-	-	-	-	4	2	-
<i>Ephedra alata</i> (E al)	-	-	-	-	-	-	3	-

Table 2. Species composition of the 144 stands in the two transects, arranged in order of occurrence in the eight TWINSPAN groups. Entries in **bold** are characteristic species in each group. Species abbreviations displayed in Figures 2, 3 and 5 are given between parentheses.

Soil variable	TWINSPAN groups								F- ratio	P
	I	II	III	IV	V	VI	VII	VIII		
EC (mS cm ⁻¹)	0.5±0.3	2.8±0.7	0.8±0.9	0.9±0.7	2.2±0.2	0.7±0.7	0.5±0.3	1.1±0.9	19.0	0.0001
pH	8.0±0.6	8.8±0.4	7.9±0.5	7.9±0.4	7.7±0.5	7.7±0.5	7.9±0.4	7.6±0.4	1.3	0.3
CaCO ₃ (%)	9.6±2.6	11.3±4.9	15.0±5.8	13.5±5.3	21.0±8.1	14.8±6.0	15.1±5.5	19.1±3.8	4.6	0.0001
MC (%)	1.5±0.3	2.0±0.6	2.12±0.7	2.3±0.5	2.5±0.2	2.6±0.8	2.9±0.7	3.3±0.7	5.4	0.0001
OM (%)	1.5±0.2	0.3±0.4	0.21±0.3	0.2±0.3	0.1±0.1	0.1±0.1	0.1±0.1	0.1±0.06	29.5	0.0001
Sand (%)	93.5±1.0	93.3±1.8	94.5±4.1	92.4±2.0	91.2±0.9	91.5±1.0	88.4±16.9	90.4±0.9	12.5	0.0001
Silt + clay (%)	6.5±1.4	6.7±1.8	5.5±2.1	7.6±2.0	8.8±0.9	8.4±1.0	11.6±1.1	9.6±1.0	8.6	0.0001

Table 3. Mean values, standard deviation errors and ANOVA F values of the soil variables in the stands supporting the 8 vegetation groups obtained by TWINSPAN. EC = electric conductivity, CaCO₃ = calcium carbonate, MC = moisture content and OM = organic matter

	Axis		
	1	2	3
Eigenvalues			
DCA	0.830	0.496	0.377
CCA	0.474	0.376	0.292
Species-environment correlation coefficients			
DCA	0.724	0.468	0.409
CCA	0.781	0.871	0.658

Table 4. Comparison of the results of ordination by DCA and CCA: eigenvalues and species-environment correlation coefficients for the first three axes are demonstrated

Soil variables	Canonical coefficient			Intra-set correlations		
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
EC	-0.48*	0.88*	0.01	-0.50	0.85	0.35
pH	-0.13	-0.16*	-0.10	-0.22	0.07	0.06
CaCO ₃	-0.08	0.02	-0.21	0.06	-0.08	-0.37
MC	0.28*	0.09	0.10	0.49	-0.10	0.24
OM	-0.33*	-0.19*	0.88*	-0.41	-0.28	0.85
Sand	0.12	-0.06	0.01	-0.09	-0.07	0.005
Silt + clay	0.53*	0.29*	0.25	0.67	0.53	0.27

Table 5. Canonical coefficients and the intra-set correlations of soil variables with the first three axes of CCA

* = t-values > 2.3 (only indicative of coefficient strength)

EC = electric conductivity, CaCO₃ = calcium carbonate, MC = moisture content and OM = organic matter

The exploratory CCA was evaluated using the intra-set correlations, since the canonical coefficients were unstable due to inclusion of highly correlated variables.

Eight soil variables were included: electric conductivity, pH, CaCO₃, soil moisture, organic matter, sand, silt and clay. The significance of differences between the different vegetation groups, as to their edaphic variables, was tested by ANOVA. CCA axes were evaluated statistically by means of a Monte

Carlo permutation test (ter Braak, 1988). All the statistical techniques were according to student SYSTAT software (STUSTATW 5: Berk, 1994).

RESULTS

Sixty plant species related to 19 families of the angiosperms and one of the gymnosperms were recorded in this study. They constituted 40 perennial and 20 annual species: Cruciferae and Chenopodiaceae (13.3%

each), Zygophyllaceae (11.7%), Caryophyllaceae, Compositae and Leguminosae (10.0% each), while the other 14 families share 31.7%. Chamaephytes are the most abundant life form and constituted 40.0% of the total flora of the study area, followed by therophytes (33.3%), hemicryptophytes (15.0%) and phanerophytes (11.7%). The most common perennials recorded were: *Prosopis farcta*, *Tamarix nilotica*, *Fagonia arabica*, *Zygophyllum coccineum*, *Salsola imbricata* subsp. *imbricata*, *Cornulaca monacantha*, *Alhagi graecorum*, *Atriplex leucoclada*, *Randonia africana*, *Deverra tortuosa* and *Capparis spinosa* var. *aegyptia* may be considered as leading dominants and characteristic species. Each of these species attains a maximum importance value (IV) of more than 140 (out of 300 for all species in a stand), and a mean of more than 60. Common but less important perennials are *Phoenix dactylifera*, *Pulicaria crispa*, *Anabasis articulata*, *Zilla spinosa* subsp. *spinosa*, *Stipagrostis plumosa* and *Pulicaria incisa*. Common annuals include: *Trigonella stellata*, *Zygophyllum simplex*, *Cotula cinerea*, *Eremobium aegyptiacum*, *Schouwia thebaica* and *Paronychia arabica* subsp. *arabica*.

The 144 stands were classified into eight vegetation groups according to TWINSPAN technique (Figure 2). The first level of the dendrogram separates all the stands into two main groups. The first group comprises 57 stands found mainly in the northern transect, and the second comprises 87 stands sampled from both transects. Table 3 summarises the mean values and the standard deviations of the measured soil variables in the eight groups derived from TWINSPAN. Generally, pH shows the least variation among groups. It can also be noted that whereas levels of lime and fine materials attain their highest values in the groups of the northern transect, the organic matter content reaches its highest levels in those of the southern transect.

The identified vegetation groups are named after the characteristic species as follows: *Prosopis farcta-Tamarix nilotica* (lower part of the southern transect in the vicinity of the lowlands of Dakhla Oasis); *Tamarix nilotica-Alhagi graecorum* (southern transect, high salinity levels favour the growth of some halophytic species, e.g. *Nitraria retusa* and *Zygophyllum album*); *Zygophyllum coccineum-Salsola imbricata* subsp. *imbricata* (in runnels and depressions of the southern transect); *Cornulaca monacantha-Fagonia arabica* (larger catchment areas of the north-

ern transect, some species of this group do not penetrate into other groups of the southern transect); *Atriplex leucoclada* (lower part of the northern transect); *Randonia africana-Deverra tortuosa* (the silty runnels, and occupying a distance of about 20 km of the middle part of the northern transect); *Deverra tortuosa-Capparis spinosa* var. *aegyptia* (occupying a distance of about 30 km in the upper stretches of the middle part of the northern transect); *Capparis spinosa* var. *aegyptia-Zilla spinosa* subsp. *biparmata* (in the low depressions between km 185 and km 198 along the lower part of the northern transect).

The four DCA axes explain 11.7%, 7.0%, 5.3% and 3.4% of the total variation in the species data, respectively. This low percentage of variance explained by the axes is attributed to the many zero values in the vegetation data set. Table 4 shows that the eigenvalue for the first DCA axis was high indicating that it captured the greater proportion of the variation in species composition among stands, but the species-environment correlation coefficients were low for DCA axes.

DCA ordination of the perennial species (Figure 3) shows that species with high positive scores on axis 1 are found mainly in stands of the southern transect, and ordinated close to the right end-point: *Prosopis farcta*, *Phoenix dactylifera*, *Nitraria retusa*, *Sarcocornia fruticosa* and *Imperata cylindrica*. The species positioned on the other end of this axis include: *Capparis spinosa* var. *aegyptia* (negative end), *Deverra tortuosa*, *Randonia africana*, *Ephedra alata* and *Helianthemum lippii*. These and many other species are commonly found in the upper and middle parts of the northern transect. In the centre of axis 1 there are many species found throughout the investigated area with no preference to any geographical aspect (e.g. *Zygophyllum coccineum*, *Tamarix nilotica*, *Alhagi graecorum*, *Fagonia arabica* and *Cornulaca monacantha*). Along axis 2, species with high positive scores include: *Atriplex leucoclada* and *Zilla spinosa* subsp. *biparmata*. These species are recorded from the lower part of the northern transect, whereas species on the other end are of common occurrence in the middle and upper parts. To compare the classification and DCA ordination results, the recognised eight TWINSPAN groups are superimposed. Significance correlations of soil variables with the first four DCA axes (results not shown) revealed greater correlations along axis 1 than the higher order axes.

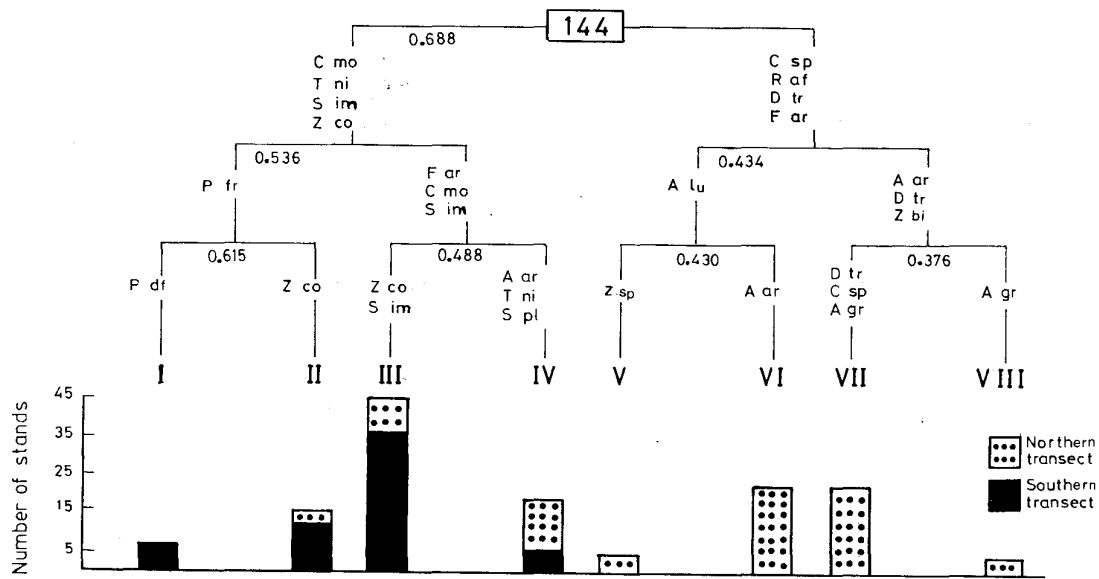


Figure 2. TWINSpan classification are indicated for the three levels of division. Indicator species are given together with pseudo-species values. The number of stands and their distribution along the two transects are indicated.

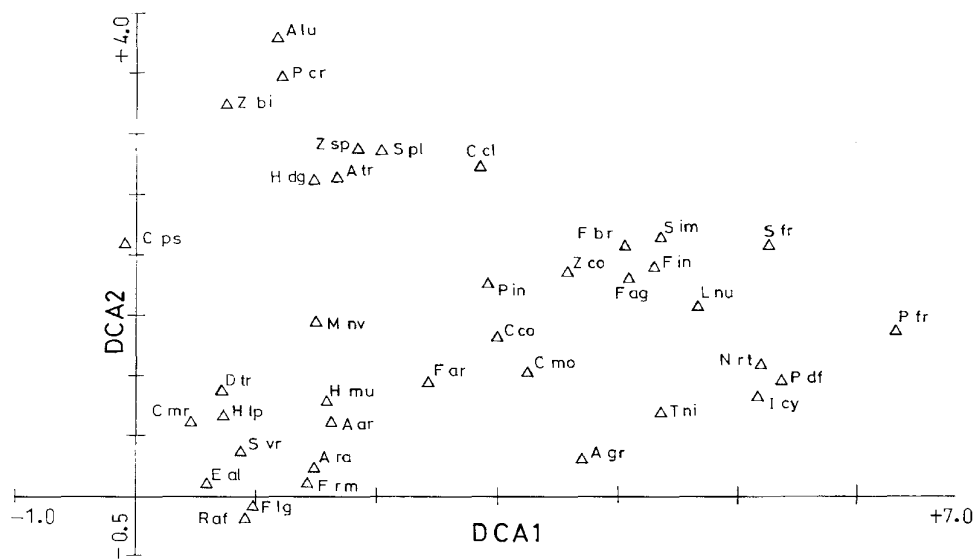


Figure 3. DCA ordination of the 40 species along axes 1 and 2

DCA axis 1 shows significant positive correlations with salinity ($r=0.37$) and organic matter content ($r=0.57$) and negative correlations with soil moisture ($r=-0.42$) and fine materials ($r=-0.71$). DCA axis 2 is negatively correlated with salinity ($r=-0.44$) and fine sediments ($r=-0.67$) and positively correlated with CaCO_3 ($r=0.52$).

The eigenvalues of the first three axes of the Canonical Correspondence Analysis (CCA) of the 144 stands decrease rapidly (Table 4). These eigenvalues

were somewhat lower than for the DCA axes, indicating that important explanatory site variables were not measured in the analysis or some of the variation was not explained by soil variables. However, the expected species-environment correlations were higher for the first three canonical axes explaining 84.1% of the cumulative variance. From the intra-set correlations of the soil factors with the first three axes of CCA shown in Table 5, it can be inferred that the first axis was shaped by fine sediments, moisture content

and salinity, while the second axis was defined by salinity and organic matter content. This fact is also evident in the ordination diagrams (Figures 4 & 5). Contribution of salinity, fine sediments, organic matter and moisture content, as indicated by the forward selection in the CCA program, to the variation in species data were 29.4%, 29.0%, 22.1% and 11.3%, respectively.

CCA ordination diagram for the species scores and canonical coefficients scores of the soil variables is presented in Figure 4. Three species grouping are evident. The first was highly associated with organic matter and sand, and includes species such as *Prosopis farcta*, *Salsola imbricata* subsp. *imbricata*, *Fagonia bruguieri*, *Zygophyllum coccineum* and *Cornulaca monacantha*. The corresponding TWINSpan groups were I, III and IV (Figure 5). A second group associated with salinity and pH and includes: *Tamarix nilotica*, *Alhagi graecorum*, *Nitraria retusa*, *Atriplex leucoxyla* and *Calotropis procera*. Vegetation groups located here are II and V. The third group was closely associated with moisture content, fine materials and lime. The associated vegetation groups are VI, VII and VIII, and include: *Deverra tortuosa*, *Randonia africana*, *Zilla spinosa* subsp. *biparmata* and *Atriplex leucoxyla*.

DISCUSSION

The vegetation groups which resulted from the application of TWINSpan in the study area, may be related in its northern transect to the *Salsolion tetrandrae* of habitats with soils derived from chalks and marls and rich in gypsum and soluble salts and the *Anabasion articulatae arenarium*, *Hammada-Anabasion articulatae* (Zohary, 1973), and *Thymelaion hirsutae* (Tadros & Atta, 1958) of the progressively less saline habitats. The associations belonging to these alliances and their characteristic species have repeatedly been recorded as abundant in ecological studies of specific habitats in the western Mediterranean coastal region of Egypt (Migahid *et al.*, 1971), and in the north-western Negev, Israel (Tielbörger, 1997). TWINSpan groups of the southern transect can be inferred to the alliance *Zygophyllion coccinei* (El-Sharkawy *et al.*, 1984) with their characteristic species are commonly recorded in the communities of the southern part of the Western Desert of Egypt (El-Hadidi, 1980b; Boulos, 1982). According to

the detailed phytosociological survey by Bornkamm and Kehl (1990), they suggested one new order: *Pituranthetalia tortuosi* to comprise all the plant communities of the Western Desert of Egypt. Within this order the northern communities can be attributed to the alliance *Thymelaion hirsutae* (Eig, 1946) and the southern one to the alliance *Zygophyllion coccinei*. The results obtained in this study largely corroborate the latter suggestion. Whereas some species, e.g., *Atriplex leucoxyla*, *Deverra tortuosa*, *Randonia africana*, *Capparis spinosa* var. *aegyptia* and *Zilla spinosa* subsp. *biparmata* are confined to the northern transect, and *Prosopis farcta*, *Fagonia bruguieri*, *Traganum nudatum* and *Salsola imbricata* subsp. *imbricata* to the southern one, some other species exhibit wide ecological amplitude of tolerance through their distribution in both transects. Consequently, it can be suggested that the vegetation of the study area represents a gradual transition from the southern Nubian communities (of the Nubian Desert *sensu* El-Hadidi, 1980a) in the south-western part to those characteristic of the northern Mediterranean coast (Libyan Desert *sensu* El-Hadidi, 1980a). The transitional character is clearly indicated by the fact that a group of species reaches its southern limit, and another group reaches its northern limit of distribution.

The habitat investigated in this study is a relatively simple one, in which the species have to withstand harsh environmental conditions. This is not only reflected by the preponderance of annuals, but also by the presence of several highly-adapted, drought-resistant species (Abdel-Razik *et al.*, 1984). In this respect, the vegetation along the two studied transects is similar to that of gorges (karkurs) of Gebel Uweinat and some neighbouring areas of south-western Egypt (Boulos, 1982; Bornkamm, 1986). A major difference between the two corresponding habitat types is the high degree of scarceness of precipitation which may fall once every seven to ten years in Uweinat, and up to twenty years or more in Gilf Kebir and the neighbouring areas. The vegetation cover of the latter landscape is less than 1% in the extreme desert (Stahr *et al.*, 1985). Thus, often just one species reaches dominance forming monotypic stands. However, monodominant stands in this study are not as common as those codominated by more than one species.

