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A survey of heath vegetation of the Iberian Peninsula and Northern Morocco: a biogeographic and bioclimatic approach

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with 14 figures, 1 table and 1 appendix

To our master and friend Salvador Rivas-Martínez

Abstract. The present study attempts to carry out a biogeographic and bioclimatic approach using a specialized vegetation type such as that of heathlands (Calluno-Ulicetea class) in the Iberian Peninsula and Northern Morocco. The territories in which this vegetation occurs have been divided into 63 small units based on the accepted biogeography of the area. The heathland flora of each unit was surveyed using phytosociological data from bibliography and other sources. Finally, each of the territorial units has a list of species drawn up being representative of the floristic composition of their heathland vegetation. The total amount of plants was limited to 289, as rare plants were discarded. Species from this list were classified into 12 groups according to their phytosociological affinity (Calluno-Ulicetea, Quercetea ilicis, Querco-Fagetea, Festuco-Brometea, etc.) in order to identify the floristic influences in each of the territories. The original matrix with 63 columns and 289 rows was set and several ordinations were carried out, particularly PCA and canonical RDA. The floristic composition of the list of total species for each territory, strongly reflects the biogeographic and bioclimatic conditions. This is valid for the genuine Calluno-Ulicetea flora as well as for the rest of the floristic groups. The main climatic parameters which explain the differences between the heathland flora of the territories considered are mostly P (annual precipitation), It (thermicity index) and Ic (continentality index). Rainy areas, located in the Cantabrian and Atlantic areas, have a large number of Calluno-Ulicetea plants, whilst continental areas, particularly in the Eastern Pyrenees, have low numbers.

1. Introduction

Heaths or heathlands are defined as a dwarf-shrub vegetation formed by heathers (*Calluna* and *Erica* species and other related plants, mostly belonging to the Ericaceae family) which grow on acidic low fertility soils. A heath is open land covered with low-growing evergreen shrubs which is particularly common in the Atlantic façade of Europe, from western Norway (DIERSSEN 1996, FREMSTAD 1997, TVERABRAAK 2004) to Northern Morocco (QUÉZEL et al. 1988, DEIL 1984, DÍAZ GONZÁLEZ 1998, BENITO

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Cebrián 1948). Heaths have attracted the interest of Administrations involved in Nature Conservation, particularly those within the European Union, and they have been included in Annex I of the Habitat Directive (92/43/CEE). This is because in many areas of the EU, heaths are retreating or even disappearing, as a result of the rural abandonment and the reduction of the disturbance regime necessary to maintain them.

Heaths have been studied over recent years from different viewpoints with variable geographic scope: syntaxonomy (Braun-Blanquet et al. 1965, Géhu 1973, Rivas-Martínez 1979, Rivas-Martínez et al. 2001, Loidi et al. 1997, Díaz González 1998, Botineau & Géhu 2005), management (Bullock & Pakeman 1997, Webb 1998, Wilson et al. 2003, Britton et al. 2005), fragmentation and species extinction (Piessens & Hermy 2006), biodiversity and disturbance regime (Arroyo & Marañón 1990, Ojeda et al. 1995) and others, but they have scarcely been studied from the biogeographic point of view; some approaches dealing only with Ericoideae species have been carried out (Ojeda et al. 1998). The present study gives some information about the conditions, structure, composition, etc. of those European (and North African) heaths.

The basic aim of this survey was to make an approach to the flora living on heathlands in order to investigate the share of the different floristic elements and draw conclusions about the origin and affinities of the different heath communities in the surveyed area. Also, an attempt was made to relate this floristic composition with the main features of the regional climate. Calluno-Ulicetea vegetation was used as the basis for a biogeographic and bioclimatic study concerning the Iberian-Moroccan territories in which it occurs.

The key aims of this survey can be summarized by considering the following questions:

1. Is there any affinity between the characteristic floristic composition of the Calluno-Ulicetea flora of each of the territories and the territorial division? i.e. to what extent is the Calluno-Ulicetea flora reflecting the territorial division and the affinities between the different territories?
2. Similarly, is the remaining flora living on heathlands (i.e. the non-Calluno-Ulicetea flora) significant with regard to the territorial division?
3. Which areas are the richest in Calluno-Ulicetea species?
4. Which are the driving bioclimatic parameters, which determine this floristic composition?

2. Material and methods

2.1. Study area

The southernmost territories of the total area of this vegetation, i.e. the Iberian Peninsula and Northern Morocco (Rif area and Tingitanean peninsula) were selected. The reason for this was that in the southern part of these territories heath vegetation is in contact with Mediterranean flora and thus is strongly influenced by it, while in Northern Iberia it is in contact with temperate flora; this enables a more contrasted analysis of the floristic influences to be carried out. In addition, the biogeographic knowledge of this area permits a more detailed analysis in terms of territorial divisions.

2.2. Source data

The basic source of information for this analysis were both published and sometimes unpublished (PhD, reports, etc.) phytosociological tables taken from 96 bibliographical sources (Annex 1). The number of relevés involved in the analysis was 1981, belonging to 77 associations and 3 plant communities. The floristic information was complemented in some cases with data from the web page ANTHOS (http://www.programanthos.org).

The climatic information was taken from the Climatic Digital Atlas of the Iberian Peninsula (Ninyerola et al. 2005). From Northern Morocco there are some available climatic data (Ajbilou et al. 2006, http://www.globalbioclimatics.org) but not in the same format as the Iberian ones (digital maps of all the parameters).

2.3. Data analysis

As data had been taken from different sources, some standardization was needed. Species names in the older relevés were updated to today's nomenclature and taxonomy, adapted basically to Flora Iberica (Aedo & Herrero 2005, Castroviejo et al. 1986–1997, Muñoz Garmendia & Navarro 1998, Nieto Feliner et al. 2003, Talavera et al. 1999, 2000), Flora Europaea (Tutin et al. 1968–1980, 1993) and the Addenda to the Vascular Plant Communities of Spain and Portugal, Part II (Rivas-Martínez et al. 2002a).

Before running the numerical analysis of the data two standardizations were performed:

1. Exclusion of companion species with a low occurrence and of taxa that were considered to be unrelated to heathland vegetation such as nitrophilous or therophytes.
2. In order to equalize the floristic content of the biogeographic territories, a second reduction was carried out due to the high diversity in the number of species listed. Such diversity was due to the different number of relevés used to build each list: some of the areas had several hundred relevés and others had only a few. There was also a divergence due to the author effect.

Finally, a total set of 289 taxa were used for the analysis, which were classified into several categories as shown in Table 1.

In the study area 63 units were defined beforehand based on the biogeographic classification for Europe and the Mediterranean area by Rivas-Martínez et al. (2002b), Costa et al. (1999), Amigo et al. (2005) and Berastegi et al. (1997). The biogeographic categories had been modified by

Table 1. Species of heathland flora from the Iberian Peninsula and northern Morocco classified according to syntaxonomical-ecological affinities into 12 categories.

