

Original article

Natural black pine (*Pinus nigra* subsp *salzmannii*) forests of the Iberian eastern mountains: development of the phytoecological basis for their site evaluation *

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Summary — A phytoecological study of the *Pinus nigra* subsp *salzmannii* forests in the dolomite-limestone mountains of eastern Spain was undertaken. Starting from several floristic and ecological data collected from 355 relevés, classification and ordination numerical analysis were realized. A typification of the different pine forest communities was thus obtained and a series of floristic groups was defined, which can be used as a basis for the classification of distinct sites. Following the phytosociological method, 2 main groups, which can be considered as climax vegetation of the high supra- and mountain-Mediterranean levels, have been defined: a continental group, *Thalictro tuberosi–Pinetum salzmannii*, and a subcontinental group, *Lonicero xylostei–Pinetum salzmannii*, which represents the southern range limit of *Pinus nigra* forests in the eastern Pyrenees.

***Pinus nigra* / numerical analysis / phytosociology / climax / floristic group**

Résumé — Typologie phytoécologique des stations forestières : les forêts naturelles de pin de Salzmann (*Pinus nigra* subsp *salzmannii*) des montagnes orientales ibériques. La présente étude concerne la caractérisation phytoécologique des forêts de *Pinus nigra* subsp *salzmannii* des montagnes orientales de l'Espagne. Des analyses numériques de classification et ordination ont été réalisées avec 355 relevés comprenant des données floristiques et écologiques. La typologie des différents groupements silvatiques de *Pinus salzmannii* a permis d'établir plusieurs groupes floristiques, susceptibles d'être utilisés dans la caractérisation des stations forestières de cette essence. Selon la méthode phytosociologique, ont été distinguées 2 associations qui représentent sûrement la végétation climatique à l'horizon supérieur de l'étage supraméditerranéen et à l'étage montagnard-méditerranéen : *Thalictro tuberosi–Pinetum salzmannii* dans la partie occidentale avec des conditions cli-

* The present work complies with the nomenclature given in Bolos *et al* (1990), Castroviejo *et al* (1986–1993) or Tutin *et al* (1964–1980).

matiques méditerranéo-continentales, et Lonicero xylostei–Pinetum salzmannii dans la partie orientale avec des conditions climatiques sub-continentales. Les forêts de pin de Salzmann qui appartiennent à la dernière association représentent la limite méridionale de ce groupement caractéristique des Pyrénées orientales.

Pinus nigra / analyse numérique / phytosociologie / climat / groupe floristique

INTRODUCTION

Pinus nigra subsp. *salzmannii* has its central core of distribution in the dolomite-limestone mountain ranges of the eastern portion of the Iberian peninsula (Sistema Ibérico) (fig 1), the main forest region of Mediterranean Spain. Exceptionally a relict population stand isolated in areas of the central-western granitic range, representing a special paleogeographic and phylogenetic interest (Regato *et al.*, 1992). The total natural populations of this species extend over approximately 380 000 hectares.

The black pine forests found in the Sistema Ibérico account for two-thirds of the total black pine formations in the Iberian peninsula. Together with *Pinus sylvestris* woods, they represent the most extensive forests of the eastern mountains. While *P. sylvestris* forests have been easily managed, resulting in good even-aged stands, *P. nigra* forests actually have critical problems due in part to the lack of basic understanding about the regeneration biology of this long life species. Furthermore, disturbance processes in the area (geomorphological dynamism, high frequency of storms, *etc*) generally resulting in uneven-aged stands and the random exploitation of woods, carried out since the beginning of the century, contribute to the present open-structured forests.

Historically, major problems have been encountered when trying to establish a site index for the different types of forests. In particular, when stands are not even-aged, have mixed species compositions or have received severe growth damage, problems with site index are greater (Monserud, 1977).

Therefore, a more ecologically oriented site classification, based on phytosociological concepts and approaches, was developed in an attempt to solve some to these specific problems. As a first attempt, Cajander's approach (1926) defines vegetation types meaningful to forest productivity. After this very early work, other vegetation-oriented studies were conducted (Maycock, 1960; Pfister, 1977; Carleton, 1980; Jeglum *et al.*, 1982; Jones, 1984; Kotar, 1984). All efforts have been conducted to develop a better understanding of natural vegetation patterns in order to establish an ecological classification of forest types. This is the basis for carrying out site evaluation in well-established stands inside each forest type.

In a first attempt to analyze the black pine wood area of Spain, Elena-Rosselló and Sánchez-Palomares (1991) found a good relationship between yield and floristic groups. Given the encouraging results of that early evaluation, a more in-depth analysis in the largest territorial area of *P. nigra* (Sistema Ibérico) was conducted (Regato, 1992) in order to characterize the different habitat types of this species, an essential element to determine the potential productivity of the different sites.