Along gradients of decreasing precipitation, vegetation varies from grasslands to shrublands (Westoby, 1980).

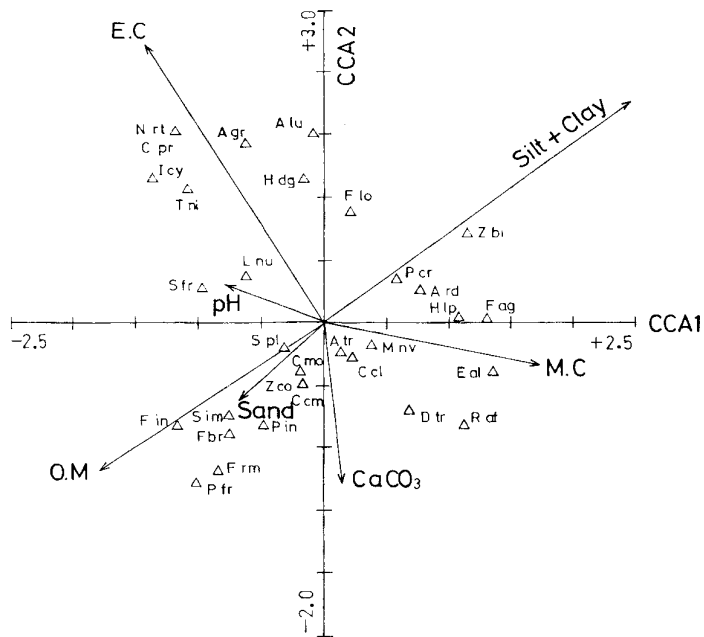


Figure 4. CCA ordination of the 40 species along the first two axes. The effective soil gradients are indicated.

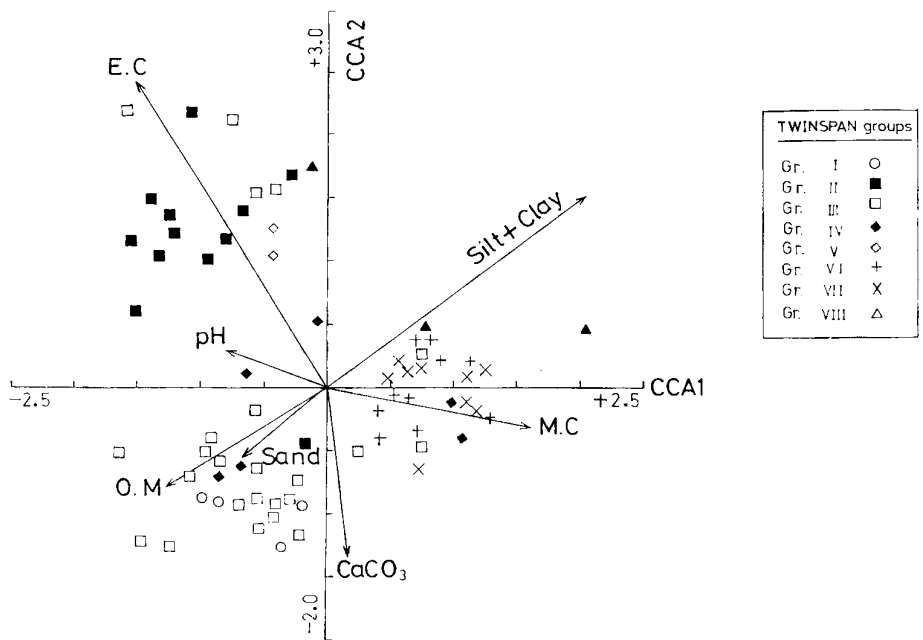


Figure 5. CCA ordination of the 144 stands along the first two axes. The effective soil gradients are indicated.

The relative advantage of shrubs over grasses when water is limiting, as in the study area, can be explained by their extensive root systems which are capable to utilise water stored in different soil depths, whereas grasses utilise the transient water stored in the upper soil synchronic with precipitation pulses. The upper dry layer of the surface deposits acts as a protective layer, moisture is stored in subsurface layers, and the underlying sandstone provides added water storage capacity. The presence of a subsurface layer that is permanently wet is well-known phenomenon in the Egyptian Deserts (Kassas & Batanouny, 1984). As presented in the results, the dominance of shrubby plant species over the grasses is evident. Chamaephytes constitute 40% of the floristic composition, followed by therophytes. The dominance of both chamaephytes and therophytes over other life forms seem to be a response to the hot dry climate and human and animal interferences. A comparison of the life-form spectrum of the same 5° of the northern latitude in the corresponding Eastern Desert of Egypt (25°N – 30°N), Abd El-Ghani (1998) showed more therophytes (38.3%) and hemicryptophytes (22.0%) and less chamaephytes (29.0%).

The vegetation that characterise the study area can be divided, according to TWINSPAN technique, into eight vegetation groups: *Prosopis farcta-Tamarix nilotica*, *Tamarix nilotica-Alhagi graecorum*, *Zygothymum coccineum-Salsola imbricata* subsp. *imbricata*, *Cornulaca monacantha-Fagonia arabica*, *Atriplex leucoclada*, *Randonia africana-Deverra tortuosa*, *Deverra tortuosa-Capparis spinosa* var. *aegyptia* and *Capparis spinosa* var. *aegyptia-Zilla spinosa* subsp. *biparmata*. Some species: *Atriplex leucoclada*, *Anabasis articulata*, *Capparis spinosa* var. *aegyptia* and *Randonia africana* common to the western Mediterranean coastal belt (Ayyad & Ammar, 1974; Abdel-Razik *et al.*, 1984) are found in the less arid sites of the northern transect where the silty soil decreases water infiltration. A group of salt-tolerant plants including *Nitraria retusa*, *Tamarix nilotica*, *Sarcocornia fruticosa* and *Alhagi graecorum* are found in the dry saline sites of the southern transect, and form phytogenic mounds of variable size. *Alhagi graecorum* is a widely distributed species that seems to grow in different habitats (Kassas, 1952). It is also considered as a groundwater-indicating plant (Girgis, 1972). According to Kassas and Girgis (1965), the growth of the desert scrub *Nitraria retusa* represents the highest tol-

erance to soil salinity conditions, and a penultimate stage in the successional development. The plant reaches its northernmost limit of distribution around Qara Oasis on the south-western edge of Qattara Depression (Abd El-Ghani, 1992) as well as in Bahariya Oasis (Abd El-Ghani, 1981). *Nitraria retusa*, however, has not been recorded beyond Latitude 28°N in Egypt (M. Kassas, pers. comm.). Further studies concerning the distribution of this plant in the country is recommended. *Prosopis farcta*, *Imperata cylindrica* and *Salsola imbricata* subsp. *imbricata* are commonly found in the dry sandy plains along the southern transect. Restriction of *Imperata* to the high sandy plains is apparently due to the inability of this species to reach the capillary fringe of the groundwater which is fairly close to the surface (Rikli, 1943). The species is considered as facultative halophyte mainly occurring on sandy soil with slight salt content. Thus, this habitat may represent a transitional zone between the less arid and dry saline habitats. The xero-psammophytes *Fagonia arabica*, *Cornulaca monacantha*, *Zilla spinosa* subsp. *spinosa*, *Calligonum polygonoides* subsp. *comosum*, *Pulicaria incisa*, *Citrullus colocynthis* and *Heliotropium digynum* were found in dry non-saline sandy sites along both transects where infiltration is higher and water accumulated in deeper layers, and the soil is highly fertile. This group of species are more widely distributed in Egypt and neighbouring countries (Batanouny, 1979; Zahran & Willis, 1992; Frankenberg & Klaus, 1980; Wojterski, 1985).

Ayyad (1976) pointed out that physiographic and edaphic factors have greatly affected the distribution of plant communities in the Western Desert of Egypt. DCA and CCA analyses of the vegetation and soil data in the present study indicated the relative positions of species and sites along the most important ecological gradients. DCA axis 1 may represent a geographical trend in the floristic data set. The main reason for this may be a gradient in the local harsh climate within the study area. Both ordination techniques emphasised that salinity, fine sediments, organic matter and moisture content are the significant factors controlling the distribution of the vegetation in this region. This has been reported in other studies such as those of El-Ghareeb and Hassan (1989), El-Demerdash *et al.* (1995) and Shaltout *et al.*, (1997). The soil texture gradient in arid desert environments results in a corresponding gradient of available soil moisture. Therefore, moisture content is probably one

of the most effective physical factors leading to vegetation variations from north to the south of the study area. The organic matter content plays an important role as a key element in soil fertility. Sharaf El Din and Shaltout (1985), and Abd El-Ghani (1998) indicated the role of soil organic matter in the Egyptian arid desert ecosystems.

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Activité cellulolytique *in vitro* de sols de deux steppes à alfa (*Stipa tenacissima* L.) d'Algérie

Soil cellulolytic activity in two Algerian alfa (*Stipa tenacissima* L.) steppes

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RESUME

La cellulose constitue une part importante de la matière organique apportée par les litières d'alfa. L'activité cellulolytique étant un bon indicateur de l'activité microbiologique des sols, différentes expériences *in vitro* ont été effectuées afin de comparer l'influence des conditions stationnelles et en particulier du gradient d'aridité dans deux stations : une steppe d'alfa aride et une steppe d'alfa semi-aride.

Des prélèvements ont été effectués sous les touffes d'alfa et entre les touffes. Différents taux d'humidité et températures ont été choisis en fonction des conditions climatiques. Deux niveaux de sol ont été étudiés. Il apparaît que l'activité cellulolytique *in vitro* est moins intense dans la station la plus aride. Les sols de la station aride sont proportionnellement plus actifs aux fortes températures et humidités faibles que ceux de la station semi-aride.

Mots-clés : cellulose, aridité, matière organique, rhizosphère, système racinaire

ABSTRACT

Cellulose represents an important part of the organic matter returned to soil with the litter of alfa. Thus cellulolytic activity is a good indicator of the soil microbial activity.

Different experiments *in vitro* compared the influence of different conditions, particularly the gradient of aridity, corresponding to two sites : arid alfa steppe and semi-arid alfa steppe.

Soil samples were collected underneath and between tufts of vegetation. Different temperature and humidity were chosen in function of climatic data. Two levels soil depth were studied. From our results, it can be concluded that cellulolytic activity in the arid alfa steppe soils is less intense than in the semi-arid ones, as determined *in vitro*.

Key-words: cellulose, aridity, organic matter, rhizosphere, roots

ABRIDGED ENGLISH VERSION

Cellulose represents a considerable part of the organic matter and *Stipa tenacissima* content ranges from 42 to 50%. Thus, the degradation of cellulose is a good indicator of the biological activity of an ecosystem.

The aim of this study was to measure the microbial fauna activity and specially cellulolytic activity, in two alfa steppes corresponding to a gradient of aridity, and study the effects of the alfa rhizosphere and depth level on this activity. All experiments were conducted *in vitro* at different temperature and moisture levels.

The study area is located in the western high plains of Algeria, where *Stipa tenacissima* is a perennial tussock grass. The most productive rangelands of the region have been degraded by successive dry years and increasing grazing pressure. Local climate is semi-arid at Rogassa station and arid at Mekalis. The mean annual rainfall in the region studied only reaches 200 – 300 mm with high variability. Other characteristics of this zone have been summarised in tables 1 and 2.

Soil samples were collected in each station underneath and between several tufts of alfa, at different depths. To es-

timate the degradation rate of cellulose, a technique based on the *in vitro* degradation on filter papers was used. The disappearing of cellulose was determined by following the ponderal changes of the filter paper residues.

The results (Figures 2 and 3) demonstrate that:

- the intensity of degradation is higher in the semi-arid than in arid conditions. The higher contents in organic matter (plant biomass) and other nutrient as nitrogen, phosphorus and calcium (Table 2) in the semi-arid could explain this behaviour.
- the cellulolytic activity decreases with depth, except under tufts of alfa which affect the distribution of micro-organisms along the profile.
- the rate of cellulose degradation is more important under the tufts than between them in both studied sites. This is probably because most indicators of soil fertility (organic matter, total and available nitrogen, phosphorus and cations, number and activity of microbial and arthropod decomposers) are much higher in the soil under tufts than elsewhere, as previously shown by Noy-Meir (1985).

INTRODUCTION

La dégradation de la cellulose est reconnue comme un bon indicateur de l'activité biologique des sols (Dommergues & Mangenot, 1970 ; Berg & Roswall, 1973 ; Labroue & Lascombes, 1975 ; Rozé, 1986). Les steppes à alfa du Sud-Oranais (Algérie) sont en voie de dégradation très rapide. Entre 1978 et 1990, la phytomasse verte de l'alfa est passée de 1750 à 75 kg Ms / ha selon Aidoud et Touffet (1996). Ces auteurs attribuent cette dégradation essentiellement au surpâturage qui s'ajoute à plusieurs années de sécheresse successives (Djellouli, 1990). Dans ces milieux en voie de désertification, le taux de matière organique dans le sol est considéré comme l'un des attributs vitaux essentiels (Aronson *et al.*, 1995) et sa réduction, un indicateur pertinent de désertification. La minéralisation de la matière organique a été prise comme indice de l'activité microbiologique des sols (Djellali, 1981) ; cependant, l'activité cellulolytique n'a pas fait l'objet d'étude particulière. Afin de mieux comprendre le fonctionnement des sols de ce type de steppe, le présent travail est une contribution à l'évaluation de la cellulolyse dans les sols alfatiers. Notre objectif a été de mettre au point un protocole selon la structure locale de l'espèce dominante et le degré d'aridité. Dans ce but, deux stations situées dans des conditions écologiques différentes ont été choisies afin de mesurer

les variations de l'activité cellulolytique et de vérifier l'importance des effets des conditions écologiques à différentes échelles spatiales.

MATERIEL ET METHODES

Stations

L'étude a été réalisée sur les steppes d'alfa des hautes plaines du Sud-Oranais dans deux stations :

la station de Rogassa se trouve à 1090 m d'altitude au nord ouest d'El Bayadh, sur un glacis de pente très faible ; cette station se place dans l'étage bioclimatique semi-aride inférieur à hiver froid (Nedjraoui, 1990). Le sol, sur croûte calcaire (à environ 30 cm de profondeur), est de type brun calcaire et de texture sablo-limoneuse. Il présente des éléments grossiers et de nombreuses racines verticales et horizontales (Nedjraoui, 1990). Le recouvrement global de la végétation (steppe à alfa pur) est de 55%, sa richesse spécifique est de 29 taxons (Bessah, 1998) ;

la station de Mékalis se situe à 36 km au nord de Aïn Sefra, à 1300 m d'altitude. Elle repose sur un glacis de pente très faible, inférieure à 2%. Elle est située dans l'étage bioclimatique aride supérieur, variante à hiver froid. Le sol à croûte calcaire est assez profond (40 cm ou plus) et sa texture est essentiellement sableuse.

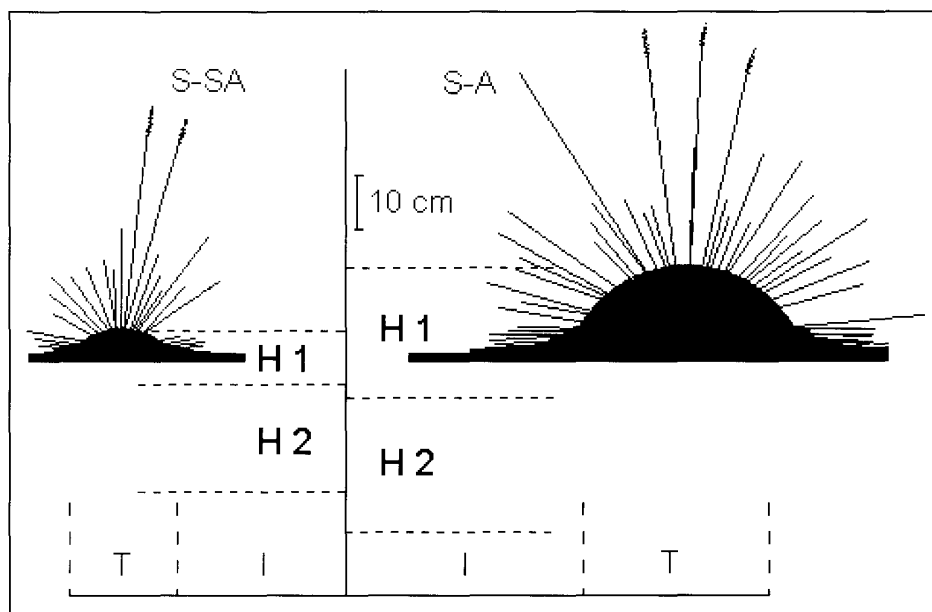


Figure 1. Niveaux de prélèvements H1 de surface et H2 de profondeur des échantillons dans les deux stations S-SA (semi-aride de Rogassa) et S-A (aride de Mékalis) par rapport aux touffes d'alfa (T : sol sous les touffes d'alfa ; I : sol entre les touffes)

	Pluviométrie annuelle moyenne (mm)	Moyenne des températures annuelles (°C)	Moyenne des maxima annuels (°C)	Moyenne des minima annuels (°C)
Rogassa*	250	14,7	34,4	-0,6
Mekalis**	200	15,9	35,7	-0,4

Tableau 1. Caractéristiques climatiques des zones d'étude ; données de pluie extrapolées à partir :

* de la station météorologique d'El Bayadh, (P = 298 mm, altitude = 1310 m)

** de la station de Aïn Sefra (P=192 mm, altitude = 1073 m)

			Mo%	C%	N%	Ca%
Rogassa	T	H1	1,42	0,82	0,11	1,07
		H2	1,93	1,12	0,15	1,68
	I	H1	0,77	0,45	0,12	1,70
		H2	1,8	1,05	0,15	1,25
Mékalis	T	H1	0,26	0,15	0,044	0,6
		H2	0,26	0,15	0,056	0,61
	I	H1	0,26	0,15	0,044	0,86
		H2	0,26	0,15	0,044	0,75

Mo : taux de matière organique ; C : taux de carbone ; N : taux d'azote ; Ca : taux de calcium

Tableau 2. Caractéristiques pédologiques de la zone d'étude (pour la légende voir également Figure 1)

Les racines sont longues et verticales, sans chevelu racinaire. La végétation est une steppe mixte à alfa (*Stipa tenacissima*) et sparte (*Lygeum spartum*). Son recouvrement global est de 50% (dont 30% d'alfa et 10% de sparte). Sa richesse spécifique est de 22 taxons.