1 Calluno-Ulicetea taxa	Agrostis curtisii, Avenula albinervis, Avenula marginata ssp. sulcata, Calluna vulgaris, Carex asturica, Cirsium filipendulum, Cistus psilosepalus, Daboecia cantabrica, Drosophyllum lusitanicum, Erica andevalensis, Erica australis, Erica australis ssp. aragonensis, Erica australis ssp. riphaeum, Erica ciliaris, Erica cinerea, Erica lusitanica, Erica mackaiana, Erica scoparia, Erica tetralix, Erica umbellata, Erica vagans, Euphorbia polygalifolia, Genista ancistrocarpa, Genista anglica, Genista berberidea, Genista carpetana, Genista micrantha, Genista pilosa, Genista triacanthos, Genista tridens, Halimium alyssoides, Halimium lasianthum, Halimium ocymoides, Halimium umbellatum, Hypericum linariifolium, Lavandula viridis, Lithodora prostrata, Luzula lactea, Pedicularis sylvatica ssp. lusitanica, Polygala microphylla, Potentilla erecta var. herminii, Pseudarrhenatherum longifolium, Pterospartum tridentatum s.l., Satureja salzmannii, Scorzonera humilis, Serratula tinctoria, Simethis mattiazzi, Stauracanthus boivinii, Stauracanthus spectabilis ssp. vicentinus, Thymelaea broteriana, Thymelaea coridifolia, Thymelaea dendrobryum, Thymelaea subrepens, Thymelaea villosa, Thymus villosus, Tuberaria globulariifolia, Tuberaria major, Ulex airensis, Ulex europaeus, Ulex europaeus f. maritimus, Ulex gallii (incl. U. cantabricus), Ulex gallii f. humilis, Ulex gallii ssp. breoganii, Ulex jussiaei, Ulex jussiaei ssp. congestus, Ulex latebracteatus, Ulex latebracteatus f. humilis, Ulex micranthus, Ulex minor, Vaccinium myrtillus, Viola lactea
2 Quercetea ilicis taxa	Arbutus unedo, Asparagus acutifolius, Asparagus aphyllus, Calicotome villosa, Carex distachya, Chamaerops humilis, Corema album, Daphne gnidium, Erica arborea, Genista tournefortii, Juniperus navicularis, Juniperus turbinata, Myrtus communis, Olea europaea ssp. sylvestris, Osyris alba, Osyris lanceolata, Paeonia broteri, Phillyrea angustifolia, Phillyrea latifolia, Pistacia lentiscus, Pistacia terebinthus, Pulicaria odora, Quercus canariensis, Quercus coccifera, Quercus ilex, Quercus lusitanica, Quercus rotundifolia, Quercus suber, Rhamnus alaternus, Rubia peregrina, Rubia peregrina ssp. longifolia, Ruscus aculeatus, Scilla monophyllos, Serratula alcalae, Smilax aspera, Teucrium fruticans, Teucrium scorodonia ssp. baeticum, Viburnum tinus
3 Cisto-Lavanduletea taxa	Arctostaphylos uva-ursi ssp. crassifolia, Astragalus lusitanicus, Cistus crispus, Cistus ladanifer, Cistus ladanifer ssp. sulcatus, Cistus laurifolius, Cistus monspeliensis, Cistus populifolius, Cistus populifolius ssp. major, Cistus salviifolius, Genista hirsuta, Genista hirsuta ssp. algarbiensis, Halimium alyssoides ssp. atlanticum, Halimium calycinum, Halimium halimifolium, Halimium halimifolium ssp. multiflorum, Halimium lasiocalycinum ssp. riphaeum, Halimium viscosum, Lavandula stoechas, Lavandula stoechas ssp. luisieri, Lavandula stoechas ssp. lusitanica, Lavandula stoechas ssp. pedunculata, Lavandula stoechas ssp. sampaiana, Lithodora lusitanica, Stauracanthus genistoides, Stauracanthus spectabilis, Thymus camphoratus, Thymus capitellatus, Thymus mastichina, Tuberaria lignosa, Ulex argenteus, Ulex australis, Ulex australis ssp. welwitschianus, Ulex baeticus, Ulex borgiae, Ulex eriocladus

Table 1 (cont.)

4 Querco-Fagetea taxa	Arenaria montana, Betula celtiberica, Blechnum spicant, Deschampsia flexuosa, Fagus sylvatica, Frangula alnus, Genista falcata, Holcus mollis, Hypericum pulchrum, Ilex aquifolium, Lathyrus linifolius, Linaria triornithophora, Luzula forsteri, Melampyrum pratense, Physospermum cornubiense, Pulmonaria longifolia, Quercus faginea, Quercus petraea, Quercus pubescens, Quercus pyrenaica, Quercus robur, Salix atrocinerea, Solidago virgaurea, Sorbus aucuparia, Stachys officinalis, Tamus communis, Teucrium scorodonia, Veronica officinalis, Viola riviniana
5 Festuco-Brometea taxa	Avenula mirandana, Brachypodium phoenicoides, Brachypodium rupestre, Briza media, Bromus erectus, Centaurium erythraea, Chamaespartium sagittale, Euphorbia cyparissias, Galium verum, Hypericum perforatum, Luzula campestris, Potentilla montana, Sanguisorba minor, Trifolium montanum
6 Cytisetea taxa	Adenocarpus complicatus, Adenocarpus lainzii, Adenocarpus telonensis, Cytisus cantabricus, Cytisus commutatus, Cytisus grandiflorus, Cytisus multiflorus, Cytisus scoparius, Cytisus scoparius ssp. bourgaei, Cytisus striatus, Cytisus striatus ssp. eriocarpus, Genista florida ssp. polygaliphylla, Genista hystrix, Genista obtusiramea, Genista polyanthos, Genista quadriflora, Teline linifolia
7 Nardetea taxa	Carex pilulifera, Danthonia decumbens, Erythronium dens-canis, Galium saxatile, Gentiana acaulis, Gentiana pneumonanthe, Jasione laevis, Jasione laevis ssp. carpetana, Juncus squarrosus, Meum athamanticum, Nardus stricta, Polygala serpyllifolia, Polygala vulgaris, Potentilla erecta, Scilla verna, Viola canina
8 Molinio-Arrhenatheretea taxa	Achillea millefolium, Agrostis capillaris, Arrhenatherum elatius ssp. bulbosum, Anthoxanthum odoratum, Cynodon dactylon, Dactylis glomerata, Holcus lanatus, Hypochoeris radicata, Lotus corniculatus, Plantago lanceolata, Prunella vulgaris
9 Orophilous taxa	Antennaria dioica, Arctostaphylos uva-ursi, Cysitus oromediterraneus, Festuca gautieri, Genista sanabrensis, Huperzia selago, Hypericum richeri ssp. burseri, Juniperus communis ssp. alpina, Lycopodium clavatum, Vaccinium uliginosum
10 Basophilous taxa	Cistus albidus, Cytisus lotoides, Genista hispanica, Genista occidentalis, Genista scorpius, Halimium atriplicifolium, Helichrysum decumbens, Helichrysum italicum ssp. seroti-

Table 1 (cont.)

	num, Helichrysum stoechas, Helictotrichon cantabricum, Lavandula angustifolia ssp. pyrenaica, Lithodora diffusa, Rosmarinus officinalis, Serratula pinnatifida, Thymus sylvestris, Thymus vulgaris
11 Coastal taxa	Angelica pachycarpa, Anthyllis vulneraria ssp. iberica, Armeria pubigera, Armeria pubigera ssp. depilata, Cheirolophus uliginosus, Crithmum maritimum, Crucianella maritima, Dactylis marina, Daphne gnidium ssp. maritimum, Daucus carota ssp. gummifer, Daucus halophilus, Euphorbia portlandica, Festuca rubra ssp. pruinosa, Helichrysum picardii, Koeleria cristata ssp. arenaria, Leucanthemum ircutianum ssp. crassifolium, Plantago maritima, Polygala baetica, Rumex acetosa ssp. biformis, Silene uniflora
12 Other taxa	Agrostis castellana, Arrhenatherum album, Carex binervis, Molinia caerulea s.l., Pteridium aquilinum, Rumex acetosella ssp. angiocarpus, Sesamoides purpurascens, Stipa gigantea, Thymus caespititius, Tolpis umbellata, Urginea maritima

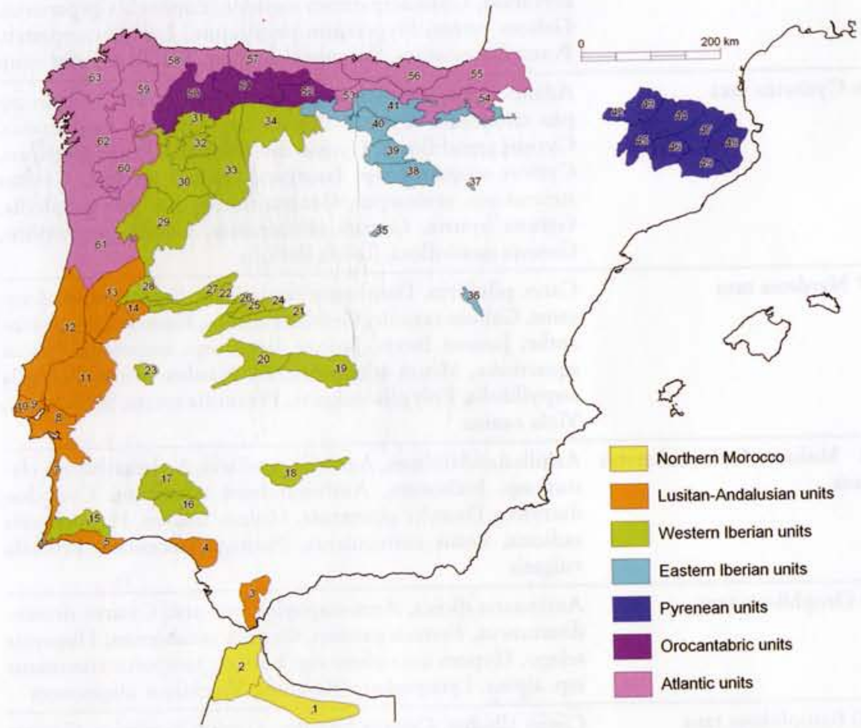


Fig. 1. Biogeographic units of the Iberian Peninsula and Northern Morocco considered in the study.

taking into account the occurrence and diversity of the different heathland community types, and therefore some of them have been reduced to the area in which heathlands occur. Each unit was inhabited by a particular heath flora, which was defined by a single list of the plants occurring in their heathland communities. This taxa list had been extracted from the phytosociological relevés corresponding to each biogeographic unit and was eventually supplemented with information from flora databases. Finally, a presence/absence matrix was obtained with columns corresponding to the 63 biogeographic units.

These biogeographic units were grouped considering bioclimatic and biogeographic affinities and built into 7 groups: Northern Morocco, Lusitan-Andalusian, Western Iberian, Eastern Iberian, Orocantabric, Atlantic and Pyrenean (Fig. 1).

In order to find the relationships between the different groups of taxa and the biogeographic units, a Principal Component Analysis (PCA) was performed using CANOCO 4.5 (ter Braak & Smilauer 2002). PCA with all the taxa was initially carried out. Two other PCA were made to determine the weight of the characteristic taxa of Calluno-Ulicetea in the ordination, one of them using only the Calluno-Ulicetea taxa and the other one with the species of the other groups (see Table 1). Relationships between environmental variables and heathland taxa or biogeographic units were investigated by constrained ordination implemented by CANOCO

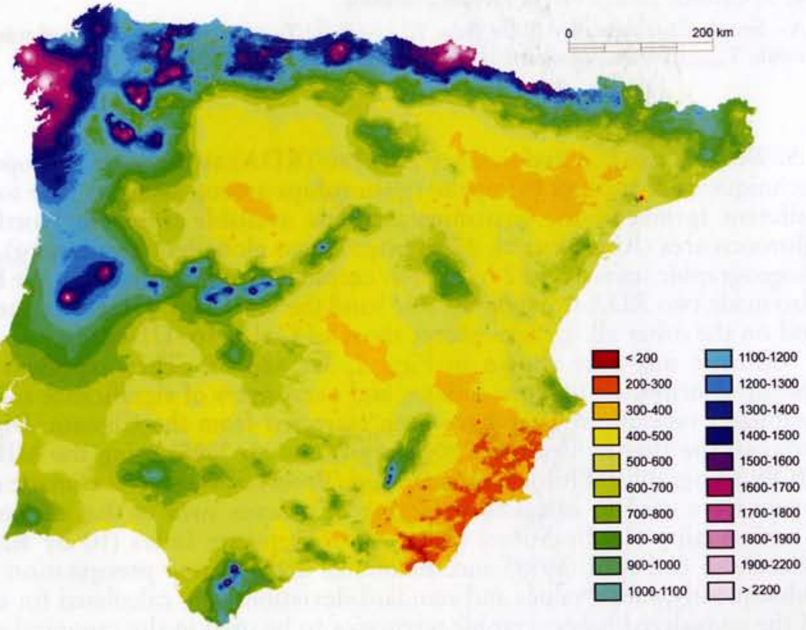


Fig. 2. Annual precipitation (in mm) of the Iberian Peninsula.

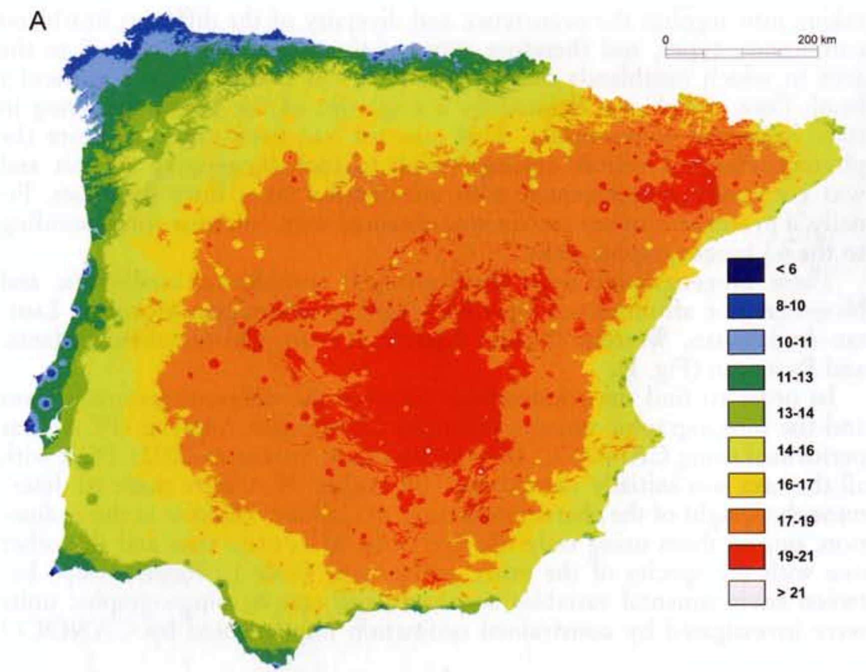
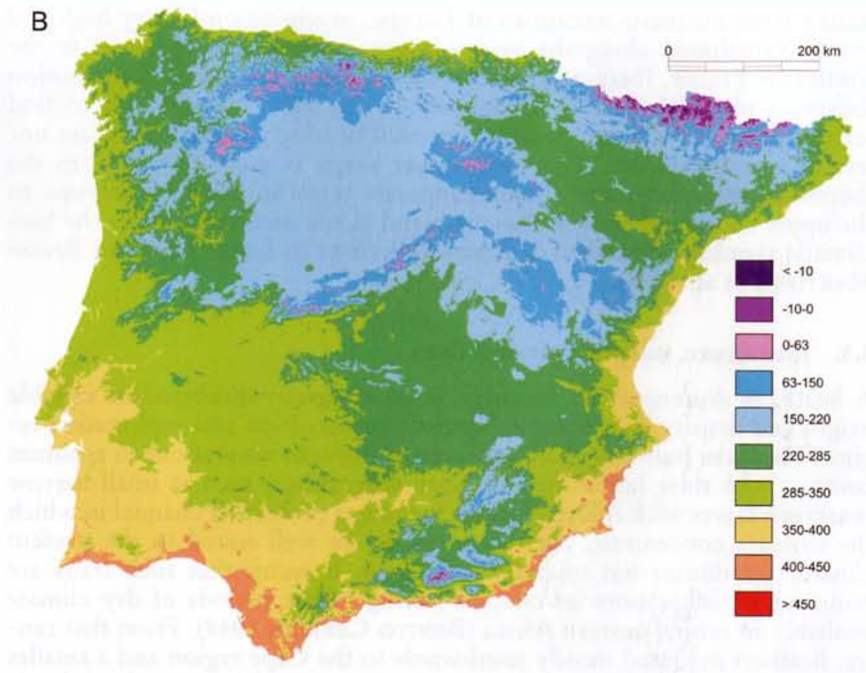


Fig. 3. Climatic pattern on the Iberian Peninsula.
3A – Simple Continentality Index (Ic = $T_{max} - T_{min}$; T_{max}: mean temperature of warmest month; T_{min}: mean temperature of coldest month)

4.5. We have selected Redundancy Analysis (RDA) as the more appropriate technique as it displays better the relationships among samples. Due to the different format of the environmental data available from the Northern Morocco area (Abijlou et al. 2006, http://www.globalbioclimatics.org), the biogeographic units 1 and 2 have been excluded from this analysis. We have also made two RDA using on the one hand the Calluno-Ulicetea species and on the other all the taxa except those of Calluno-Ulicetea.