Les caractéristiques climatiques et édaphiques ont été résumées dans les tableaux 1 et 2.

Prélèvements et techniques d'étude

Les prélèvements ont été effectués selon la profondeur du sol : de 0 à 10 cm (H1) puis de 10 à 30 cm (H2) dans la station semi-aride et de 0 à 25 cm (H1) et de 25 à 50 cm (H2) dans la station aride (Figure 1). Ces prélèvements ont été réalisés sous les touffes (T) ou entre les touffes (I) d'alfa.

L'activité cellulolytique a été suivie *in vitro* selon le protocole suivant : dans des boîtes de Pétri stériles on introduit environ 100 g de terre, sans tamisage préalable. Le papier filtre servant de substrat cellulosique a été humecté puis mis en sandwich entre deux couches de terre. Les boîtes ont été mises à incuber à différentes températures (5, 15 et 30° C) et humidités (5%, 15% et 30%). La perte d'eau appréciée par pesée a été compensée périodiquement par l'apport d'eau distillée. Après 90 jours d'incubation, les papiers filtres ont été recueillis puis nettoyés selon la méthode de Rashid et Schaefer (1984). Le poids de cellulose pur restant après incubation a été calculé comme la différence de deux pesées : une première réalisée après séchage à 105°C et une deuxième après incinération à 500°C.

RESULTATS

Le papier filtre est passé par différentes étapes de dégradation sous l'effet des micro-organismes cellulolytiques. Cette évolution s'est manifestée par l'apparition de taches jaunes, grises, brunes et même rougeâtres.

Entre les touffes d'alfa

L'activité cellulolytique mesurée *in vitro* de la microflore est plus intense pour le sol de la station semi-aride que pour celui de la station aride et ceci, aussi bien pour les échantillons prélevés en surface qu'en profondeur. En effet, le pourcentage de dégradation varie de 20 à 85% pour la première station et de 11 à 42% pour la seconde. Cette cellulolyse diminue avec la profondeur du sol dans les deux stations. Dans la station semi-aride, les taux de dégradation enregistrés (Figure 2) sont de 22 à 85% en surface et de 20 à 70% en profondeur. Dans la station aride, ces taux varient de 15 à 42% dans l'horizon superficiel et de 11 à 38% en profondeur.

Sous les touffes

En surface, l'activité cellulolytique est plus marquée pour le sol de la station semi-aride que pour celui de la station aride, avec des taux de dégradation va-

riant de 9 à 94% pour la première station et de 13 à 63% pour la seconde.

Pour la station semi-aride, cette cellulolyse diminue avec la profondeur du sol. Le pourcentage de dégradation passe de 9 à 94% dans l'horizon de surface et de 9 à 47% en profondeur. Par contre pour la station aride l'activité cellulolytique ne diminue pas avec la profondeur du sol : elle a même tendance à augmenter puisque le taux de dégradation est en moyenne de 13 à 53% en surface et de 17 à 63% en profondeur (Figure 3).

L'influence du taux d'humidité et de la température sur l'activité cellulolytique en fonction des conditions d'incubation connaît la même évolution sous les touffes et entre les touffes : le maximum d'activité cellulolytique pour la station semi-aride est atteint à 30% d'humidité quelle que soit la température d'incubation. Pour la station aride, un maximum d'activité a été observé à 15% d'humidité et pour des températures d'incubation de 15 et 30°C. A 5°C et 5% d'humidité, le papier filtre semble peu altéré, si ce n'est dans sa coloration, les évolutions pondérales étant alors peu marquées.

DISCUSSION

L'activité cellulolytique des sols de steppes à alfa, mesurée *in vitro*, apparaît relativement faible par rapport à celle des sols des régions tempérés. Par exemple, des mesures réalisées dans les mêmes conditions pour les sols de la forêt d'Orsay (Rashid & Schaefer, 1984) ont donné des taux de dégradation de l'ordre de 90% (mull) et de 58% (anmoor) au bout d'un mois d'incubation, alors que dans notre cas ces valeurs n'ont été atteintes qu'au terme de trois mois d'incubation en conditions moyennes.

L'intensité de l'activité cellulolytique de la microflore dépend des conditions stationnelles, micro-stationnelles (sol sous la touffe et entre touffes), de la profondeur du sol et des conditions d'incubation réalisées au laboratoire. D'après nos résultats, elle semble être plus importante dans la station semi-aride que dans la station aride, ce qui peut être lié aux caractéristiques climatiques et édaphiques des stations. L'aridité de la station de Mékalis serait non seulement climatique, mais également édaphique en raison de caractères pédologiques (Pouget, 1980).

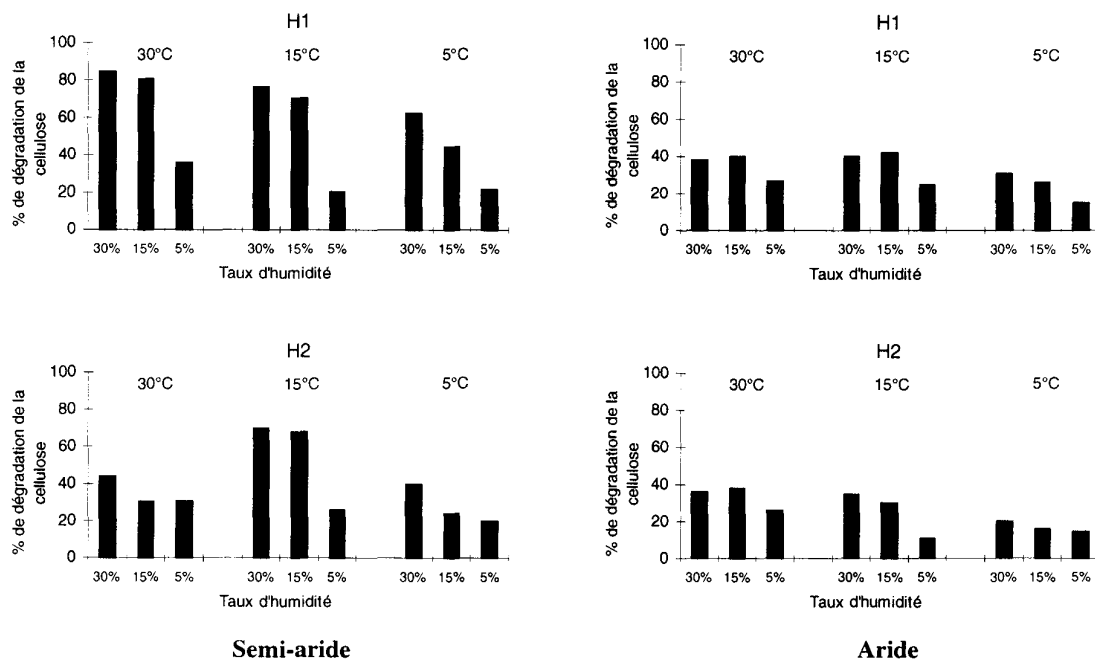


Figure 2. Evolution de l'activité cellulolytique des sols prélevés entre les touffes d'alfa à deux niveaux de profondeur (H1 et H2) dans une station semi-aride et une station aride en fonction des températures (30, 15 et 5°C) et des taux d'humidité d'incubation

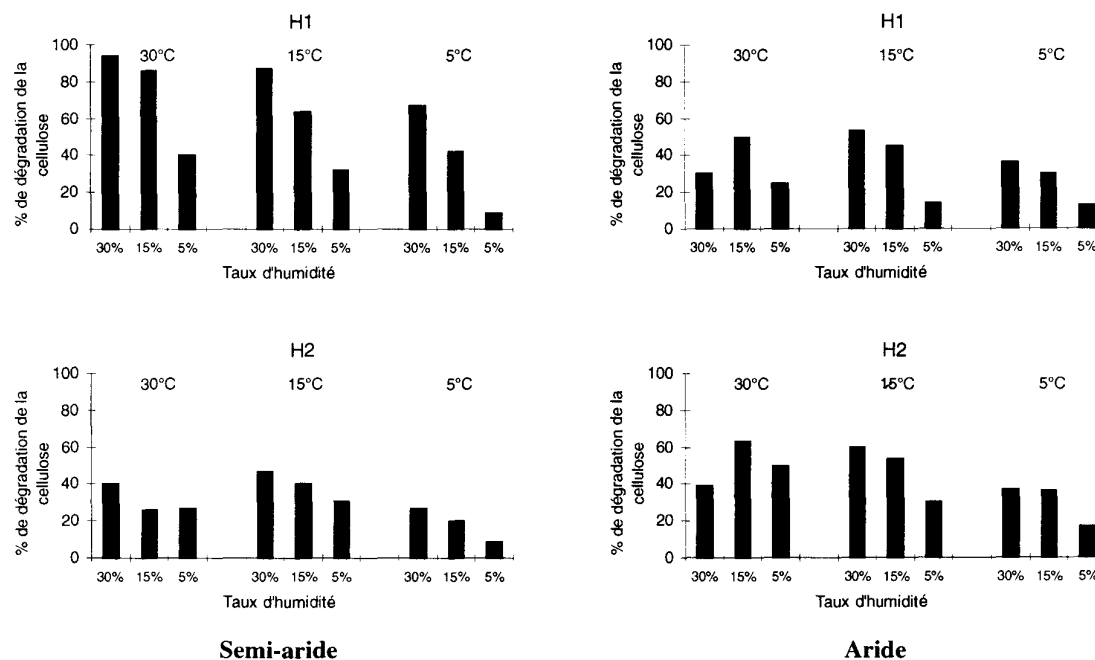


Figure 3. Evolution de l'activité cellulolytique des sols prélevés sous les touffes d'alfa à 2 niveaux de profondeur (H1 et H2) dans une station semi-aride et dans une station aride en fonction des températures (30, 15 et 5°C) et des taux d'humidité d'incubation.

Les résultats expriment la capacité de réaction et de résistance des micro-organismes vis-à-vis de ces conditions écologiques qui deviennent vraisemblablement limitantes le long du gradient d'aridité croissant caractérisant les deux stations.

La biomasse végétale marque une baisse importante entre les deux stations. La phytomasse aérienne a été évaluée à 8040 kg Ms / ha dans la station semi-aride et à 3525 kg Ms / ha dans la station aride (Nedjraoui, 1990). Cette différence peut, outre les conditions écologiques, être attribuée en partie à l'intensité d'exploitation. La biomasse végétale représente la source principale de matière organique (Pouget, 1980 ; Kadi-Hanifi, 1998). La diminution de celle-ci entraîne une baisse du taux de matière organique dans le sol. Ce taux passe en moyenne de 1% dans la station semi-aride à 0,1% dans la station aride. Or l'incorporation de la matière organique dans le sol influe sur la stabilité structurale et donc sur l'aération du sol et sa perméabilité (Duchaufour, 1970 ; Duthil, 1973 ; Guckert *et al.*, 1975 ; Kadi-Hanifi, 1990, 1998). Elle stimule également le développement de la microflore (Dommergues & Mangénot, 1970 ; Le Houérou, 1995). L'effet favorable de la matière organique sur les germes cellulolytiques a été mis en évidence dans des sols au Maroc par Bryssine (1967). A partir de ces travaux, nous pouvons supposer que la diminution de la matière organique en fonction de l'aridité du climat (Pouget, 1980) est à l'origine de la faible activité de la microflore dans la station aride.

La cellulolyse plus importante dans le cas de la station semi-aride peut être influencée également par d'autres constituants chimiques du sol. En effet, Duchaufour (1970), Rozé (1986) et Widden *et al.*, (1988) ont mis en relation la sensibilité de l'activité cellulolytique et la richesse du sol en azote : la cellulolyse est plus rapide dans les milieux bien pourvus en cet élément, elle est par contre lente dans les milieux pauvres en azote. De plus, Berg et Rosswall (1973) ont montré que le phosphore est l'élément qui favorise le plus la cellulolyse, l'azote et le calcium venant ensuite. Nos résultats concordent avec ces données bibliographiques : la cellulolyse est plus active dans la station semi-aride dont les sols sont notablement mieux pourvus en ces nutriments que ceux de la station aride (Tableau 2).

L'activité cellulolytique est plus marquée dans les échantillons de sol prélevés sous les touffes (sol rhizosphérique) que dans ceux prélevés entre les touffes

d'alfa (sol nu). Cette plus forte activité doit être liée à la quantité de matière organique plus élevée sous la touffe et au microclimat améliorant les conditions édaphiques créées par la touffe. En effet, la plupart des indicateurs de la fertilité du sol dans les zones arides (matière organique, azote total, phosphore, nombre et activité des micro-organismes) sont plus importants sous les touffes qu'entre celles-ci (Garcia-Moya & McKell, 1970 ; Tiedmann & Klemmedson, 1973 ; Charley & West, 1975 ; Barth & Klemmedson, 1978 ; Doescher *et al.*, 1984 ; Noy-Meir, 1985 ; Klopatek, 1987 ; Bolton *et al.*, 1990). Ainsi, les racines peuvent enrichir le sol en matière organique et stimuler leur colonisation par les micro-organismes rhizosphériques (Warembourg, 1975 ; Haller & Stolp, 1985 ; Gorissen, 1994). Les produits néoformés de la litière racinaire, très importante chez l'alfa, et les produits simples issus de l'exsudation racinaire (polysaccharides), favorisent la prolifération de bactéries et de champignons (Dommergues & Mangénot, 1970 ; Zeriahène, 1987). De plus, Djellali (1981), Ali-Haimoud (1982) et Kihal (1986) ont démontré que la rhizosphère de l'alfa présente une action positive sur la microflore des sols de steppes.

La profondeur du sol influe également sur l'activité cellulolytique. Entre les touffes, l'activité de la microflore diminue avec la profondeur dans la station aride comme dans la station semi-aride. Cette différence d'activité entre surface et profondeur serait en relation avec la distribution verticale des micro-organismes. Ces derniers se trouvent en majorité dans la couche superficielle du sol, mieux aérée et plus riche en substances nutritives et leur nombre diminue progressivement avec la profondeur (Boullard & Moreau, 1962 ; Gaucher, 1968 ; Dommergues & Mangénot, 1970). Les mêmes résultats ont été obtenus dans les landes bretonnes (Rozé, 1986) où l'activité cellulolytique mesurée *in situ* est de plus en plus réduite en fonction de la profondeur du sol. Les travaux de Djellali (1981) et Ali-Haimoud (1982) confirment ce fait pour des sols alfatiers d'Algérie.

Sous les touffes, l'activité cellulolytique augmente avec la profondeur du sol dans la station aride. Par contre, sous conditions semi-arides, cette activité cellulolytique diminue avec la profondeur du sol. Cette différence de fonctionnement de la microflore en fonction de la profondeur est probablement liée à la morphologie racinaire de l'alfa. En effet, les racines d'alfa présentent des modifications qui leur permettent

de mieux s'adapter aux conditions hydriques et édaphiques de leur biotope (Zeriahène, 1987 ; Aidoud, 1989 ; Nedjraoui, 1990). En fonction de l'aridité, les racines deviennent de plus en plus longues et épaisses : 33,76 cm de longueur et 2,5 mm de diamètre pour l'alfa des régions pré-sahariennes, 24,5 cm de longueur et 1 mm de diamètre pour l'alfa provenant des régions semi-arides (Nedjraoui, 1990).

Dans la station semi-aride, les sols sont peu profonds et la croûte calcaire est proche de la surface, constituant ainsi un obstacle au développement des racines en profondeur. Celles-ci parviennent difficilement à franchir la croûte calcaire et forment un réseau dense au niveau de l'horizon superficiel. Le développement racinaire se fait donc latéralement. Dans la station aride, les sols à texture essentiellement sableuse sont assez profonds. Les racines sont essentiellement pivotantes et pénètrent profondément dans le sol à la recherche de zones plus humides. Ainsi la répartition des germes cellulolytiques suit celle des racines ; leur activité diminue avec la profondeur dans la station semi-aride et augmente avec celle-ci dans la station aride. Cette dernière observation rejoint celle de Labroue et Lascombes (1975) qui ont trouvé dans les sols de l'étage alpin une activité cellulolytique *in situ* plus importante en profondeur qu'en surface. Selon ces auteurs, cette intensité de l'activité cellulolytique serait liée à l'enracinement profond des graminées colonisant la station étudiée.

L'intensité de l'activité cellulolytique varie également en fonction de l'humidité. En effet, les résultats obtenus après incubation à différents taux d'humidité montrent que les micro-organismes caractéristiques de la station semi-aride, probablement adaptés à un taux d'humidité relativement important, réagissent mieux à 30% d'humidité. Par contre, dans la station aride où les micro-organismes sont probablement adaptés à une certaine sécheresse du milieu, la réaction est maximale à 15% d'humidité.