Climatic maps are shown in Figs. 2, 3A and 3B. They represent the Iberian distribution of some indexes and parameters of significance for the heathland vegetation. They have been extracted from the Climatic Digital Atlas of the Iberian Peninsula (Ninyerola et al. 2005) using the MIRAMON Geographical Information System (Pons 2004). Several climatic data layers were used to calculate a number of indexes such as that of Simple Continentality (Ic) by Supan (1884), the Thermicity Index (It) by Rivas-Martínez & Loidi (1999) and the annual accumulated precipitation (P). Subsequently, mean values and standard deviation were calculated for each of the considered biogeographic territories to be used in the canonical analysis.



3B – Thermicity Index (It = (T + M + m) × 10; T: mean annual temperature, M: mean highest temperature of coldest month, m: mean lowest temperature of coldest month).

3. Site conditions, distribution, dynamism and syntaxonomy of Atlantic and western Mediterranean heaths in Europe and Morocco

3.1. Soil

Heaths develop on poor acidic soils often on siliceous substrates such as sandstone, granite, gneiss, quartzite and others. Sometimes this vegetation also develops on carbonate rocks like limestone or marl, provided that leaching of soluble bases is intense enough to provoke acidification in the upper layers of the soil. Under high rainfall conditions, podzolization can also occur in Atlantic areas, particularly in northern parts of Europe. However, in the South it occurs mostly in mountain areas. As an adaptation to this oligotrophy, mycorrhizae develop extensively on heaths. Some types of heaths can resist a certain degree of hydromorphy in the soil, especially within the numerous waterlogged areas.

3.2. Climate

The typical climate features associated with the territories in which heaths occur are high humidity levels and a low continentality (high oceanity). In heaths from northern territories of Europe, precipitation is very high and evenly distributed along the year without a dry season, whereas in the south (South France, Iberian Peninsula and Morocco) the rainfall distribution follows a more Mediterranean pattern. In any case, it is difficult to find territories below 600 mm of annual rainfall bearing a heath vegetation unless in swampy places. The temperature range is quite broad, from the thermomediterranean and thermotemperate types in Southern Europe to the upper supratemperate in the north and in the mountains (after the bioclimatic typology described in RIVAS-MARTÍNEZ & LOIDI 1999 and RIVAS-MARTÍNEZ et al. 1999).

3.3. Structure, adaptations and flora

A heath, as dominated by heathers, is an evergreen shrubland of variable height and density depending on floristic composition and exploitation regime. Heathers bear a typical syndrome of drought adaptations in apparent contrast with their humid habitat. Such adaptations, such as small narrow evergreen leaves with folded margins forming a protecting channel in which the stomata concentrate, etc., seem not to be well suited to the present climatic conditions but to more xeric ones. It seems that such traits are remnants of adaptations of ericoids during earlier periods of dry climate probably in central-eastern Africa (BENITO CEBRIÁN 1948). From that centre, heathers migrated mostly southwards to the Cape region and a smaller portion northwards towards the Atlantic Europe and Macaronesia (Atlantic islands of Canary, Madeira and Azores) through a connection between Mediterranean regions and the Cape (QUÉZEL 1978). It is important to highlight that most modern ericoid species live under Mediterranean climatic conditions, i. e. under a dry summer, not only in the Cape region but also in the Atlantic European and Macaronesian area. The representation of these species in the northern part of Atlantic Europe (Britanny, British Isles, Norway), where climate becomes more summer-rainy, is relatively small in terms of species number although they cover large areas in vast territories. It is thought that such extensive representation has been largely enhanced by human impact. Other interpretations consider that the morphologic adaptation of heather leaves correspond to the bending force of wind (WILLMANNS 1993). In any case, the drying effect of the wind should also be considered.

Woody legumes are often present in heaths, particularly gorses (*Ulex*) and some *Genista* species (CUBAS 1984, GIBBS 1966). In such cases the structure becomes more complex because the number of layers and size of the vegetation increases. It is important to mention that those legumes are atmospheric N fixers and substantially improve the trophic conditions of the soil (THORNTON et al. 1995). Direct grazing or harvesting of the above ground material from these heaths for cattle foraging or compost elaboration, provides a more valuable material than heaths without legumes.

Herbs and grasses constitute another important element of heaths. There are some grass species, which are irrevocably linked to heathlands (*Agrostis*

curtisii, Pseudarrhenatherum longifolium, Avenula marginata subsp. *sulcata, Avenula albinervis*, etc.), particularly in southern territories, and are characteristic of their communities. Those grasses and herbs can even dominate the heath if conditions and the disturbance regime are appropriate. In wet soils, under hydromorphic conditions, heaths increase the amount of herbs, grasses and bryophytes as they are often in contact with mires. The northern territories bear a much higher quantity and diversity of mosses and lichens.

3.4. Syntaxonomy

The term heath has been frequently used in a broad sense, including almost all the shrubs having heathers, particularly *Calluna vulgaris*. This has included subalpine heathlands in the mountains of central and Northern Europe as well as boreal heaths in the north (RODWELL 1991, DIERSSEN 1996, SCHAMINÉE 1993). Those shrublands, often with plants like *Vaccinium uliginosum, V. vitis-idaea, Loiseleuria procumbens, Arctostaphylos alpinus*, etc. actually belong to the Vaccinio-Piceetea or Loiseleurio-Vaccinietea classes. In the South, *Calluna* and some *Erica* species also occur in Mediterranean shrublands dominated by *Cistus* ("jaras" in Spanish), in communities belonging to Cisto-Lavanduletea under substantially drier conditions (RIVAS-MARTÍNEZ 1979). Those "jarales" represent the Mediterranean vicariant of the true Atlantic heaths and will not be included in this survey. Thus, we restricted our concept of heath to the class Calluno-Ulicetea in the strict sense (DÍAZ GONZÁLEZ 1998, BOTINEAU & GÉHU 2005, GÉHU 2000); this excludes a broad range of plant communities in which *Calluna* occurs, particularly in the Northern European territories, as well as grasslands dominated by *Nardus stricta*, which many authors group together with heaths to form the Nardo-Callunetea class.

3.5. Dynamism

Nowadays, heaths mostly develop in disturbed areas. Historically within Europe, fire has been the main tool used to remove forests in order to gain areas for grazing. This has been the disturbance regime which has enabled the broad expansion of heathlands in Atlantic Europe on acidic substrata, thus replacing forests of diverse composition (LAWSON et al. 2004). Furthermore, heaths have become pasture in most of the areas in which they occur. Grazing and harvesting heaths have been common practices for peasants in the area. The most common trees which form the forests which are replaced by heaths are *Fagus sylvatica, Betula pendula, Quercus robur, Q. petraea, Q. pyrenaica* and *Q. suber*, the latter mostly in the southern territories.

But, which are the primary stations of heaths? Considering the actual dependence of this vegetation on severe disturbance, we have to accept that the vast majority of today's heaths are secondary (GÉHU 2000). Before human disturbance expanded heaths in Western Europe, they probably occupied never forested areas such as cliffs and rocky slopes unless natural disturbance (landslides, wildfires, etc.) could also occur in forests, giving a chance to heaths to participate in the earlier stages of secondary succession. Thus, coastal fringes (coastal cliffs) and mountains (rims, ridges and shallow soil places) should have been the areas providing most primary stations for this vegetation in a pre-Neolithic time. Chromosome number studies in *Ulex* show that diploids in *U. europaeus* (Fernández Prieto, Vera et al. 1993) and in the *U. gallii* group (Fernández Prieto, Nava et al. 1993) concentrate mostly on the coastal fringe, suggesting that those species expanded from ancestor refugees on the Atlantic coasts.

3.6. Distribution

From central Norway to Northern Morocco, all the Atlantic countries throughout Europe are involved: Denmark, north-western Germany, The Netherlands, Belgium, Western France, The British Isles and north-western and western Iberian Peninsula (Cross 2003, Díaz González 1998). The limits in the central European area are rather diffuse, as the climatic east-west gradient is gentle and heaths gradually diminish eastwards. In the south, the limits are much sharper, particularly in the Mediterranean Region where heaths are restricted to the numerous rainy areas. A decrease in precipitation means a sudden disappearance of heaths. For that reason, in Northern Spain, heaths still have an impoverished representation in the eastern Pyrenees, but in central and Southern Iberian Peninsula, heaths become scarce and are only found in rainy mountains or in locations with wet soils (Loidi et al. 1997). In eastern Iberia, except the north-eastern corner (Catalonia), heaths are completely absent. Rif mountains in Northern Morocco also exhibit some areas with heathlands in their wet western territories.

4. Results and discussion

In order to search the affinities or groupings of the biogeographic territories, a first PCA ordination with the complete species list was carried out (Fig. 4). In this ordination axis 1 explains the variability due to precipitation. The rainiest temperate climate territories concentrate on the extreme right of this axis, whilst those with mediterranean climate remain on the left. Axis 2 separates units after continentality, the Pyrenean being the most continental one opposite the Atlantic territories.

To check if the groupings suggested by PCA with all species (Fig. 4) were due to species characteristic of other vegetation types (Cisto-Lavanduletea, Querco-Fagetea, Quercetea ilicis, Festuco-Brometea, etc) which can be transgressive to heathland communities, two other PCAs were carried out (Fig. 5 and 6)

The diagram of Fig. 5 is a PCA performed without the Calluno-Ulicetea species. The pattern of Fig. 4 is repeated here: most of the Mediterranean territories such as the Lusitan-Andalusian and the Western Iberian are

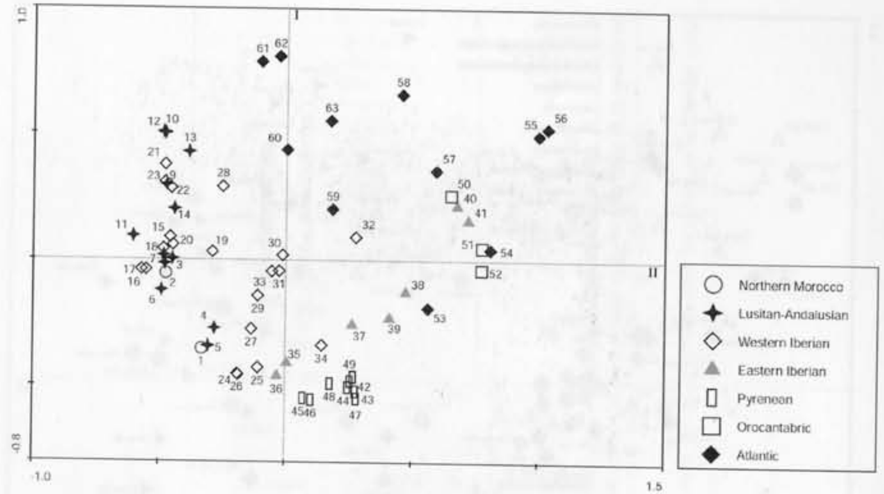


Fig. 4. Ordination (PCA) diagram of biogeographic units. All species present in heathland communities have been used for the analysis.

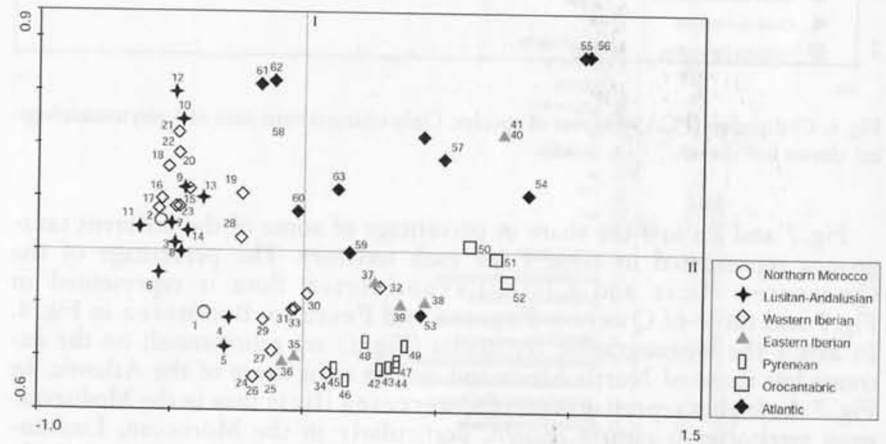


Fig. 5. Ordination (PCA) diagram of biogeographic units. Calluno-Ulicetea taxa have been excluded from the analysis.

opposite the Atlantic and Orocantabric ones along axis 1. The analysis of the taxa in the ordination carried out with the complete species list (Fig. 6) shows a clear segregation between species characteristic of Mediterranean syntaxa (Quercetea ilicis, Cisto-Lavanduletea) and the Eurosiberian ones (Querco-Fagetea, Festuco-Brometea) along axis 1. The rest of the groups (Table 1) add no relevant information in the analysis and have not been represented in the diagram.

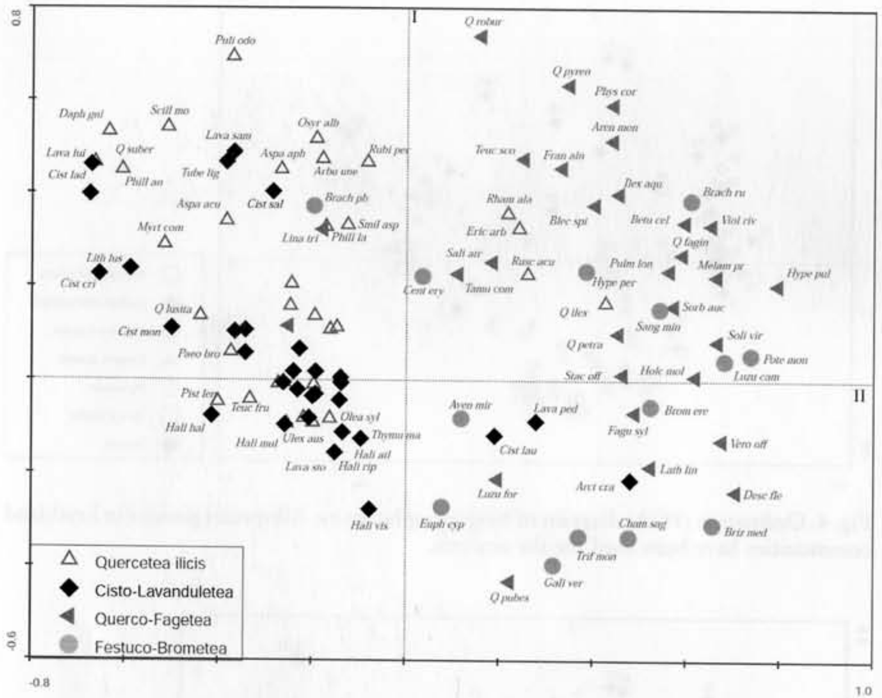


Fig. 6. Ordination (PCA) diagram of species. Only characteristic taxa of 4 phytosociological classes are shown.

Fig. 7 and 8 show the share in percentage of some of the different taxa-groups represented in table 1 for each territory. The percentage of the Quercetea ilicis and Cisto-Lavanduletea flora is represented in Fig. 7 and those of Querco-Fagetea and Festuco-Brometea in Fig. 8. In axis 1 the biogeographic territories (Fig. 1) are represented; on the extreme left those of North Africa and on the right those of the Atlantic. In Fig. 7 the higher representation of Quercetea ilicis taxa in the Mediterranean territories is clearly shown, particularly in the Moroccan, Lusitan-Andalusian and Western Iberian territories, but they are also relatively abundant in the Atlantic units due to the existence of *Quercus ilex* forests. This is also indicated in the diagram of Fig. 6 where species such as *Quercus ilex, Rhamnus alaternus, Erica arborea* and *Ruscus aculeatus* are located on the right hand side of axis 1, together with other plants of Querco-Fagetea and Festuco-Brometea. In the more continental territories such as the Pyrenees, Quercetea ilicis and Cisto-Lavanduletea species are very scarce.

The high percentage of Querco-Fagetea species in the heathland communities of all the temperate territories (Fig. 8) reflects the seral stage condition of the latter in relation to those forests.