L'activité cellulolytique est maximale parfois à 30° et parfois à 15°C dans les deux stations. Ces résultats seraient liés aux exigences de la microflore vis à vis de la température. Dommergues et Mangenot, (1970) signalent une activité des bactéries cellulolytiques à partir de 15-20°C avec des valeurs optimales de 28-30°C. Le minimum d'activité cellulolytique est observé à 5°C. Nous avons déjà montré (Rozé, 1986) que des températures trop basses induisent une faible activité cellulolytique.

CONCLUSION

Cette étude a permis de quantifier l'activité cellulolytique dans les sols de steppes et de rechercher les principaux facteurs de sa variation. Elle aborde un volet particulier du fonctionnement qui vient s'ajouter aux travaux antérieurs réalisés dans les steppes à alfa par Aidoud (1989), Nedjraoui (1990) et Kadi-Hanifi (1998). Les résultats obtenus ont montré que l'activité cellulolytique diminue avec l'aridité et la profondeur du sol. La morphologie de la touffe d'alfa semble modifier la distribution verticale de la microflore cellulolytique. Le taux d'humidité constitue un facteur essentiel qui n'est pas indépendant de la structure de la touffe d'alfa.

L'activité cellulolytique met en relief des différences entre les stations qui avaient déjà été évoquées : il s'agit donc d'un bon indicateur de la dégradation des sols. Cet indicateur devra être confronté à d'autres, tels que la protéolyse et la minéralisation de l'azote, afin de déterminer son niveau de pertinence.

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The climate of the Mediterranean Basin and of Eurasia of the last glacial maximum as reconstructed by inverse vegetation modelling and pollen data

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ABSTRACT

Classical climate reconstruction based on statistical method implicitly assumes that the atmospheric CO₂ concentration, which has greatly fluctuated during the Quaternary, has no influence on the vegetation. In order to attenuate this assumption, we propose to use a process-based vegetation model (BIOME 3.5) in inverse mode to reconstruct from pollen data the most probable climate under lowered CO₂ concentration in the biosphere. Appropriate tools to match the model outputs with the pollen data are developed to generate a probability distribution associated with the reconstruction (Monte Carlo sampling and neural network techniques). The method is validated with modern pollen data from Europe and Northern Eurasia: it is able to reconstruct modern climate with a sometimes large error bar from pollen data. The error bar depends in fact on the tolerance of the vegetation to the corresponding climatic variable. The application to 71 pollen assemblages from these regions, representing the last glacial maximum (LGM: 18,000 ¹⁴C-yr B.P.), is done through two experiments: modern and LGM CO₂ concentration. We show that there is a good agreement between previous results based on statistical methods and inverse modelling in the northern part of the studied region. In the Mediterranean region and southern Siberia, the summer temperatures and the water availability parameters could be higher than previously reconstructed, because of the CO₂ effect.

Key-words: vegetation model, Monte-Carlo sampling, palaeoclimatology, last glacial maximum, Europe, Eurasia

RESUME

La reconstruction climatique classique, basée sur la méthode statistique, suppose implicitement que la concentration atmosphérique en CO₂, qui a considérablement fluctué pendant le Quaternaire, n'a aucune influence sur la végétation. Afin de tempérer ce postulat, nous proposons d'utiliser un modèle fonctionnel de végétation (BIOME 3.5) en mode inverse pour reconstruire, à partir des données polliniques, le climat le plus probable sous faible concentration de CO₂ dans la biosphère. Des outils adaptés permettant de faire coïncider les sorties des modèles avec les données polliniques sont développés afin d'établir une distribution de probabilité associée à la reconstruction (échantillonnage de Monte Carlo et réseaux neuronaux). La méthode est validée avec les données polliniques actuelles d'Europe et d'Eurasie du nord : il est possible de reconstruire le climat actuel, avec parfois une marge d'erreur importante, à partir des données polliniques. L'erreur dépend en fait de la tolérance de la végétation à la variable climatique correspondante. L'application à 71 assemblages polliniques de ces mêmes régions représentant le dernier maximum glaciaire (DMG: 18,000 ans ¹⁴C B.P.) est réalisée au travers de deux expériences : concentration en CO₂ actuel et glaciaire. Nous montrons qu'il y a une bonne concordance entre les résultats précédents basés sur les méthodes statistiques et la modélisation inverse, dans la partie nord de la région étudiée. En région méditerranéenne et en Sibérie méridionale, les températures estivales et les paramètres de disponibilité de l'eau pourraient être plus élevés que ceux reconstruits précédemment en raison de l'effet du CO₂.

Mots-clés : modèle de végétation, échantillonnage de Monte-Carlo, paléoclimatologie, dernier maximum glaciaire, Europe, Eurasie

INTRODUCTION

During the last decades, transfer functions have been used to reconstruct past environments from terrestrial data (pollen, diatoms, tree-rings, insects, molluscs ...) as well as from ocean data (foraminifera, diatoms, dinoflagelates ...). The methods primarily used were based on modern distribution of one or several species in a climatic domain (Iversen, 1944; Grichuk, 1984; Atkinson *et al.*, 1987; Zagwijn, 1994; Fauquette *et al.*, 1998) or on a statistical calibration of modern assemblages in terms of climatic variables, using (i) multivariate statistical analyses (Imbrie & Kipp, 1971; Gasse & Tekaya, 1983; Koç *et al.*, 1993; Rousseau, 1991; Roux *et al.*, 1991) or using (ii) the concepts of best modern analogues (Hutson, 1979; Prell, 1985; Guiot *et al.*, 1989; Bonnefille *et al.*, 1990; de Vernal *et al.*, 1994; Pflaumann *et al.*, 1996) and/or that of response surfaces (Bartlein *et al.*, 1986; Prentice *et al.*, 1991; Waelbroeck *et al.*, 1998).

The reliability of these methods depends on the validity of explicit assumptions. First, it is accepted that the distributions of taxa and their associated assemblages reflect the climate variables to be reconstructed. Although there are some biases such as, for instance, that pollen data could also register potentially human-induced disturbances in long-settled regions or that foraminifer assemblages could be strongly influenced by local variations in productivity, appropriate statistical methods and sampling of modern data can minimise these distortions (e.g. Huntley *et al.*, 1989). Second, the climate reconstruction assumes also that the biological assemblages are in equilibrium with climate without significant delay in species migration (e.g. Prentice, 1986; Prentice *et al.*, 1991; Webb, 1986). Lastly, none of the reconstruction methods explicitly uses known physiological processes of the biological assemblages.

Recently, Jolly and Haxeltine (1997) have shown that the low glacial atmospheric CO₂ concentration can explain the shift of the vegetation belts observed in the intertropical African highlands. Thus, the pollen-derived temperature reconstructed by calibration on modern data, and thus under modern CO₂ concentration, could be considered as maximum anomalies, because they are not able to take into account the direct effect of the low CO₂ level on the vegetation. To solve that problem (among others), we propose a new

concept of climate reconstruction that allows physiological processes to be included.

After a brief description of the new method (details are published in Guiot *et al.*, in press) and its test on modern pollen, we apply it to the last glacial maximum (LGM, 18,000 ¹⁴C-years ago) in Europe, especially the Mediterranean Basin (Peyron *et al.*, 1998), and in Eurasia (Tarasov *et al.*, 1999).

DATA SET

A data set of 1245 original modern pollen samples located in Europe, the Mediterranean region, Kazakhstan, and Siberia has been compiled by Peyron *et al.* (1998) and Tarasov *et al.* (1999). From these original pollen counts, 64 taxa, including trees, shrubs and herbs, have been extracted. Pollen percentages for all the data (modern and fossil) were calculated on the basis of the total pollen sum minus the pollen and spores of aquatic, exotic and anthropogenic taxa. These surface samples are carefully selected so we can assume that they represent the potential vegetation around the sampling site. The percentages of the 64 pollen taxa are transformed into scores of 15 plant functional types (pfts) using the method defined by Prentice *et al.* (1996) and slightly modified by Peyron *et al.* (1998).

Monthly mean climatic variables (temperature, precipitation and cloudiness) have been interpolated for each modern pollen sample, using a global climate data set (Leemans & Cramer, 1991). The absolute minimum temperature is interpolated from the dataset compiled by Spangler and Jenne (1988). We use, for interpolation technique, a 2-layer backpropagation (BP) artificial neural network technique (see for example Caudill & Butler, 1992) as described by Guiot *et al.* (1996).

A set of 15 LGM sites has been studied by Peyron *et al.* (1998) in Europe and Mediterranean region. A set of 56 LGM has been studied by Tarasov *et al.* (1999) in the former Soviet Union and Mongolia. We use the pft scores calculated in these papers.

METHODS

A pollen spectrum that reflects the composition and structure of the regional vegetation, can be correlated with vegetation model outputs as net primary production (NPP) of various plant functional types

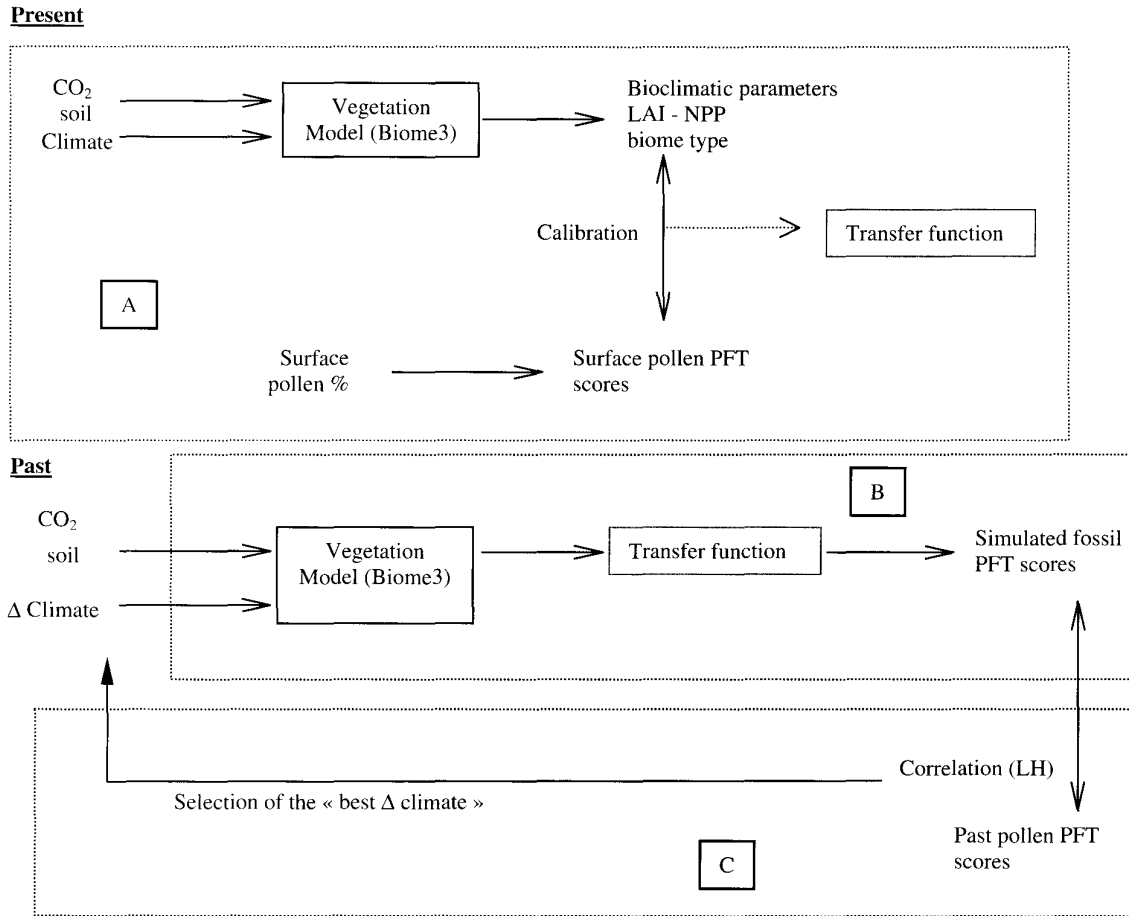


Figure 1. Diagram of inverse modelling approach to reconstruct past climates. LAI = leaf area index; NPP = net primary productivity; PFT = plant functional type; LH = (modified) likelihood function

(pft). For this purpose, we use a modified version of BIOME3 (Haxeltine & Prentice, 1996), called BIOME3.5 (Kaplan, unpubl.).

The method devised proceeds in several steps (Figure 1).

The first step (Figure 1A) is to define a set of transfer functions able to transform the model output into values directly comparable with pollen pft scores. Among the 15 pfts, three (ctc1, ts1, wte1) are grouped with respectively bctc, ts and wte (Table 1) because they were not frequent enough in the dataset. For each pft, an affinity score is calculated as the sum of the square-root of the percentage of the taxa (when it is greater than 0.5%) belonging to the pft. This transformation, used to minimize the distortion due to large differences in the pollen productivity, is applied to both the surface and the fossil data. Then, a relationship is calibrated between pollen-derived pft scores

and a few outputs of BIOME3.5 (detailed in section 2.1).

The second step (Figure 1B) is to try a large variety of climatic changes (Δ climate) as the input of the vegetation model. For each climatic combination, we obtain a set of simulated pft NPP values. Using the transfer function defined above, a set of simulated pft scores is then obtained. A correlation measurement is necessary to assess the quality of fit of the simulated pft scores to the pollen-derived pft scores (Figure 1C). The set of the " Δ climate" that gives the best correlation is the final result of the climate reconstruction.

The BIOME3.5 model is driven by monthly variables that are used to calculate a set of bioclimatic variables: GDD5 (growing degree-days above 5°C), MTCO (mean temperature of the coldest month), MTWA (mean temperature of the warmest month), E/PE (actual to equilibrium evapotranspiration ratio).

Pollen pft	Code	R
Boreal summergreen	bs	0.85
Boreal conifer	bec	0.84
Cool temperate conifer (including ctc1)	ctc	0.81
Temperate summergreen (including ts1)	ts	0.79
Temperate summergreen (warmer)	ts2	0.55
Warm temperate evergreen (including wte1)	wte	0.85
Warm temperate evergreen (warmer)	wte2	0.76
Alpine-arctic shrubs	aa	0.80
Cool grass/shrub	cogs	0.79
Heath	h	0.41
Warm grass/shrub	wags	0.79
Desert forbs	df	0.55

Table 1. Results of the transfer translating NPP into pollen pft scores. We use 8 neurones in the intermediate layer and a log-sigmoid at the intermediate as well as at the output layer. The 13 inputs are transformed each into 5 classes by "fuzzification" (see Guiot *et al.*, 1996). R is the correlation between observations and predictions on the 1245 spectra used for calibration.

Our final goal is to reconstruct these bioclimatic variables that constrain the vegetation by a kind of inversion of the model.

The vegetation model

BIOME3.5 is a process-based terrestrial biosphere model which includes a photosynthesis scheme that simulates acclimation of plants to changed atmospheric CO₂ by optimisation of nitrogen allocation to foliage and by accounting for the effects of CO₂ on net assimilation, stomatal conductance, leaf area index (LAI) and ecosystem water balance. It assumes that there is no nitrogen limitation.

The inputs of the model are soil texture, CO₂ rate, absolute minimum temperature (T_{min}), monthly mean temperature (T), monthly total precipitation (P) and monthly mean sunshine (S) *i.e.* the ratio between the actual number of hours with sunshine over the potential number (with no clouds). From these input variables, BIOME3.5 computes bioclimatic variables (growing degree-days, ratio of actual evapotranspiration to evapotranspiration at the equilibrium and precipitation minus evapotranspiration) that represent energy and water constraints on the vegetation. Then, the model calculates the maximum sustainable leaf area index and the NPP (in kg m⁻² yr⁻¹) for the pfts able to live in such an input climate. Competition among pfts is simulated by using the optimal NPP of each pft as an index of competitiveness. We use the 10 pfts present in our modern pollen dataset: temperate broad-leaved evergreen (tbe), temperate summergreen (ts), temperate evergreen conifer (tc), boreal evergreen (bec), boreal deciduous (bs), temperate grass (tg), woody desert plant type (wd), tundra shrub type (tus),

cold herbaceous type (clg), lichen/forb type (lf). The pollen pfts are slightly different in such a way that some of these pfts are sometimes subdivided.

We retain as predictors the NPP of these 10 pfts, the total annual net absorbed photosynthetically active radiation (APAR in MJ.m⁻².yr⁻¹) and the LAI of the dominant pft (with a maximum NPP). For a better discrimination, we use also an additional predictor related to the rank of the pft in the above list, so that forest pfts have a lower rank than the herbaceous pfts.

Transfer function (TF) from BIOME3.5 to pollen

BIOME3.5 is run, on the 1245 modern pollen samples, to estimate the 13 predictors described in section 2.1. Then we use a backpropagation neural network technique (as in section 1) to calculate a set of non-linear relationships between the 12 pollen-derived pft scores and the 13 predictors. The correlation coefficients are greater than 0.55 and often greater than 0.8 (see Table 1) except for the heaths (mainly *Calluna*) which is a really ubiquitous pft.

The likelihood function (LH)

The inverse modelling problem consists in finding the value of an input parameter vector for which the model output fits as much as possible a set of observations (Mosegaard & Tarantola, 1995). Here, the parameters of the model are a set of climatic variables which constrain properly the pollen pft scores.