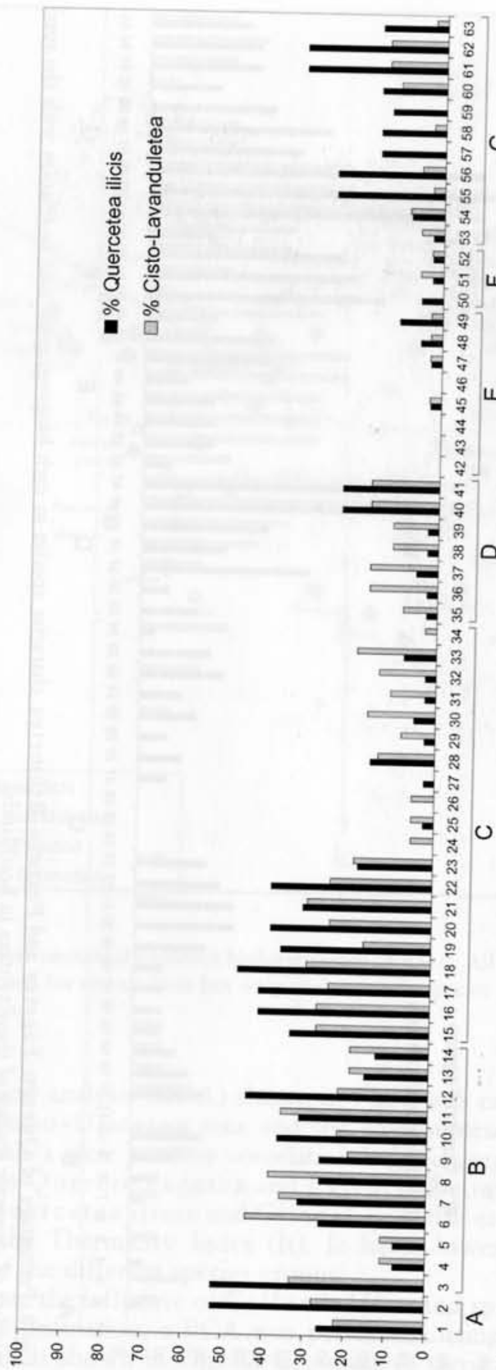


Fig. 7. Percentage of Quercetea ilicis and Cisto-Lavanduletea character species in each biogeographic unit in relation with the total number of character species of these syntaxa in heathlands.

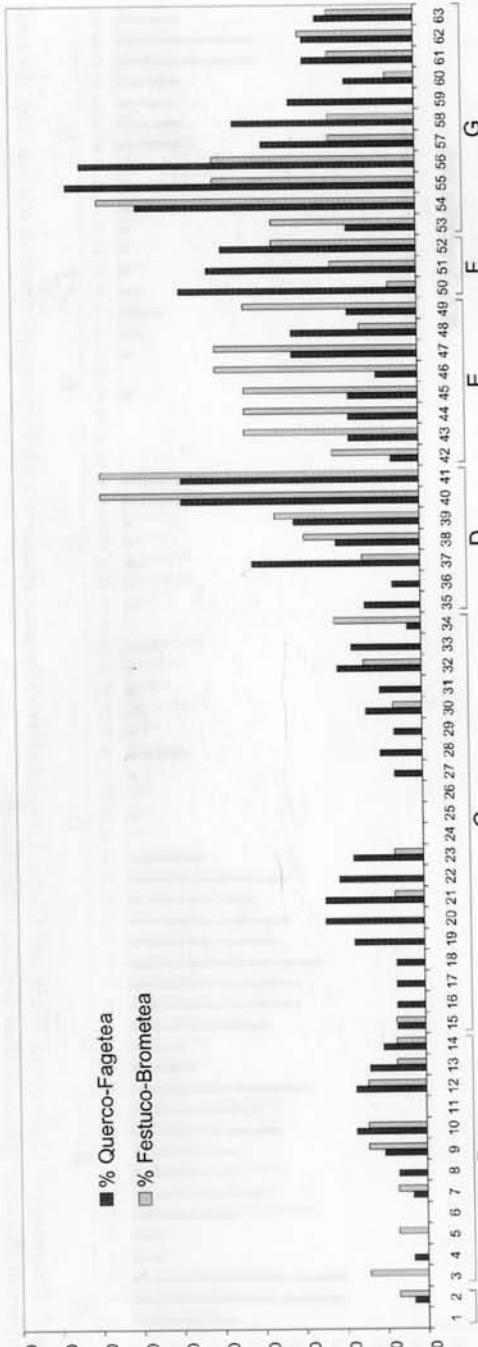


Fig. 8. Percentage of Querco-Fagetea and Festuco-Brometea character species in each biogeographic unit in relation with the total number of character species of these syntaxa in heathlands.

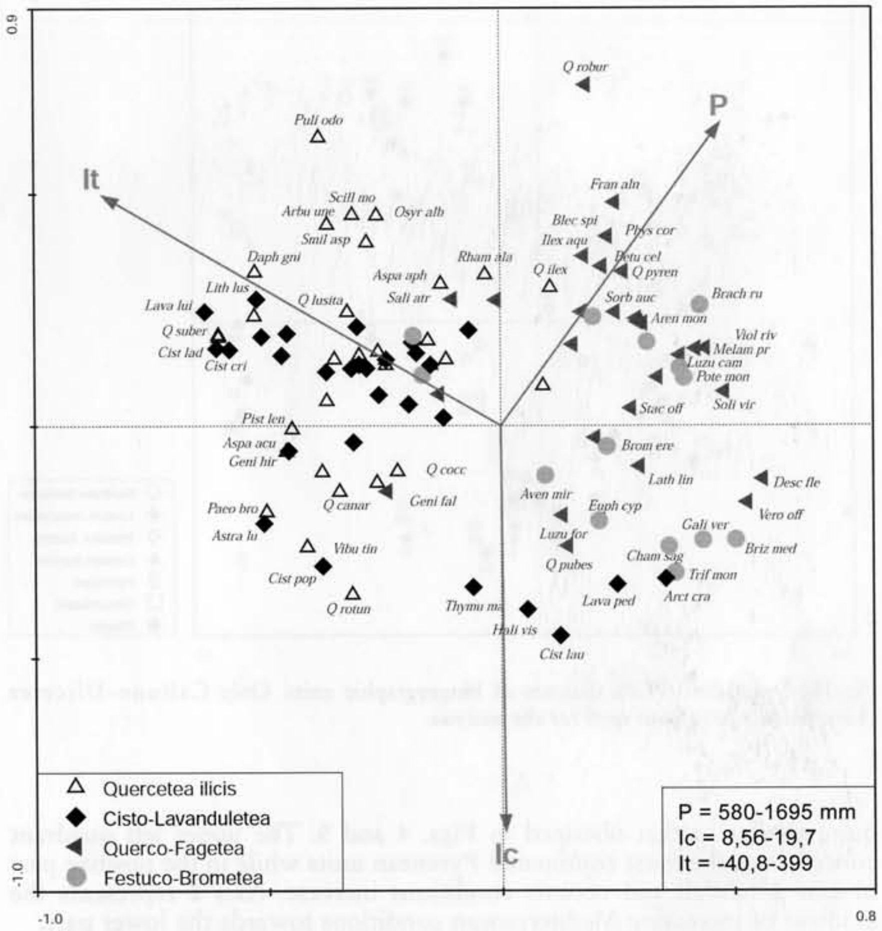


Fig. 9. Species-environmental variables biplot diagram of RDA. All non-Calluno-Ulicetea taxa have been used for the analysis but only characteristic species of 4 phytosociological classes are shown.

The canonical analysis (RDA) shown in Fig. 9 was carried out using all the non-Calluno-Ulicetea taxa and the environmental variables Ic, It and P. It reveals a clear positive correlation between precipitation and the majority of the Querco-Fagetea and Festuco-Brometea taxa. On the other hand, Quercetea ilicis and Cisto-Lavanduletea species are correlated with the Thermicity Index (It). Ic has a lower influence on the distribution of the different species groups.