The crudest approach is the exhaustive sampling, where all the points in a dense grid, covering the model space, are visited. This method is not recommended if the number of parameters is high. An

alternative approach is the Bayesian approach which describes the "*a priori* information" we may have on the parameter vector by a probability density. Then it combines this information with the information provided by the comparison of the information provided by the model to that provided by the observations in order to define a probability density representing the *a posteriori* information. The likelihood function, which roughly measures the fit between observed data and data predicted by the model, links the *a posteriori* probability to the *a priori* one.

To give a maximum weight to cases where the correct biome is predicted, we adopt a likelihood function LH which is proportional to the difference between predicted and observed pft and also to the difference between predicted and observed biomes. More details are given in Guiot *et al.* (in press).

Definition of the parameter vector

The parameters of interest in this study are temperature and precipitation. We add to the modern monthly temperatures a term ΔT_j and we multiply the modern monthly precipitation by a given ΔP_j (all being either positive or negative). It is not necessary to sample independently the 12 monthly parameters because they are linked by the seasonal cycle. Thus, we vary first the January and July climatic parameters; then, we deduce the value for the other months ($j=1, \dots, 12$) by linear interpolation (Guiot *et al.*, in press).

The sunshine parameter cannot be processed independently from temperature and precipitation as it relates more or less strongly to the latter ones (see Table 4 in Guiot *et al.*, in press).

Consequently, for each parameter vector (ΔT_{Jan} , ΔT_{Jul} , ΔP_{Jan} , ΔP_{Jul}), we calculate 12 monthly temperature values ($T_j + \Delta T_j$, $j=1, 12$), 12 monthly precipitation values ($P_j * \Delta P_j$, $j=1, 12$) and 12 monthly sunshine values which are then used as input into the vegetation model.

Monte-Carlo sampling (Metropolis-Hastings algorithm)

Let us consider a multi-dimensional mathematical domain where each dimension represents a parameter range. A vector of parameters is an element of the

multi-dimensional domain. The Metropolis-Hastings (MH) algorithm is an iterative method which browses the domain of the parameters according to an acceptance-rejection rule (Metropolis *et al.*, 1953 ; Hastings, 1970). Strictly speaking, the MH algorithm is not an optimisation method of the posterior joint density function, but a method for browsing the prior definition domain of the parameter vector in order to simulate its posterior distribution. The histograms of the parameters are incremented according to the candidate or the actual value, according to the fact that it is accepted or not. These histograms are estimates of the posterior probability distribution of the parameters.

The MH algorithm was applied with the LH function presented in section 2.3 and with a multivariate uniform distribution as a prior of the hyper-parameter. LH is not *sensu stricto* a likelihood function in the probability sense, but it has the form; numerous empirical tests have shown its suitability in our application.

RESULTS

Before applying the method to LGM pollen data, a test was performed on 591 pollen data selected among the 1245 spectra of the modern data set. These 591 spectra are more or less equally distributed in Europe and Eurasia.

Validation with modern data

The CO₂ concentration was set to 340 ppmv. The input parameters were allowed to vary within the following ranges:

- ΔT_{Jan} : [-10, 10]°C in terms of deviations of the observed value
- ΔT_{Jul} : [-10, 10]°C in terms of deviations of the observed value
- ΔP_{Jan} : [-60, 60]% of the modern value
- ΔP_{Jul} : [-60, 60]% of the modern value

The number of iterations is set to 2400 for each sample. The value of LH converges most of the time towards -3. We select the 10% iterations giving the highest LH (note that LH is defined as negative). Among them we select the iterations which simulates the most frequent biome. Only these selected iterations (generally between 500 and 1000) are used for

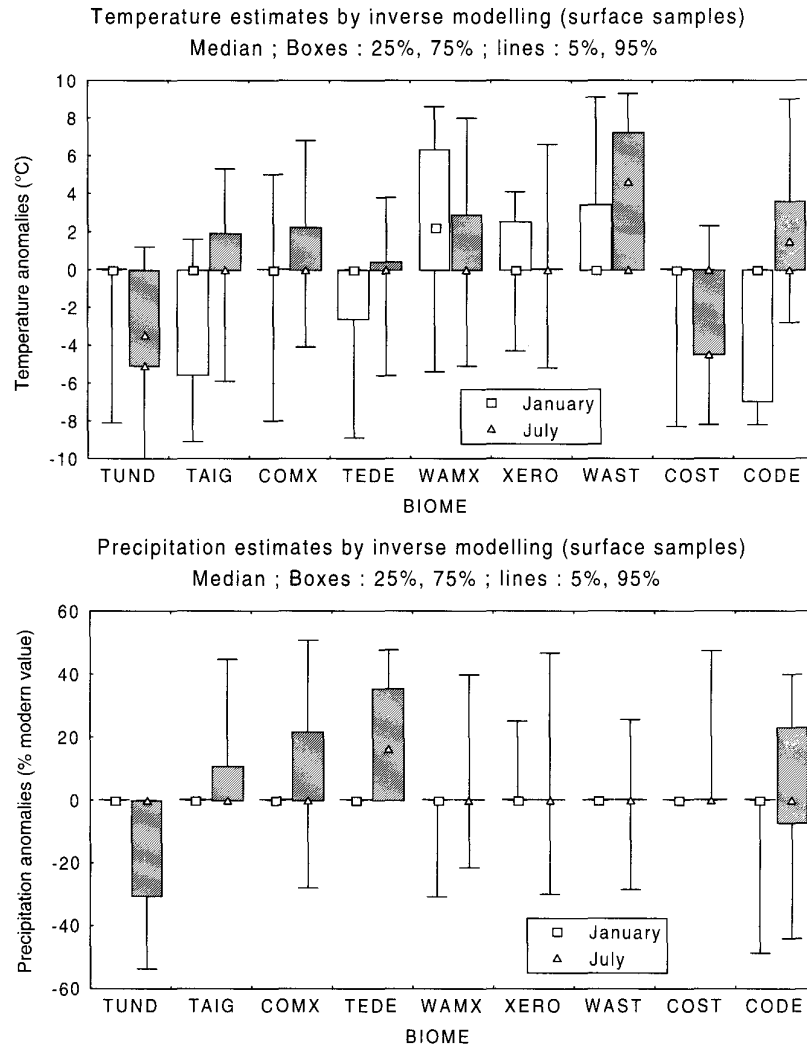


Figure 2. Box plots of the deviation between reconstructed and observed modern climate (January, July temperature and precipitation) according to the biome from which is sampled the pollen assemblage. Expected values are 0. The boxes indicate the inter-quartile intervals and the bars the 90%-intervals. These statistics are calculated on all the sites belonging to the biome (TUND = tundra; TAIG = taiga; COMX = cool mixed forest; TEDE = temperate deciduous forest; WAMX = warm mixed forest; XERO = xerophytic wood/scrub; WAST = warm steppe; COST = cool steppe; CODE = cool semi-desert)

Climatic variable	all biomes	Cool steppes/Tundra
MTCO	3.6°C	3°C
MTWA	3.7°C	3.8°C
E/PE	6.2%	6%
P-E	65mm	37mm
GDD5	680°C*days	590°C*days
Annual	2.8°C	2.9°C
Pannual	69mm	30mm

Table 2. Root of mean squared errors (RMSE) for several reconstructed climatic variables taken in all biomes and in the dominant biomes of the LGM

building the *a posteriori* probability distribution. We calculate then the probability distribution of the four input parameters (ΔT_{Jan} , ΔT_{Jul} , ΔP_{Jan} , ΔP_{Jul}).

For a given site, the results are summarised as follows: (1) we look for the mode of the distribution; (2) if it is positive we calculate the probability that it is significantly larger than 0 by summing the probabilities above 0 (if it is negative, we proceed in the same way with the probability to be negative); (3) if that probability is less than 75%, the reconstructed value is zero, otherwise it is equal to the mode. For the next step, we retain that reconstructed values which are distributed in function of the reconstructed biome. Figure 2 shows the box plots of the reconstructed anomalies of temperature and precipitations along a gradient from the coldest to the warmest biome (the three last biomes being the driest ones).

Most of the medians are zero, which shows that the mean bias is null. There are a few exceptions:

- ΔT_{Jul} is underestimated for tundra and overestimated for warm steppes, which is maybe due to the fact that the modern dataset is dominated by samples taken in very cold tundra and very warm steppes;

- ΔT_{Jan} is generally overestimated for warm mixed forest maybe because, in our modern dataset, that biome mainly occurs with mild winters;

- ΔP_{Jul} is overestimated for temperate deciduous forest, which is hard to interpret as that biome is not frequently reconstructed in our dataset (the corresponding pollen assemblages are often similar with those sampled in cool mixed forest);

- ΔP_{Jan} is reconstructed as zero everywhere because it corresponds to probabilities less than 75%.

We have also to consider the interquartile interval which is related to dispersion of the reconstructions around the median. A weak dispersion around a null median means that the parameter is extremely well reconstructed: it is the case for ΔT_{Jan} in tundra, cool steppes and cool mixed forest, ΔP_{Jan} everywhere, ΔP_{Jul} in the driest biomes (warm mixed forest, xerophytic vegetation, steppes). The dispersion is generally weak, which encourages us to apply the method to the fossil data.

The final objective of the method is to reconstruct the bioclimatic variables which drive the model. To have an idea of its precision, we use the root mean squared error (RMSE) statistic. It is calculated over all

the modern samples and over the two dominant biomes of the LGM (Table 2).

The last glacial maximum

After validation, the method can be applied to the 71 fossil spectra of Europe and Eurasia. The first experiment is based on the LGM CO₂ concentration (200 ppmv: Barnola *et al.*, 1987). Figure 3 shows the geographical distribution of the three major bioclimatic variables. The western part of the continent seems to have been colder than the eastern part. The moisture variable (E/PE) does not seem to have been much lower than present except in some sites. These results must be compared with those obtained with the same data by Peyron *et al.* (1998) and Tarasov *et al.* (1999). For that, we divide the continent into four regions: Mediterranean (9 sites of Peyron), western Europe (the other 6 sites of Peyron), northern Eurasia (the sites of Tarasov at north of 53°N), Southern Eurasia (the sites of Tarasov at south of 53°N). We do not mix the reconstructions of the two papers because there is a difference in the number of variables reconstructed. We compare also these reconstructions to a second experiment based on 340 ppmv of CO₂. The results are summarised as box plots in Figure 4.

Figure 4 shows well the west-east gradient of MTCO and GDD5. It shows also the good agreement between the results of the pft method and those of the two experiments (200 and 340 ppmv). For E/PE, the agreement is also good except for western Europe, where the vegetation model is able to produce cool steppes with a small decrease of available water (and a large decrease of temperature), while, for the pft method, it is necessary to decrease E/PE to values less than 65%.

The box plots of Figure 4 are not enough detailed to compare the results between 200 and 340 ppmv CO₂. Indeed, it has been shown (Guiot *et al.*, in press) that the response of pollen pft to climatic change could appear as multimodal distribution. To analyse these responses in more detail, we have selected a few sites in each of the four zones and we have represented these distributions for the three bioclimatic parameters (Figure 5).

MTCO: there is no significant deviation between the two distributions except in Mediterranean region where anomalies of -25°C are more probable under low CO₂ than higher anomalies;

GDD5: in Mediterranean region, the most probable anomalies are [-3300, -2300 °C*days] for both CO₂ concentrations, but, under low concentration, warmer summer climate [-2300, 500°C*days] has a probability of 33% to occur, which is far to be negligible; we find the same situation for Southern Siberia where a warmer climate is more probable under low CO₂ (mode=-750°C*days) than cooler one (mode<-900°C*days);

E/PE: in all regions, there is a displacement of the peaks toward the wetter climates, which can be explained by the fact that low concentrations of CO₂ amplify the aridity effect of the climate on the vegetation.

DISCUSSION

The method described in this paper, involving the use of new mathematical tools in palaeoclimatology (a process-based vegetation model, artificial neural network and a Monte- Carlo sampling), is able for the first time to reconstruct in a probabilistic way, several potential climatic conditions, and to integrate external constrains directly in the simulated physiological process. This approach relies on the possibility to match the pollen data (pft scores) to the vegetation model output (pft net primary productivity), as expressed by the modern data set with a high correlation value. Using the same conceptual procedure, we can expect other improvements by the use of more recent mathematical tools, such as future versions of more sophisticated vegetation models.

This method is designed to reconstruct the probability of distribution of past climates and to identify different potential climates that explain best the occurrence of a palaeoecosystem. Conventional statistical approaches take into account only one climatic combination while in our physiological-based climatic reconstruction, different palaeoclimatic scenario (including the CO₂ effect and changes in the precipitation seasonality) are reconstructed. This is a crucial change from previous studies, as we accept the concept of multi-equilibrium status between environmental conditions (climate, CO₂, soil ...) and the vegetation. The multimodal distribution could be due to the large uncertainties associated to the pollen data

(e.g. difficulty to distinguish a tundra assemblage from a steppe).

If we consider the climate reconstruction by the pft method carried out by Peyron *et al.* (1998) and Tarasov *et al.* (1999), and if we compare it with our results, it appears that the temperature reconstruction is broadly in agreement with our results. E/PE reconstruction may be 5-10% too low when we do not take into account the fact that, under low CO₂, more open stomatas could induce an amplified aridity for the vegetation.

These results are important for the problem of climate model validation as done by the Paleoclimate Modelling Intercomparison Project (PMIP) (Jousaume & Taylor, 1995). It compares the climate model simulations during several key periods of the past, and in particular the LGM, with climate reconstructions from paleodata. A part of the discrepancies can be explained by weaknesses of the models, but a part also can be explained by biased interpretations of the data. That inverse modelling approach can be used to solve a part of the data problems: climate reconstructions confirmed by inverse modelling can be considered as robust. Nevertheless, it does not solve everything as it is model-dependent. Further verifications need to use different vegetation models.

Concerning the multimodal responses, the use of additional climatic constraints, as $\delta^{13}\text{C}$ or lake-levels reconstruction, in the physiological process or in the water balance process increases the probability of one of the modes and thus helps to choose between them. In the future, all the information relative to the soils (nature but also texture), seasonality, atmospheric composition, and even information about human activities could be used to elaborate more sophisticated experiments, and to reconstruct past climates with the highest reliability.

We are convinced that this new approach has a great potential for an application to inter-tropical areas, where the vegetation is often associated with monsoon seasonality of the rainfall and where low glacial atmospheric CO₂ concentration may have induced major vegetation changes. It has also great potential for use in periods with smaller climatic change, as the Holocene, but it requires complementary data (lake-level curves, $\delta^{13}\text{C}$...) to refine the confidence intervals.

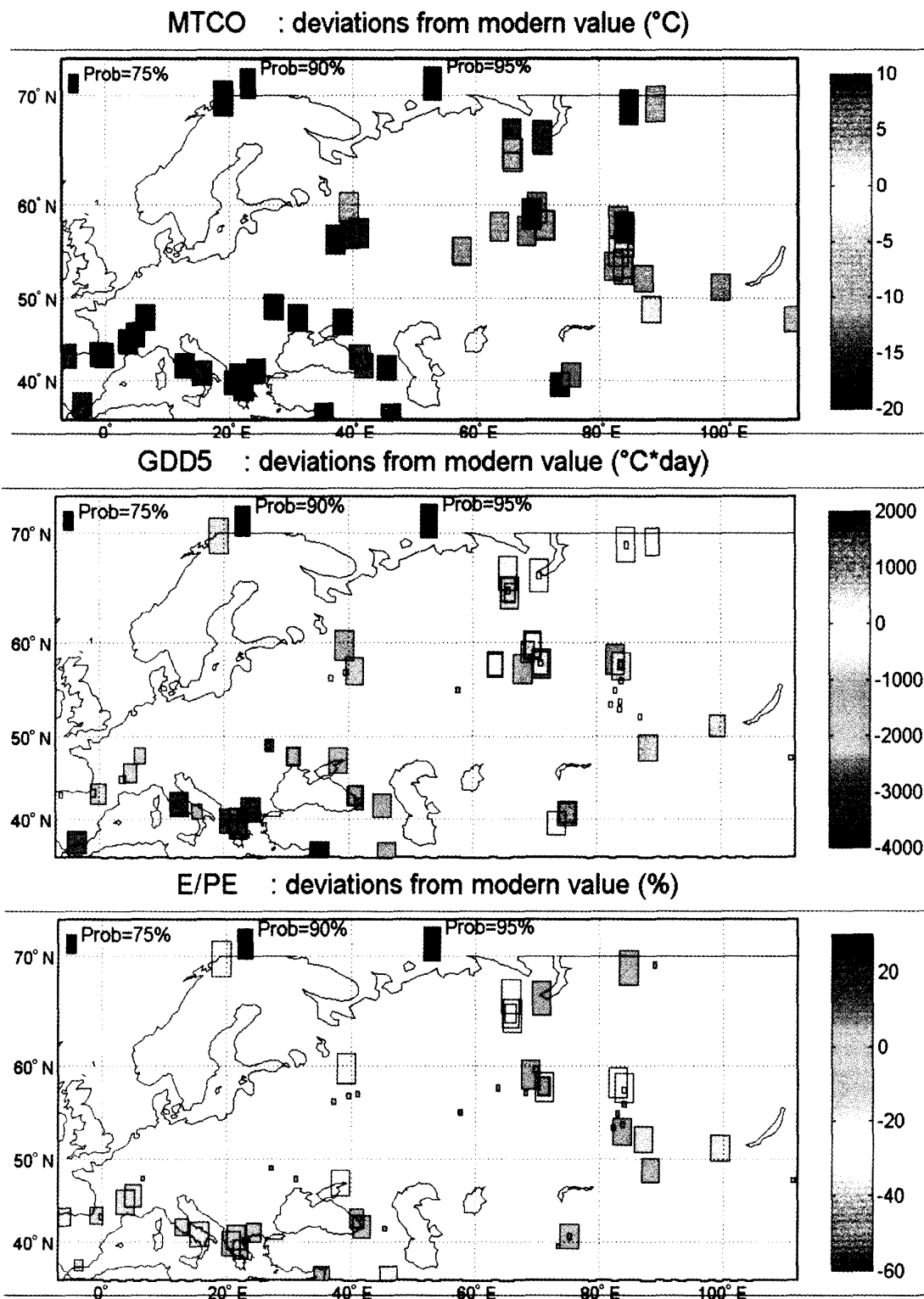


Figure 3. Reconstruction of three bioclimatic parameters using inverse modelling of pollen spectra for the last glacial maximum

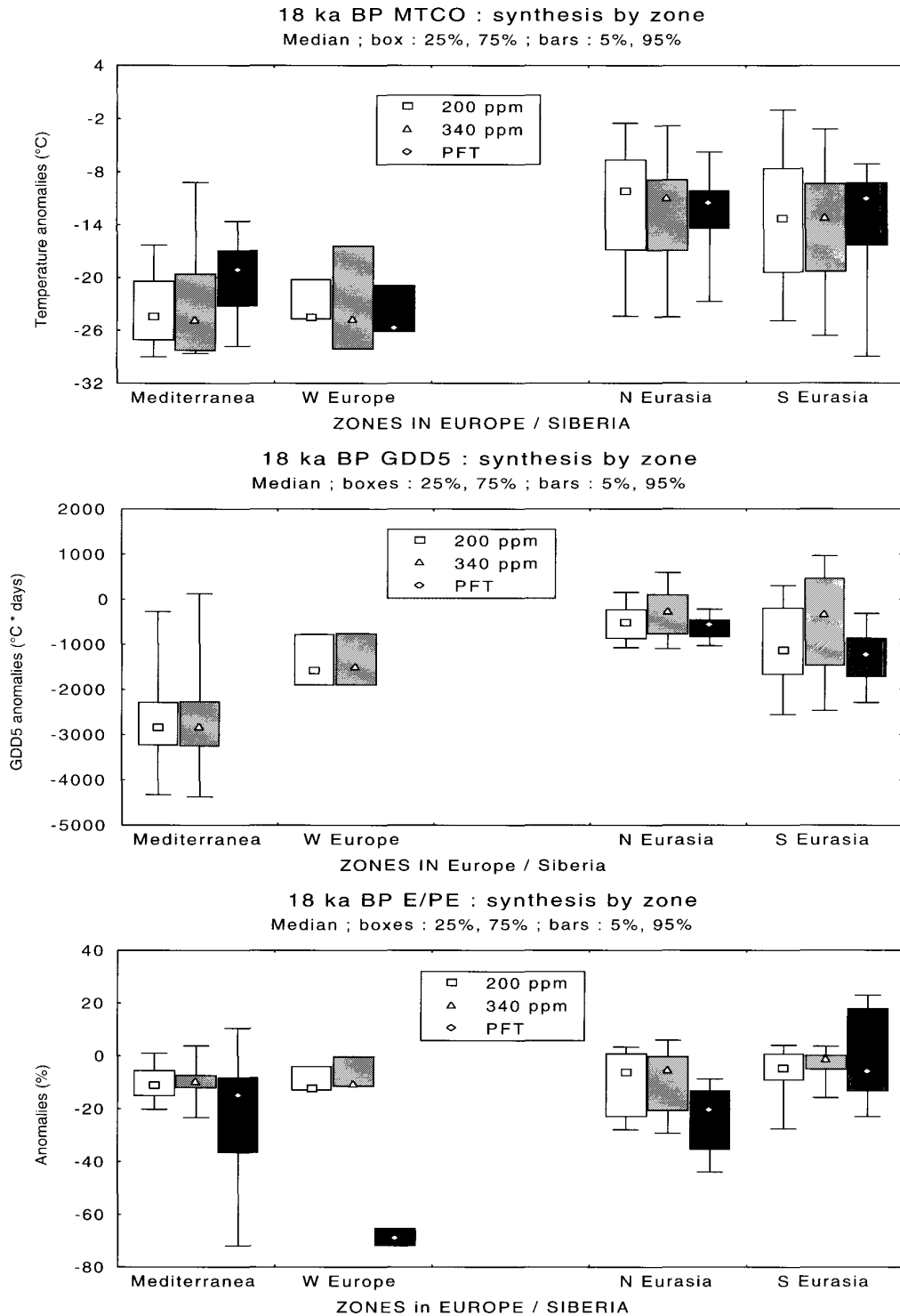


Figure 4. Box plots of the deviation between reconstructed and observed LGM bioclimatic parameters according to the region from which is sampled the pollen assemblage. The boxes indicate the interquartile intervals and the bars the 90%-intervals. Three experiments (200 and 340 ppmv CO₂) are compared to the results published by Peyron *et al.* (1998)

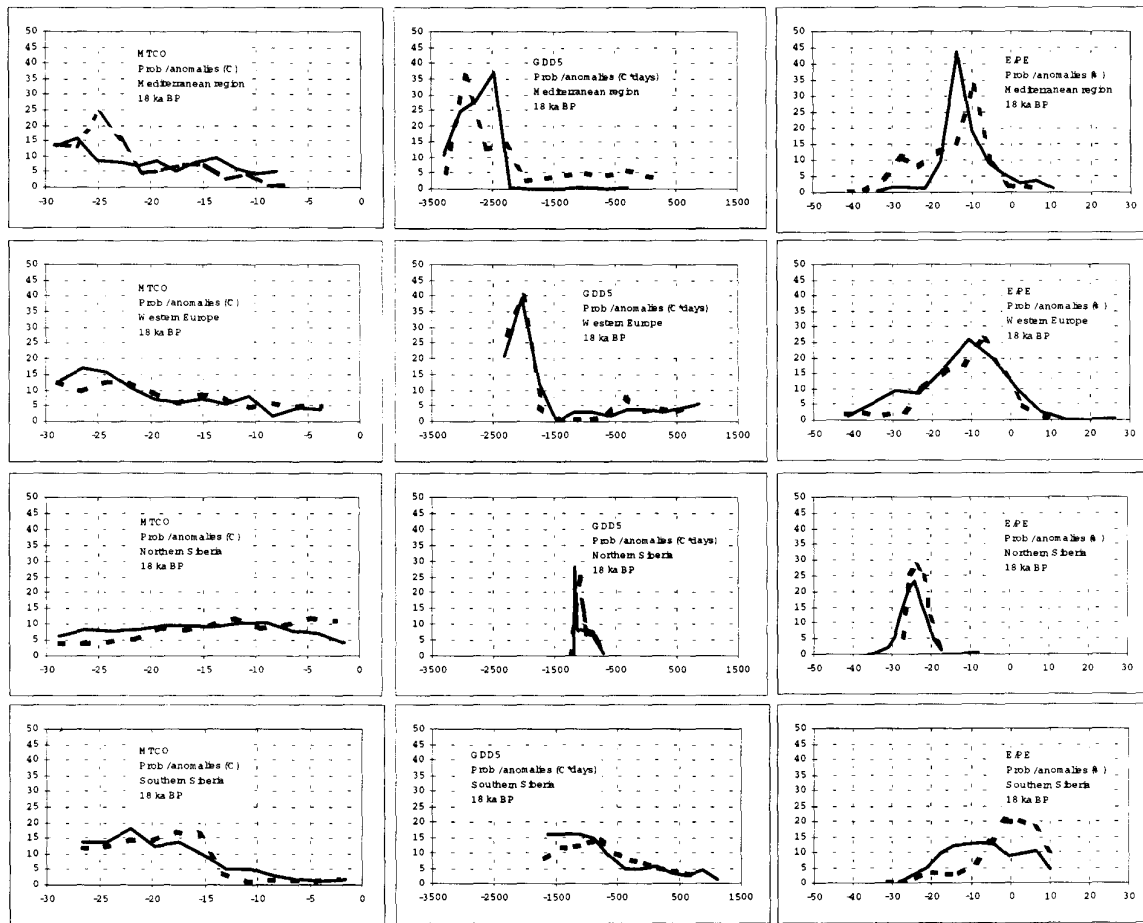


Figure 5. Probability distribution of reconstructed bioclimatic parameters using inverse modelling under 200 (light) and 340 (dark) ppmv CO₂ for a few sites selected in the four studied geographical zones

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Influence of study scale on the characterisation of plants community organisation in a Mediterranean grassland (Mont Ventoux, France)

Influence de l'échelle d'étude sur la caractérisation de l'organisation d'une communauté végétale dans une pelouse méditerranéenne (Mont Ventoux, France)

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ABSTRACT

By sampling plant species in a Mediterranean grassland, the authors examine the influence of the study scale on: (i) the detection of ecological gradients by the correspondence analysis, and (ii) the validation of one of the two models: core-satellite hypothesis or Kolasa's model. These models concern the frequency distribution of species. The size of the quadrats varies from 1.56 to 100 m². Results show that the study scale does not influence the detection of the principal ecological gradient. Nevertheless, species with high contribution to factorial axes change as study scale varies. Authors relate this fact to the abundance variability of individuals of a species according to the « point » of a gradient. On the other hand, results on a small scale are consistent with Kolasa's model, and on a large scale they are consistent with the core-satellite hypothesis. The discussion underlines the role of quadrats size in the character « core » or « satellite », and the « saturation » of large quadrats in certain species. Whatever the scale, a large category of species are infrequent (present in few quadrats). This shows that the mechanisms which lead to a weak frequency of species (mass effect, survival in favourable patches...) are essential whatever the scale.

Key-words: core-satellite species, frequency, gradient, study scale, community ecology

RESUME

Grâce à un échantillonnage des espèces végétales dans une pelouse méditerranéenne, les auteurs étudient l'influence de l'échelle d'étude sur : (i) la détection de gradients écologiques au moyen de l'analyse factorielle des correspondances, et (ii) la validation de l'un des deux modèles : le modèle « core-satellite » ou le modèle de Kolasa. Ces modèles concernent la distribution des fréquences des espèces parmi les relevés. La taille des relevés varie de 1,56 à 100 m². Les résultats montrent que l'échelle d'étude n'a pas d'influence sur la mise en évidence du principal gradient écologique. Cependant, les espèces à forte contribution ne sont pas les mêmes lorsque l'échelle d'étude change. Les auteurs expliquent ce fait par la variation de l'abondance des individus d'une espèce à un point du gradient. D'autre part, le modèle de Kolasa est compatible avec l'échantillonnage des petits quadrats, et le modèle « core-satellite » est compatible avec l'échantillonnage des grands quadrats. La discussion souligne l'importance de la taille des relevés sur le caractère « core » ou « satellite » d'une espèce, et la saturation des grands relevés en certaines espèces. Quelle que soit l'échelle, beaucoup d'espèces ne sont pas fréquentes (présentes dans peu de relevés). Cela montre que les mécanismes qui sont responsables de la faible fréquence d'une espèce (effet de masse, survie dans des « taches » favorables) sont essentiels quelle que soit l'échelle envisagée.

Mots-clés : espèce core-satellite, fréquence, gradient, échelle d'étude, écologie des communautés

Nomenclature: Kerguelen, 1993

INTRODUCTION

Patterns of species distributions, at the community, the landscape, or the region level first focused mainly on the response of the species to an *environmental gradient* (see in particular Clements, 1916, 1936; Gleason, 1917, 1926; Whittaker, 1951, 1967; Curtis, 1959, and see also the recent synthetical model of Collins *et al.*, 1993). An *environmental gradient*, or *complex gradient* (Whittaker, 1967) is the factors as a whole -including biotic factors- changing in space and governing the species distribution.

In later studies, the pattern analysis of species distributions took factors other than environmental axes into account, what Whittaker (1975) called « noise » in quantitative analysis was carefully studied. In particular, at the community level, *patch dynamics* (Levin & Paine, 1974; Whittaker & Levin, 1977; Connell, 1978, 1979) has had a considerable impact on the understanding of the community functioning. According to this concept, a plant community is a mosaic of patches of differing successional stages. The existence of these successional stages would be caused by disturbances. The *hierarchical organisation* of the community, or of the region (Allen, 1987; Kolasa, 1989; Pickett *et al.*, 1989) develops this concept by considering (*Kolasa's model*) the habitat as hierarchically heterogeneous. For example, patches are made of smaller patches; the latter are made of even smaller patches. The species are distributed in these patches according to their specialisation level. The *core-satellite hypothesis* (Hanski, 1982, 1991) distinguishes *core species* - frequent and abundant - from *satellite species* - sparse and rare. A few abundant species are infrequent - *urban species* - and a few rare species are frequent - *rural species*.

This body of theories (*hierarchical organisation* and *core-satellite hypothesis*) predicts that species which constitute the largest category would be the least *frequent* ones (to be found in less than 10 % of sites). Discrepancies appear for other maxima: Kolasa's model (1989) predicts other peaks of species number which are weaker and weaker towards the highest frequencies (Figure 1A), while Hanski's model (1982) predicts only a second maximum, for the most frequent species (Figure 1D). These latter models loosely relate to gradients. Hanski (1982) stresses that her theory is applicable when sites are in similar habitats, but Collins *et al.* (1993) introduce an

environmental gradient (Figure 2) in their *hierarchical continuum concept*, a synthesis between the *individualistic hypothesis* (Gleason, 1917, 1926), the *hierarchical structure of community* (Kolasa, 1989), and the *core-species hypothesis* (Hanski, 1982, 1991).

The purpose of this study is to appreciate the effect of sampling scale on predictive and explaining value of various models at the level of the community. The impact of scaling is examined through two different problems:

- the detection of ecological gradients through the means of Correspondence Analysis (CA);
- the validation of one of the two contradictory models: core-satellite hypothesis or Kolasa's model.

About the first point, the area-richness curves show the key-role of the area investigated for measuring richness (e.g. Arrhenius, 1921; Connor & McCoy, 1979; Williamson, 1988; Rey Benayas *et al.*, 1999). Then one must consider how the census of new species influences the detection of ecological gradients, as sample size increases. According to the *hierarchical organisation* theory, patches of various sizes could generate changing interpretation for gradients by changing scale. Several cases can occur: (i) the detected ecological gradients are the same at all the scales, in the same order of importance; (ii) they are the same but in different orders; (iii) they are not the same. The ordination of samples on axes must also be considered. It can vary as the size of the sample varies.

The second point has been studied by varying the level of organisation. Hanski (1982, 1991) originally put forward the *core-satellite hypothesis* for regional distribution patterns, then Gotelli & Simberloff (1987), Collins & Glenn (1990) proved that community-level data and small-scale study data supported this model. But what about scaling at the same level (here the community)? Collins & Glenn (1990) legitimately suspect a strong influence of scaling on frequency measures, but this must be tested.

METHODS AND STUDY SITE

Study site

The study was carried out in a Mediterranean limestone grassland. This grassland lies on the western ridge of the Massif du Ventoux (Provence, France) at a height of 835 m.

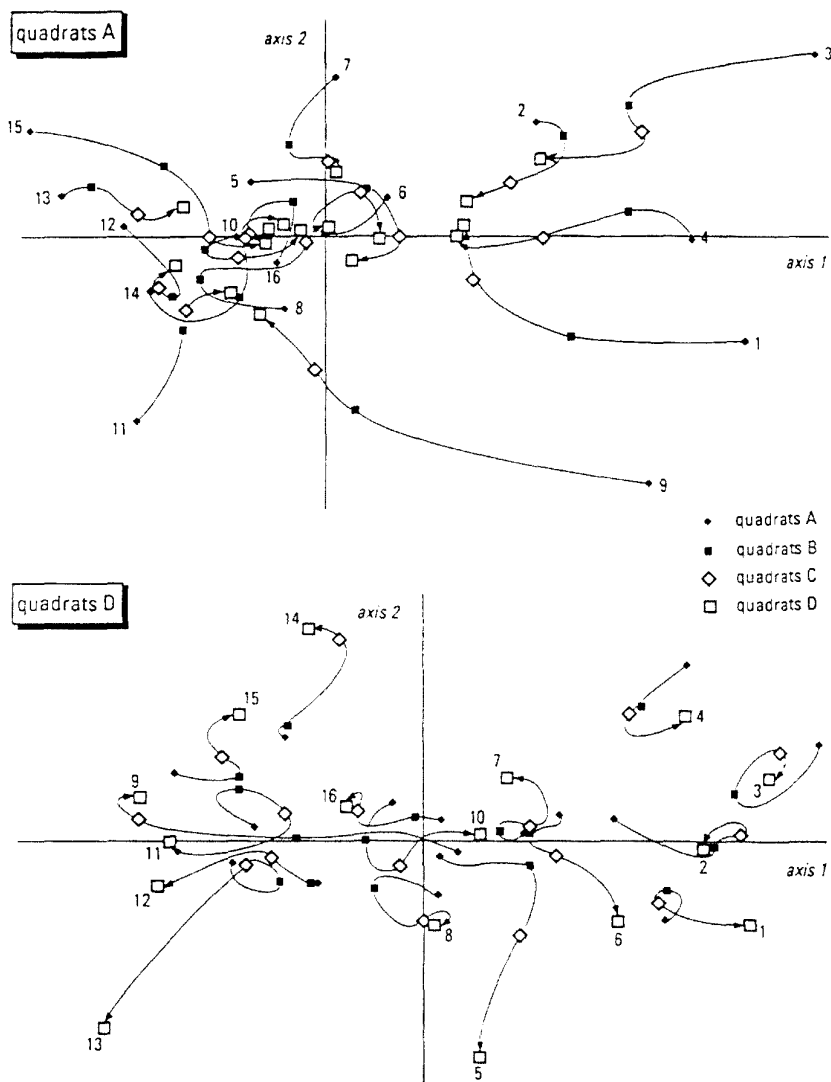


Figure 1. Correspondence analyses at two scales. Active points are quadrats A (above) and quadrats D (lower); other quadrats are non active. For each group (numbered from 1 to 16), the 4 quadrats are connected, and arrows show the progression from small to large quadrats within a group.