To investigate the influence of Calluno-Ulicetea species on the biogeographic units ordination, a PCA was performed using only taxa of this class; the result is shown in Fig. 10. Grouping of territories appears to be

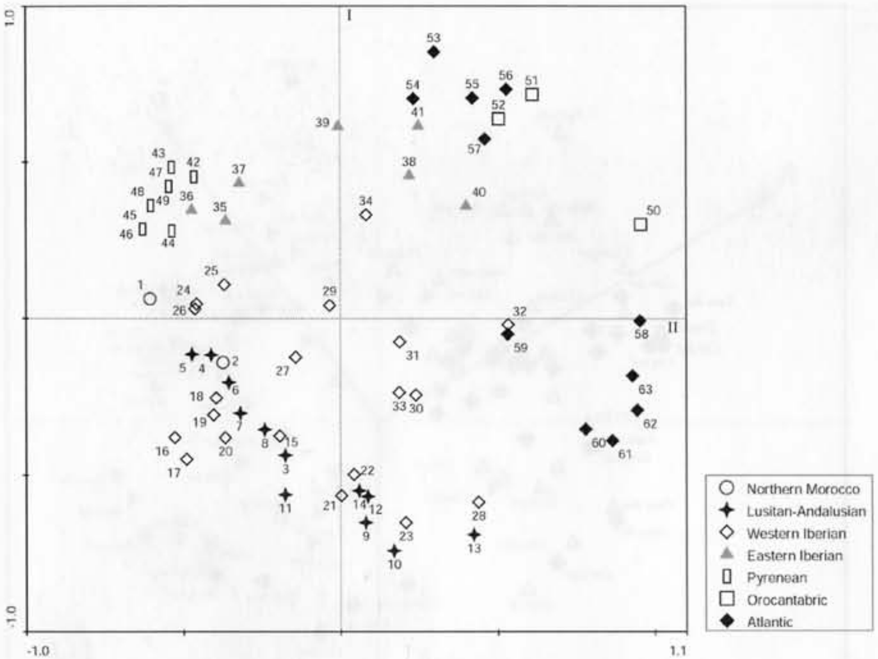


Fig. 10. Ordination (PCA) diagram of biogeographic units. Only Calluno-Ulicetea character taxa have been used for the analysis.

quite similar to that obtained in Figs. 4 and 5. The upper left quadrant concentrates the most continental Pyrenean units while in the positive part of axis 1 rainfall and oceanic conditions increase. Axis 2 represents the gradient of increasing Mediterranean conditions towards the lower part.

Two more canonical analysis (RDA) were carried out using Calluno-Ulicetea species with It, Ic and P. Fig. 11 shows the richness in Calluno-Ulicetea taxa of each territory represented by the size of the corresponding circles (see also the map of Fig. 13). There exists a positive correlation between this richness and the rainfall, as is shown in Fig. 11. On the other hand, Fig. 12 shows the correlation between the biogeographic units and these environmental variables; the Atlantic and Orocantabric units are more correlated with high rainfall, Lusitan-Andalusian and Western Iberian ones with thermicity and Pyrenean and Orocantabric ones with continentality.

Finally, Fig. 14 shows a canonical ordination (RDA) that represents the affinities of the heathland species for the parameters P, Ic and It; it only includes Iberian species characteristic of Calluno-Ulicetea (Moroccan endemics have been removed as there was no climatic data available from that territory in a digital format). Southern taxa such as *Genista tridens* and *Erica australis* are strongly correlated with thermicity (It); rainfall is

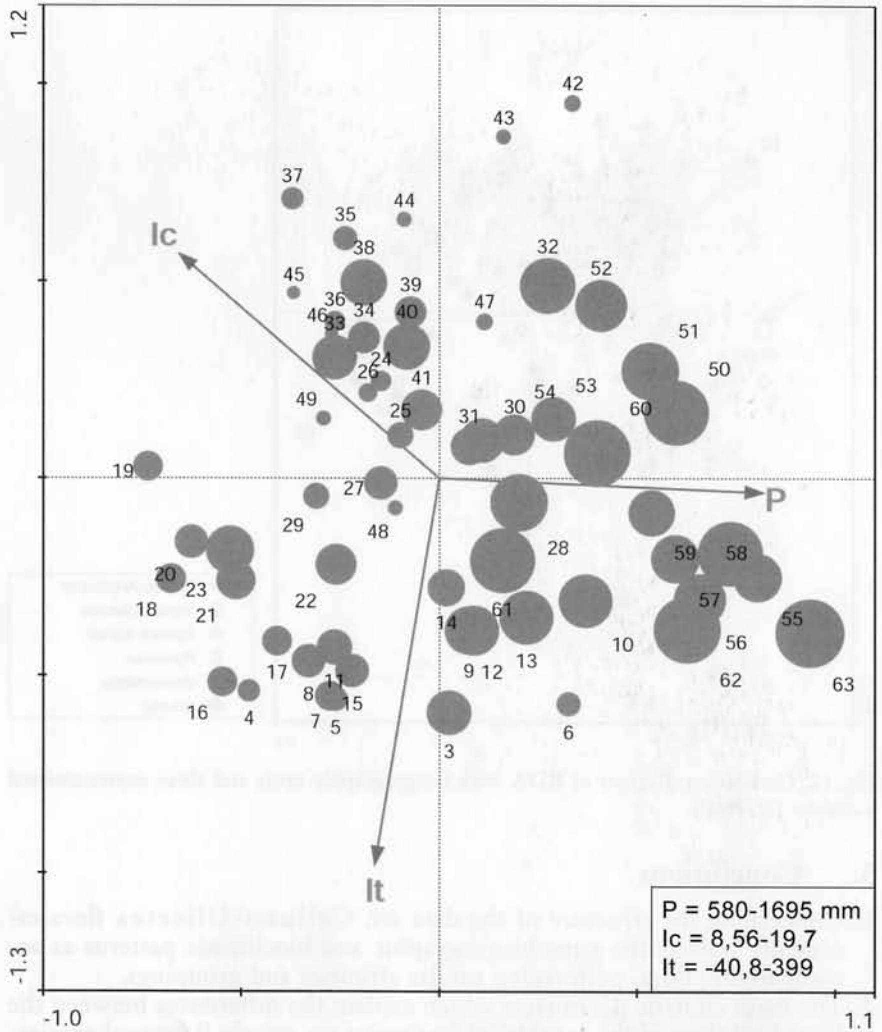


Fig. 11. Biplot diagram of RDA with environmental variables and biogeographic units. Size of symbols corresponds to Calluno-Ulicetea species richness (number of species of Calluno-Ulicetea in each unit).

influencing northern plants such as *Ulex europaeus, Carex asturica, Pseudarrhenatherum longifolium* and *Daboecia cantabrica*, while continentality actually excludes almost all of the plants.

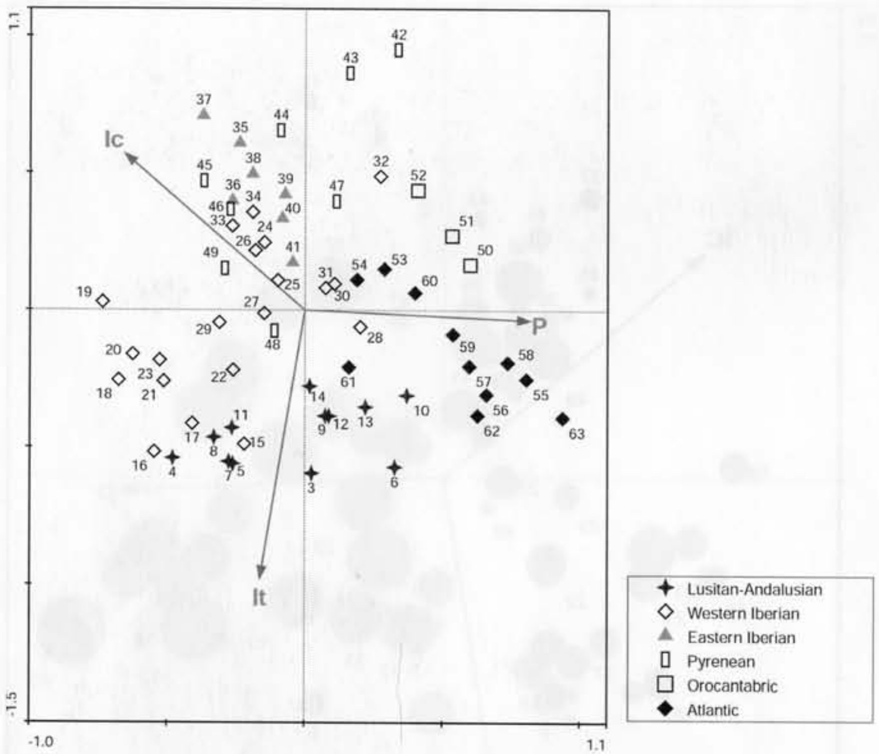


Fig. 12. Ordination diagram of RDA with biogeographic units and three environmental variables (Ic, It, P).