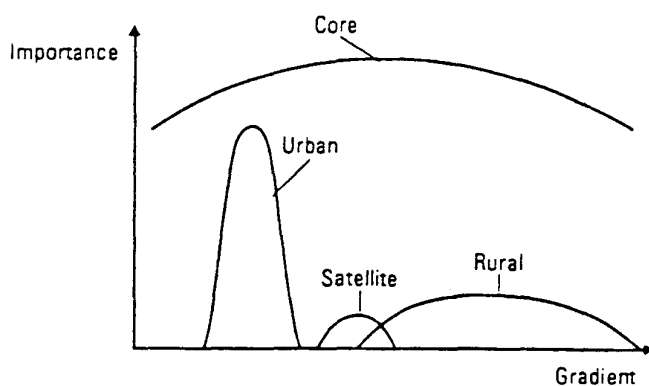


Figure 2. Distribution of core, satellite, urban and rural species along a hypothetical gradient (from Collins *et al.*, 1993)

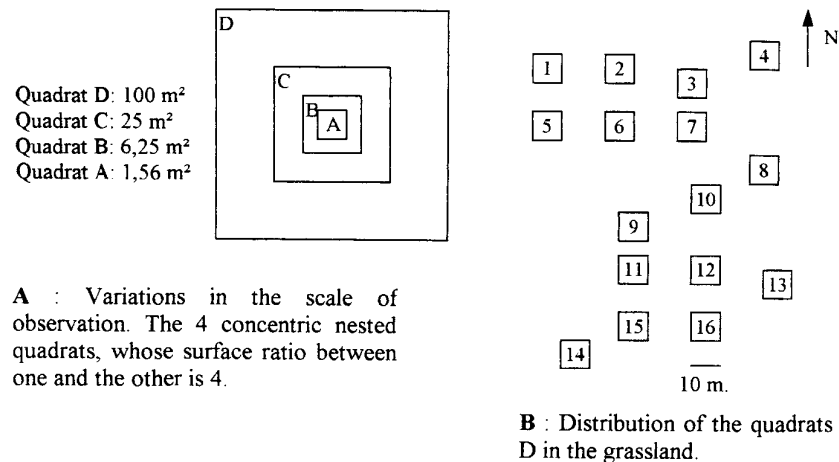


Figure 3. Sampling in the grassland

The ground is almost flat, and is slightly below the ridge itself, screened from the dominant wind. It had been reforested with conifers after deep plowing, hence notably homogenised. That plantation burned some time later (August 1989), the trunks were removed, and the plot has subsequently evolved without grazing. The extent of the study area is about 1 hectare, and its plants cover is about 90 %. The dominant species are *Aphyllanthes monspeliensis*, *Potentilla cinerea*, *Festuca gr. ovina*, *Melica ciliata* and *Buxus sempervirens* (shoots).

The annuals were mainly located in patches, associated with substrate not yet colonised after fire, or with decaying tufts, or with places disturbed by animals.

Methods

We established 16 groups of 4 nested quadrats placed at random on the grassland (Figure 3B). The area of each successive quadrat increases by a factor of four and ranges in size from 1.56 to 100 m² (Figure 3A).

Species coverage was assessed visually for each quadrat. We used a cover scale with a geometric progression. Such a scale is commonly used in animal biology and plankton biology (Frontier & Pichod-Viale, 1991). This type of scale highlights the rare species. The survey was made in June 1993, when

most of the flower-plants were easily visible and identifiable, apart from two or three vernal species.

We have conducted four Correspondence Analysis (CA): one for each scale (i.e. one for quadrats A, one for quadrats B, and so on). These analyses were based on the transformed abundance as mentioned above. For each CA, we have added quadrats of other sizes in non-active points (quadrats which don't contribute to determine factorial axes). This allowed the placement of quadrats of other sizes relatively to the factorial axes of CA for quadrats of a given size. The correlations between axes of the different CA were also made with the BIOMEKO software program (AVENIX, Montpellier). We name contribution the value :

$$f_i \cdot GH_i(k)^2 \cdot \lambda_k^{-1} \cdot 1000$$

where f_i = weight of species; i , $GH_i(k)$ = coordinate of species; i -point on axis k ; λ_k = eigenvalue of axis k .

RESULTS

Interpretation of factorial axes of CA

The relative inertia of the first three axes are given in table 1 for each scale. Axes 2 and higher numbered ordination axes present weak percentages, thus we expect the axes 1 to display the biologic relevant information for each scale (Ter Braak, 1987).

Table 2 indicates the species with a strong contribution for axis 1 to the different scales, and their contributions.

	Axis 1	Axis 2	Axis 3	Species number
Quadrats A	14,65	11,36	10,01	56
Quadrats B	18,16	12,40	10,14	61
Quadrats C	17,21	11,12	9,98	76
Quadrats D	16,07	11,46	11,18	86

Table 1. Relative inertia partition on the three first axes of CA for the four sampling scales

	Positive contributions				Negative contributions				
	A	B	C	D	A	B	C	D	
<i>Petrorhagia prolifera</i>	99				<i>Argyrolobium zanonii</i>	43			
<i>Centaurea paniculata</i>	58				<i>Teucrium montanum</i>	38	36	49	
<i>Koeleria vallesiana</i>	62				<i>Fumana procumbens</i>	50	38	29	37
<i>Crupina vulgaris</i>	38	52	40		<i>Genista hispanica</i>	51	42	74	81
<i>Trinia glauca</i>	82	69	38	31	<i>Leuzea conifera</i>		33	28	
<i>Cerastium arvense suffruticosum</i>	100	74	53	46	<i>Aster sedifolius</i>		56	44	
<i>Echium vulgare</i>		40			<i>Amelanchier ovalis</i>			54	40
<i>Lactuca perennis</i>		60			<i>Quercus humilis</i>				74
<i>Anthericum liliago</i>		54		31	<i>Dactylis glomerata</i>				28
<i>Bupleurum baldense</i>		51	35	34	<i>Potentilla hirta</i>				62
<i>Sedum acre</i>			57	32					
<i>Helianthemum nummularium</i>			41						
<i>Asperula cynanchica</i>			38						
<i>Armeria arenaria</i>			72	74					
<i>Genista X martinii</i>				39					

Table 2. Highest plant species contribution for axis 1 to the different scales

Quadrats	Axes	A		B		C		D	
		1	2	1	2	1	2	1	2
A	1	1.000							
	2	0.033	1.000						
B	1	0.758	0.399	1.000					
	2	-0.104	0.543	0.134	1.000				
C	1	0.532	0.290	0.681	0.196	1.000			
	2	0.176	0.080	0.110	-0.237	-0.123	1.000		
D	1	0.348	0.080	0.406	0.055	0.638	-0.185	1.000	
	2	-0.021	0.015	0.018	0.015	-0.042	-0.001	0.068	1.000

Table 3. Correlations between axes 1 and 2 on the different scales (correlations for axes 1 in bold)

The positive pole is characterised for each scale by species of xeric grasslands (Thero-Brachypodietalia), in particular with some annuals (*Petrorhagia prolifera*, *Crupina vulgaris*, *Bupleurum baldense*). The negative pole is characterised for each scale by species which are less xerophytic and often belong to more mature communities.

Axis 1 appears to represent a gradient linked to the water balance. The analysis of the plot-points (Figure 1) indicates that their projection onto axis 1 of each CA is closely linked to their geographic arrangement along a north-south axis. The northern plots correspond to the xeric pole. This gradient can be explained by the topography, the northern plots being more ele-

vated than southern ones by about 1 meter. Alternatively the mass effect (Shmida & Ellner, 1984) from the ridge itself should not be dismissed. The xeric species on the ridge can scatter into the windward portion of the grassland, thus increasing the xericity gradient.

Axis 1 leads to the same interpretations, irrespective of the scale of data collections. This result is in keeping with the correlations between the axes 1, which are relatively strong (Table 3). These correlations are discussed below.

Axis 2 always presents a weak inertia (Table 1), as regards the number of species. It has not been possible to interpret it at any scale. Additionally, axes 2 at the different scales show weak correlations between one

another (Table 3), except between scales A and B. However, concerning CA of quadrats D, plots which are close in space are most of the time also close on factorial axis 2. Similarly, we were unable to interpret axis 3.

These results indicate that only one physical gradient can be identified at the different scales we examined. The organisation of the plot-points is slightly different on axis 1 according to the size of the quadrats (plot 9 in particular shows an important move along axis 1).

Interpretation of species contributions by their patterns of distribution

If we examine the species with a strong contribution for axis 1 (Table 2), we can make out 3 groups:

Species characterising the poles (positive or negative) only on a fine scale (*Petrorhagia prolifera*, *Argyrobium zanonii*...). We hypothesise that these species are simply more scattered in one environment than another (at one geographic pole than another). In a limited sampling, they would tend to appear in one type of environment only, in such a way that they largely contribute to determine axis 1. On the contrary, when sampling scale increases, they would also appear in the other environment and their contribution would decrease, *i.e.* they would take a lesser part in the discrimination between one environment and the other.

Species characterising the poles at all the scales (*Cerastium arvense* subsp. *suffruticosum*, *Genista hispanica*...). We suggest they are almost absent from quadrats of one geographic pole whatever the scale, at least at the selected scales.

Species characterising the poles only on a large scale (*Sedum acre*, *Amelanchier ovalis*...). These species are exclusively present in one environment but they are represented by individuals or groups of individuals quite sparse in this environment. Consequently, they tend to appear only in larger sample size only.

The analysis of species presence-absence data among the plots at the different scales enabled us to clearly see the interpretation proposed for each point above. A few species have a high contribution only on middle scales (*Echium vulgare*, *Asperula cynanchica*...). That means that their distribution is linked to the gradient, but that the frequency gap from one pole

to the other is of relatively little importance. Let us stress the fact that axis 1 retains its meaning across scales. Table 3 shows, however, that the correlations of axes 1 between one another are better between two successive scales.

Interpretation of plot-points distribution in factorial planes by species patterns

The organisation of the plot-points in the factorial planes 1-2 is very characteristic (Figure 1): the active point of a group of 4 plots (the other 3 being non active) clearly shows a trend to be the furthest from the origin, whatever the CA. For an active point representing a quadrat of a given size, we can underline:

The smallest quadrats (non-active) tend to be placed closer to the origin for they contain less often the species with a strong contribution. Indeed, we verified above that some of these species don't occur in most of the small quadrats because they are too scattered.

The largest quadrats (non-active) also tend to come closer to the origin for, on the contrary, they all tend to contain some species with a strong contribution. Indeed, some of the « discriminating » species at the concerned scale are no more « discriminating » at a larger scale (see above).

Patterns of species frequency

We have represented in histograms the distribution of the taxa among classes of frequency (presences in the plots) (Figure 4). It appears clearly that on the smallest scale (quadrats A), collections are dominated by scarce species (lowest frequency). Secondary maxima are visible, but their distribution depends on the classes of frequencies used. When the observation scale goes up, a second peak emerges in the class of most frequent species. Thus, in larger squares, there is a large proportion of species present in one quadrat only, and a large proportion of species present in all the quadrats.

On all the scales, there is a very good positive correlation between abundance and frequency of species (Figure 5; quadrats A: $r=0.81$; quadrats B: $r=0.79$; quadrats C: $r=0.81$; quadrats D: $r=0.82$; for each test $p<10^{-5}$), a general property of most of the systems at different levels of organisation (e.g. Collins & Glenn, 1990; Collins *et al.*, 1993).

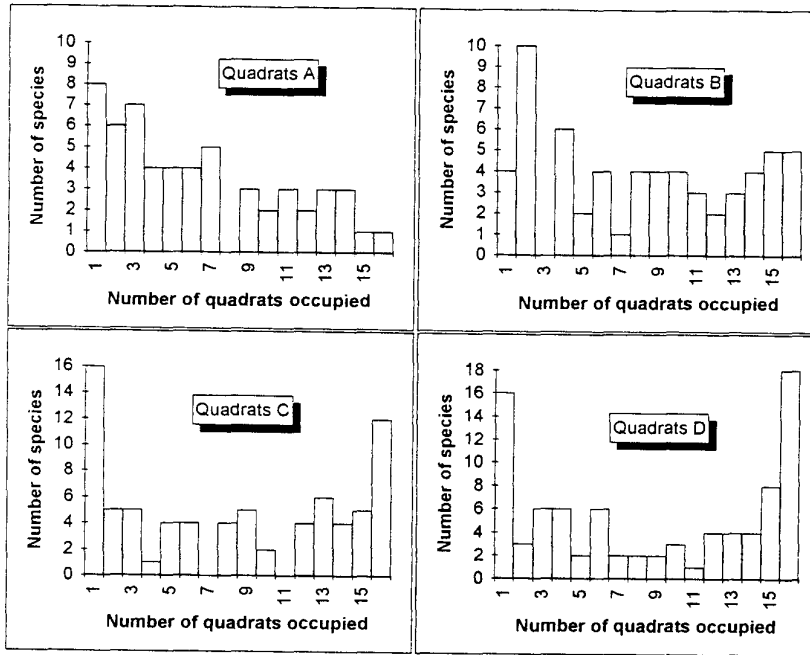


Figure 4. Distribution of species in 16 classes of frequency

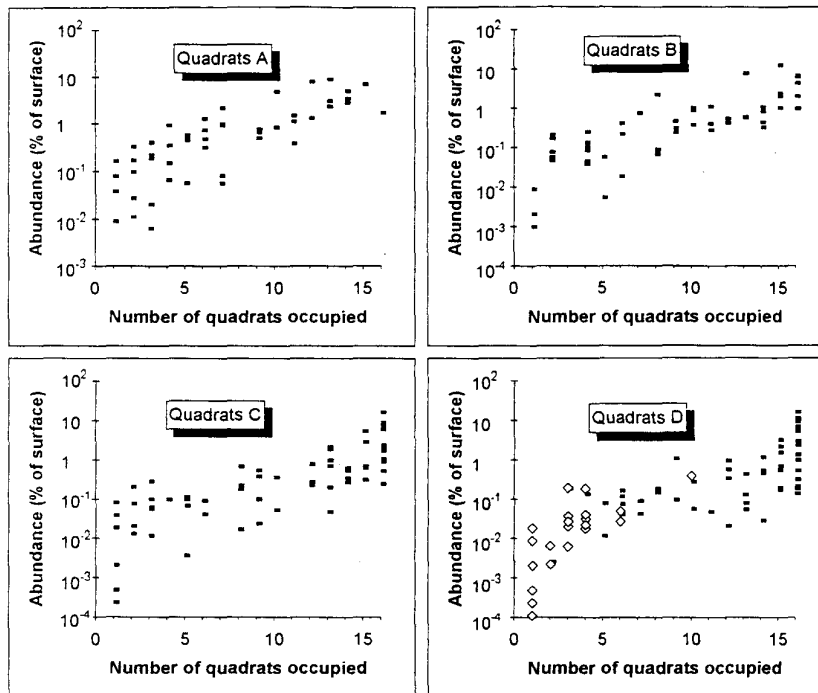


Figure 5. Abundance-frequency relations. Points correspond to species. There is a very good correlation between species frequency and their abundance in quadrats: quadrats A: $r=0.81$; quadrats B: $r=0.79$; quadrats C: $r=0.81$; quadrats D: $r=0.82$; for each scale: $p < 10^{-5}$.

This property is consistent with expectations of Hanski's (1982) and Kolasa's (1989) models.

DISCUSSION

Detection of the gradients

In our data, only one ecological factor was detected, and it always corresponds to axis 1 whatever the study scale. In these data set, a small grain is thus sufficient to detect the ecological gradient. At the examined scales, the organisation of the vegetation in *patches* (Whittaker & Levin, 1977) does not influence strongly the detection of a gradient whatever the scale. Nevertheless, correlations between axes 1 are weaker and weaker as the difference of scale increases. This underlines the risks there are to introduce different size plotting in a multi-dimensional analysis.

In our study, the organisation of the plot-points which is slightly different on axis 1 according to the size of the quadrats can be linked to the existence of patches. These moves correspond to a mosaic organisation of the vegetation. In any case, patches of various sizes are visible in the physiognomy of the community. For example, some Crassulaceae and annuals are confined in microhabitats of 1 to 3 dm². These microhabitats cannot be detected with the grain of resolution we have used. They are linked to disturbances and stress (Madon & Médail, 1997), and life in them is very difficult because of ranges of temperature, drought and the possible accumulation of litter (Fowler, 1988; Bergelson, 1990; Ryser, 1993). They are more close at the north part of the grassland than at the south part.

Models of distributions of frequency

Figure 4 clearly shows that, on a small scale, the results are consistent with Kolasa's model (1989): one mode for infrequent species and other secondary modes weaker and weaker towards classes of strong frequency. On the contrary, towards the large scales, the results become consistent with Hanski's model (1982) for the communities: two important modes for the two extreme classes of frequency. This result shows that even at the same level of organisation

(within the community), simply by changing the study scale, data can support one or the other model.

On a small scale (quadrats of 1 m²), Collins & Glenn (1990) found a second maximum in the group of high frequency. But in this study, the quadrats were adjacent: numerous species have a strong probability to occur in most of the quadrats. Indeed, the higher similarity of geographically close plots has been acknowledged for a long time (Curtis, 1959; Whittaker, 1972; Barbour et al., 1980). Shmida & Ellner (1984) attribute this feature to mass effect, but recognise that the existence of cryptic gradient is not to be dismissed.

Williams (1950) and Collins and Glenn (1990) suggested the possibility of a « saturation » of large quadrats in a great number of species. Figure 5 (quadrats D) clearly confirms this suggestion: the species plotted on a small scale tend to move towards the right on the large scale graph; therefore a certain number is present in all the quadrats (« saturation »). This is relevant to our conclusion about the influence of species patterns on species contributions in CA according to the scale.

On the contrary, there is always an important group of infrequent species whatever the scale. But these infrequent species are not necessarily the same from one scale to the other. That is to say that the character core or satellite depends on the observation scale. Figure 6 presents a model showing that at a small scale, a species can be infrequent (satellite or urban), and at a large scale, the same species can be frequent and even « saturate » quadrats (core or rural).

Hanski (1982, 1987) explains the peak for scarce species by a stochastic model of colonisation and extinction. The environmental stochasticity would tend to push the species either to superabundance or to rarity. Rare species may go disappear, or may survive in favourable patches, or may survive because of the dispersal from more favourable environments (mass-effect). The latter considerations are suitable, but the peak of frequent species appears only at a given scale. The existence of a global gradient in the community is also crucial: it necessarily limits the height of the peak of frequent species, since there are species which characterise one geographic pole (cf. results) and which are not therefore present in all the plots.

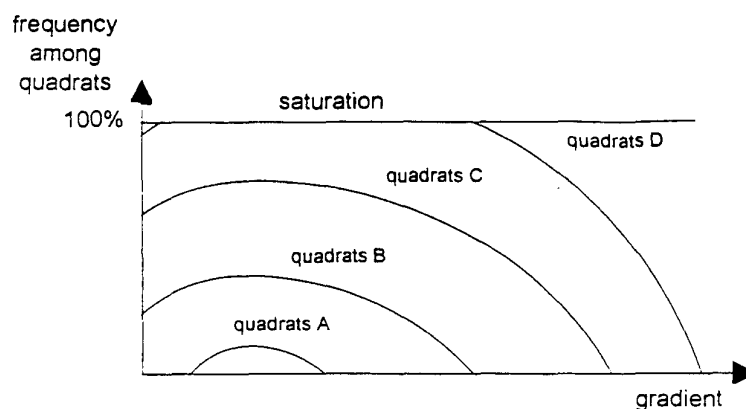


Figure 6. Influence of quadrat size on the character core or satellite of a species. The size of quadrats increases from A to D. At a small scale (quadrats A), the species can be unfrequent (satellite or urban) and at a larger scale (quadrats D), the species can saturate quadrats (it is core or rural).

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Plant systematics: a phylogenetic approach

W.S. JUDD, C.S. CAMPBELL, E.A. KELLOGG & P.F. TEVEN

Sinauer associates, Inc., 464 p. (1999)

Ce livre est une synthèse de tous les travaux récents en matière de phylogénie ainsi que de leurs applications directes dans la systématique des plantes. Le résultat est vraiment exceptionnel, compte tenu de la multitude des travaux ponctuels actuellement publiés, tant d'un point de vue moléculaire que morphologique (cette dernière approche retrouvant un certain essor du fait des limitations de la précédente). Ce livre se présente comme une sorte de précis de systématique moderne articulé en deux parties. Le lecteur se familiarisera dans un premier temps avec les techniques générales de la phylogénie, avant de découvrir les clades dégagés de ces approches.

Nous commençons de manière simple: qu'entend-on par plante, par systématique et par approche phylogénique? Et l'on se rend compte rapidement que les réponses ne sont pas si évidentes et la pertinence des nouvelles questions qu'elles entraînent nous invite à poursuivre la lecture.

Nous abordons dès lors les divers principes de la systématique biologique et phylogénique, avec des exemples concrets, basés principalement sur des caractères morphologiques, qui nous aident à appréhender les notions d'arbre (et des groupes monophylétiques qui

les constituent), les diverses méthodes de reconstruction (distances, parcimonie, maximum de vraisemblance) et la confiance que l'on doit leur accorder (Homoplasy Index, Bootstrap, Decay Index...).

Dès lors est posé le délicat problème des groupes reconnus par ces approches évolutives: on manque de manière évidente d'un certain recul et d'une vision globale d'ensemble. Par conséquent, les clades dégagés actuellement ne peuvent tous être nommés et bien souvent leurs rangs systématiques sont arbitraires ou provisoires.

Le troisième chapitre constitue une approche historique avec tous les grands noms de la systématique et leur poids dans l'approche évolutive de cette science. Une mention spéciale pour la galerie de portraits rarement publiés dans les ouvrages classiques.

Nous poursuivons par une description détaillée de tous les caractères taxonomiques utilisables, véritable lexique actualisé de tous les termes importants à connaître en botanique, qu'ils soient anatomiques, caryologiques ou basés sur la biologie de la reproduction ou l'étude des métabolites secondaires et des protéines.

Pour contrebalancer ces caractères dits "classiques", le chapitre 5

nous renseigne sur toutes les subtilités concernant les données moléculaires (description des différents génomes, différentes techniques de recherche et de reconstruction des arbres phylogéniques), avec un accent sur les problèmes d'introgession et d'hybridation, principaux artefacts dans ces approches encore considérées, il y a peu comme quasi irréprouvables.

Suit un chapitre concernant l'approche populationnelle proprement dite, avec les problèmes de diversification intraspécifique et de notion d'espèce.

Nous abordons enfin la partie purement systématique avec ses clades parfaitement définis par diverses approches et d'autres groupes encore incertains (par manque de recul): des Trachéophytes hors Angiospermes, (Lycopodes, Sélaginelles et autres fougères) jusqu'aux Cycadaceae, conifères et Ephedraceae.

Le chapitre suivant, de loin le plus important, traite des relations entre Angiospermes. Cette partie mérite d'être lue par tous les botanistes, depuis les naturalistes de terrain jusqu'aux spécialistes, car à tous les niveaux les surprises sont au rendez-vous. Parmi les faits marquants, voire surprenants, notons la proximité des Monoco-

tylédones et des Laurales avec d'autres groupes longtemps considérés comme basaux au sein des Angiospermes. Citons également l'admission de la plupart des ex-Scrophulariaceae au sein des Plantaginaceae, ou des Anthirrinaceae, selon les avis, ainsi que la fragmentation des Liliales - Liliaceae en un grand nombre de familles et genres.

Ces nombreux exemples éloignés des croyances classiques peuvent évidemment donner naissance à certaines critiques plus ou moins légitimes. Quelle valeur peut-on vraiment accorder aux groupes

considérés dans ce livre, dans la mesure où n'ont été envisagées que des approches partielles, avec des gènes et des caractères classiques variants selon les études ?

Nous pouvons conclure avec les propos des auteurs eux-même, conscients des limites de cet ouvrage :

"Les étudiants apprécieront l'abandon des rangs classiques... Avec ces bases, ils pourront avancer de manière sûre dans la compréhension de la diversité des plantes" ou encore "...dans ce livre, nous pensons que certains des groupes décrits seront peut-être

modifiés, voire détruits, dans les années à venir".

Quoiqu'il en soit, malgré ces bémols, ce livre peut être considéré sans retenue comme une référence fondamentale pour le botaniste du prochain millénaire.

Ajoutons une bibliographie pour le moins monumentale, à la fois très récente et complète, qui justifie à elle seule l'achat de ce livre, deux appendices très intéressants et un CD Rom richement illustré et nous obtenons une bible dans le domaine, avec en prime un excellent rapport qualité/prix. A se procurer absolument !

Ghilem MANSION

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Biology and Wildlife of the Mediterranean Region

J. BLONDEL & J. ARONSON

Oxford Univ. Press, Oxford, 328 p. (1999)

S'engager dans la rédaction d'un ouvrage sur la biodiversité du monde méditerranéen, était à la fois courageux et ambitieux ; les auteurs le reconnaissent, comme ils indiquent en préface avoir volontairement axé leurs discussions et illustrations sur les questions et les groupes qui s'inscrivaient dans le domaine de leurs activités, tout en tentant de rester clair et d'éviter un jargon hermétique aux non-spécialistes. Il faut reconnaître qu'ils y sont parvenus, et que cet ouvrage se lit facilement et avec intérêt. Je pense que le but souhaité par les auteurs est atteint, et qu'en quelques 300 pages, ils sont arrivés à dresser un bilan clair et quasi-exhaustif des problèmes relatifs à la biodiversité du monde méditerranéen.

C'est volontairement que les auteurs restent sur des thématiques

souvent générales, et, ils le soulignent, au niveau de la semi-vulgarisation, car ils ne veulent nullement faire oeuvre de spécialistes. Ceci assurera certainement une plus large diffusion à cet ouvrage, même si le scientifique reste parfois sur sa faim.

Les bilans et les exemples choisis illustrent clairement les caractères majeurs du monde méditerranéen, depuis son individualisation climatique et biologique, en passant par sa mise en place actuelle et ses traits de vie, et en s'ouvrant sur les challenges que posent son avenir. Le rôle de l'action humaine est fort justement souligné, comme l'indique joliment le titre du chapitre 8 "*Humans as sculptors of mediterranean landscape*".

Il n'est question ici, ni de résumer un ouvrage extrêmement

dense, ni de le critiquer, car je ne puis que souscrire, dans leurs grandes lignes, et souvent dans le détail, aux conclusions des auteurs qui, contrairement à un certain nombre de leurs prédécesseurs, donnent une idée claire et juste des critères fondamentaux du monde méditerranéen et de sa diversité.

Cependant, je ne puis que regretter quelques oublis ou imprécisions. C'est ainsi, par exemple, que si définir les limites de la région méditerranéenne pose bien des problèmes, mais reste nécessaire, les auteurs ne contribuent guère à régler cette question. Ils proposent dans les figures 1.4, 1.5 et 1.6, des solutions variables, excluant le S-E tunisien pour la première, et incluant toutes les bordures méridionales de la mer Noire qui en fait s'intègrent dans la zone euxinienne (pontique) à *Fagus orientalis* et

Rhododendron ponticum dont le climat et la flore n'ont rien de méditerranéen. La carte de la figure 1.6 dont je récusé toute paternité, comme cela est indiqué dans la légende, est la plus critiquable. Par exemple, la région saharo-arabe grignote une grande partie du Maghreb, dont les Atlas, alors que la province pontique cette fois englobe les Hauts Plateaux anatoliens et s'étend jusque sur les rivages de la Cilicie. De même, l'idée des quatre quadrants (fig. 1.4) dans le monde méditerranéen est intéressante, mais les limites proposées restent critiquables, surtout pour la péninsule italienne et ses îles annexes, écartelées entre trois d'entre eux.

Du point de vue historique, mon passé hélas réduit et lointain de biospéléologie me fait toutefois regretter que cette facette n'ait pas été analysée, pour rendre compte de certaines mises en place pré-Miocène, à partir de la répartition d'espèces cavernicoles sur lesquelles existe une bonne documentation. Parmi les "habitats" caractéristiques du monde méditerranéen, un bon bilan a été dressé, encore que la distinction entre forêt sclérophylle et forêt laurifoliée aurait gagné à être étoffée et discutée

en raison de leur signification écologique fort différente. De même, les mares transitoires, un des joyaux du monde méditerranéen, selon le mot de Braun-Blanquet, avec les adaptations remarquables de leur faune et de leur flore, ne sont pas évoquées.

Au niveau des traits de vie, les données relatives à l'origine de la sclérophylle et de son rôle dans le climat méditerranéen, de même que le problème du haut pourcentage de thérophytes dans la flore, sont analysées, mais je demeure pour ma part sur mes incertitudes, quant aux explications et aux résultats exposés. A propos du rôle et des modes de dissémination des espèces et en particulier des diaspores, l'exemple des îles macaronésiennes (Canaries et Madère), aurait gagné à être développé.

Les auteurs, à juste titre, ont mis l'accent sur les données historiques et le rôle de la région méditerranéenne en tant que capital biologique de base pour l'éclosion des civilisations néolithiques. Ils montrent une culture littéraire et historique qui mérite d'être soulignée, et ont rendu en particulier à Theophraste, un juste hommage en tant qu' "inventeur" de la spécificité du monde méditerranéen ;

mais pourquoi alors ne pas avoir au moins évoqué son remarquable chapitre sur la biologie du figuier...

Même si l'on pourrait citer encore quelques imprécisions ou quelques oublis, il n'en reste pas moins que le travail de BLONDEL & ARONSON, restera pour longtemps, une référence et une mine de renseignements, pour tous ceux qui aiment la région circum-méditerranéenne, et étudient sa faune et sa flore. Ce n'est pas l'un de leur moindre mérite, que d'avoir su regrouper et intégrer à la fois des groupes animaux et végétaux, parfois fort différents quant à leurs significations historiques et à leurs réactions face aux contraintes écologiques méditerranéennes. Les auteurs ont donc su dresser un bilan cohérent, tout en soulignant la richesse biologique incomparable du monde méditerranéen, et le rôle qu'il a joué dans l'éclosion de nos civilisations. Ils terminent fort justement en soulignant les gravissimes menaces de tous ordres qui pèsent sur lui et l'assaillent de toutes parts, et qui font certainement de cette région, à l'heure actuelle, une des plus menacées de la planète, "*a microcosm of world problems*".

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Instructions aux auteurs

Ecologia Mediterranea publie des travaux de recherche originaux et des mises au point sur des sujets se rapportant à l'écologie fondamentale ou appliquée des régions méditerranéennes, à l'exception des milieux marins. La revue exclut les articles purement descriptifs ou de systématique. Ecologia Mediterranea privilégie les domaines scientifiques suivants : bioclimatologie, biogéographie, biologie de la conservation, biologie des populations, écologie génétique, écologie du paysage, écologie microbienne, écologie végétale et animale, écophysiologie, paléoclimatologie, paléoécologie. La revue accepte également la publication d'actes de colloques, d'articles de synthèse, de notes méthodologiques, de comptes-rendus d'ouvrages, ainsi que des commentaires sur les articles récemment parus dans Ecologia Mediterranea.

Les manuscrits sont soumis à des lecteurs spécialistes du sujet, ou à des membres du Comité de Rédaction, ou aux Editeurs. La décision finale d'accepter ou refuser un article relève des Editeurs. L'article proposé doit être envoyé en triple exemplaire à l'adresse de la revue. Une fois leur article accepté, les auteurs devront tenir compte des remarques des lecteurs, puis ils renverront leur texte corrigé au secrétariat de la revue, sous 3 mois, imprimé en un exemplaire et informatisé (disquette 3.5', si possible PC et au format Word 7 ou .RTF). Les auteurs devront s'assurer de la correspondance entre le texte imprimé et le texte informatisé. Les illustrations originales seront jointes à l'envoi. Les épreuves corrigées doivent être retournées au secrétariat de la revue sans délai. Les livres et monographies devant être analysés seront envoyés aux Editeurs.

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L'article doit être complet : titres français et anglais, auteur(s) et adresse(s), résumés en français et anglais (au minimum), version anglaise abrégée (si le texte n'est pas en anglais), mots-clés, texte, puis remerciements, bibliographie, figures et tableaux. Le texte des articles originaux de recherche devrait normalement comporter quatre parties : introduction, méthodes, résultats, discussion.

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Résumés, mots-clés et version abrégée

Les résumés doivent comporter 300 mots au maximum et la version anglaise abrégée 1000 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.

Bibliographie

La bibliographie regroupera toutes les références citées et elles seules. Les références seront rangées dans l'ordre alphabétique des auteurs et de façon chronologique. Les abréviations internationales des titres des revues doivent être utilisées (sauf en cas de doute). Vérifier attentivement le manuscrit pour s'assurer que toutes les références citées dans le texte apparaissent bien en bibliographie et inversement. La mise en forme doit suivre les exemples suivants :

- article : Andow D.A., Karieva P., Levin S.A. & Okubo A., 1990. Spread of invading organisms. *J. Ecol.*, 4 : 177-188.
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- article d'ouvrage : May R.M., 1989. Levels of organization in ecology. In : Cherret J.M. (ed.), *Ecological concepts*. Blackwell Scientific Public., Oxford : 339-363.
- actes d'un colloque : 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.

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 ; Dupont & 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.*

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L'usage d'une abréviation technique doit être précédée 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.).

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Il est fourni 25 tirés-à-part par article, même lorsqu'il y a des auteurs multiples. Des tirés-à-part supplémentaires peuvent être obtenus à la demande : ils seront facturés.

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The manuscript must be complete: French and English titles, author(s) and address(es), French and English abstracts (at least), an English short version (only if it is not the language used in the article), key-words, text, references, acknowledgements, figures and tables. For research papers, the text should normally consist of 4 sections: introduction, methods, results and discussion.

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- book section:

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

- conference proceedings:

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.

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The words « figures » and « tables » announced in-text should be written *in extenso* and in lower-case letters. In the text, refer to the author's name and year of publication (followed by pages only if it is a quotation). If a publication is written by more than two authors, the name of the first author should be used followed by « *et al.* » (this indication, however, should never be used in the list of references : first author and co-authors should be mentioned). Examples: « Since Dupont (1962) has shown that... », or « This is in agreement with previous results (Durand *et al.*, 1990 ; Dupond & Dupont, 1997) ... ».

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Explanation of a technical abbreviation is required when first used. International convention codes for nomenclature should be used. Latin words should be in italics (*et al.*, *a priori*, *etc.*), particularly for taxonomic classifications (the first time, please state the author's name: for example, *Olea europaea* Linnée).

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