5. Conclusions

1. Concerning the structure of the data set, Calluno-Ulicetea flora essentially reflects the same biogeographic and bioclimatic patterns as accompanying flora, performing similar affinities and groupings.
2. The main climatic parameters which explain the differences between the heathland flora of the considered territories are mostly P (annual precipitation), It (thermicity index) and Ic (continentality index).
3. The richest areas in Calluno-Ulicetea plants are the rainiest ones, located in the Cantabrian and Atlantic areas, and the poorest the most continental ones, particularly in the eastern Pyrenees. Maps of Figs. 2 and 3A compared with the map of Fig. 13 clearly indicate that high rainfall is a very important condition for heaths, particularly in Mediterranean Iberia, as well as strong oceanic conditions. The floristic impoverishment of heaths towards the east and towards Northern Europe is parallel to what has also been reported from genetic variability in *Calluna vulgaris* at a European scale (Mahy et al. 1997) and to the results of the chromosomic studies carried out in *Ulex* (Fernández Prieto,

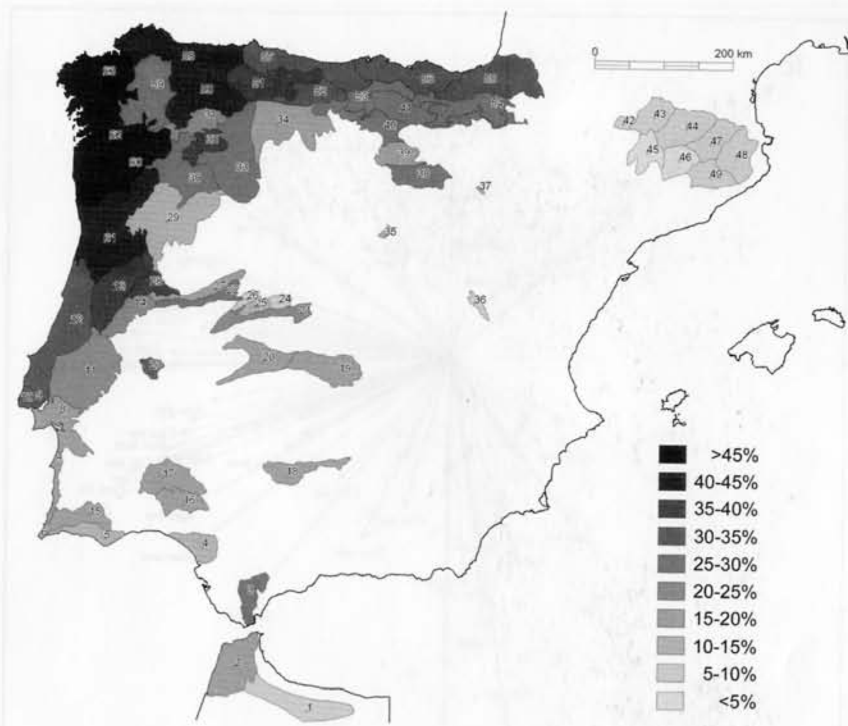


Fig. 13. Calluno-Ulicetea species richness of each biogeographic unit.

Vera et al. 1993, Fernández Prieto, Nava et al. 1993). This statement is a quite generalised opinion (Géhu 2000) and could be related with the Quaternary history of Europe, in which during cold periods this vegetation had to refuge in the coastal shelters of the Southern Atlantic shore, probably located in the Iberian Peninsula. In each of the warm periods (interglacial) it expanded northwards and eastwards, as is the case at the present time, but originating a gradient of impoverishment in terms of the flora and of the genetic variability. In any case, apart from the recent historic considerations, it seems that this vegetation finds its modern climatic optimum in the Cantabrian and Atlantic areas of the Iberian Peninsula.

4. Southwestern and Southern Iberian and Northern Moroccan heaths are only found in exceptionally rainy areas or on wet soils. They are always in contact with Mediterranean xerophytic vegetation (often Cisto-Lavanduletea) and for climatic reasons this vegetation type occupies a reduced surface. In these areas heaths are not so rich in flora as those of the Cantabrian and Atlantic territories, but they bear several endemic taxa suggesting an ancient establishment of this vegetation type. Time and isolation have probably enhanced speciation, but reduction of area

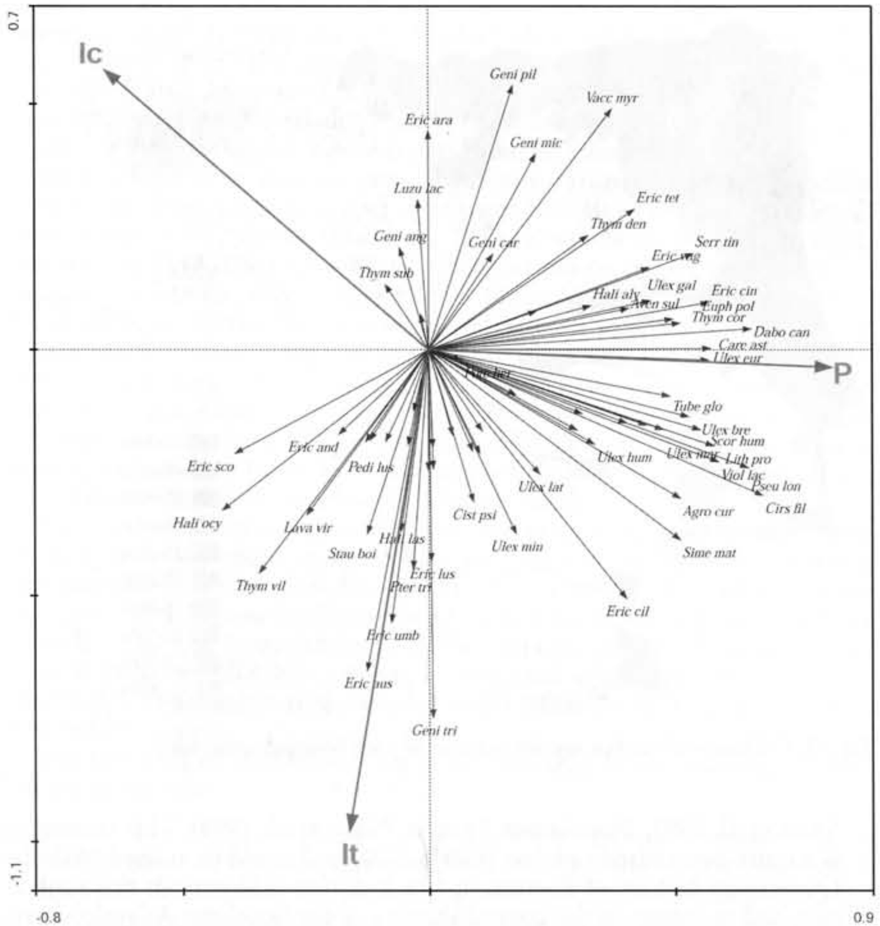


Fig. 14. Biplot diagram of RDA with Calluno-Ulicetea species and environmental variables. Only Calluno-Ulicetea species have been used for the analysis.

and the Mediterranean climatic conditions prevailing for a long time should have impoverished its flora. Human activity expanded both heaths (Calluno-Ulicetea) and *Cistus* scrubs (Cisto-Lavanduletea) on siliceous territories in the southern areas but high fire frequency probably favoured the latter more, enhancing the area reduction of the heaths.

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Annex 1. List of bibliographical sources of the relevés used to form the basic matrix of data

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