Geobotanical background

The most important geobotanic studies were conducted by Willkomm (1844, 1852, 1896), and they provided very accurate descriptions of the main forests of this species. When describing black pine woods along the Sistema Ibérico, he mentioned the exis-

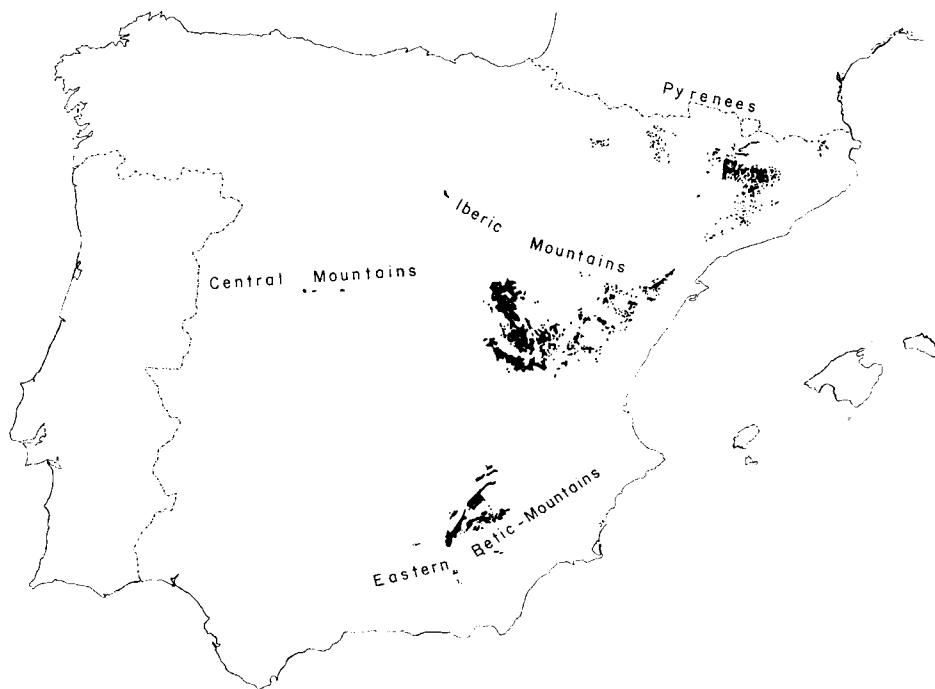


Fig 1. Distribution area of *Pinus nigra* subsp. *salzmannii* in Spain.

tence of pristine forests, which he described as a shady canopy of gigantic trees, including several specimens with an estimated age of more than 1 000 years. As far as the structure and degree of development are concerned, he claimed these woods to be perfectly comparable to the best preserved ones in Central Europe. Twenty years later, the same author regretted the serious degradation of these pine woods; today, it is difficult to find mature formations with an average age of more than 150 years.

Since the beginning of phytosociological studies in Spain, the role of Spanish *Pinus nigra* forests has been undervalued, if not neglected. Gaussen (1945) originally defined a potential vegetation series for the Pyrenees, headed by *P. nigra* subsp. *salzmannii*, while Rivas-Godoy (1946) described a vegetation level, *Pinetum lar-*

ciosis, which is characteristic of the Sistema Ibérico, and located between the upper woods of *Pinus sylvestris* and the mixed oak forests (*Quercus faginea* and *Q. ilex* subsp. *ballota*). Nevertheless, such considerations were eventually invalidated, and the sites occupied by the *Pinus nigra* woods were considered to be either potential oak forests (*Quercus faginea*, *Q. pubescens* and *Q. ilex* subsp. *ballota*) or potential *Juniperus thurifera* steppic forests.

Under this prevailing theory, black pine is just an accessory species in such types of forests, and its populations are considered as a consequence of anthropogenic expansion. Thus, a deep phytosociological and ecological study of these pine woods was largely neglected.

Recently, all over western Europe, woods of *Pinus nigra* subsp. *salzmannii* were reval-

ued and given greater ecological and phytosociological importance in France (Quezel and Barbero, 1988) and in Spain (Gamisans and Gruber, 1988; Gamisans *et al.*, 1991; Elena-Rosselló and Sánchez-Palomares, 1991; Regato, 1992). Starting from a number of historical elements, as well as the ecological, biogeographic and biological features of this species, it is thought that *Pinus nigra* subsp *salzmannii* stands are an important element of the potential vegetation of Spain, defining climatic forests which constitute a special vegetation level. It seems therefore appropriate to revive the initial proposals of Gaussen and Rivas-Goday, and to determine with greater precision the eco-

logical value of *Pinus nigra* in the Spanish vegetation landscape.

Ecological features

The Sistema Ibérico is a range of mountains with moderate high elevations often over 2 000 m, surrounded by high plateaus with an average height of 1 200 m. Most of the *Pinus nigra* forests are located in the supra- and mountain-Mediterranean levels, between 1 000 to 1 500 m, ranging from the lowest points at roughly 400 m, to the highest ones in the oro-Mediterranean level (fig 2). Under particular conditions and in the

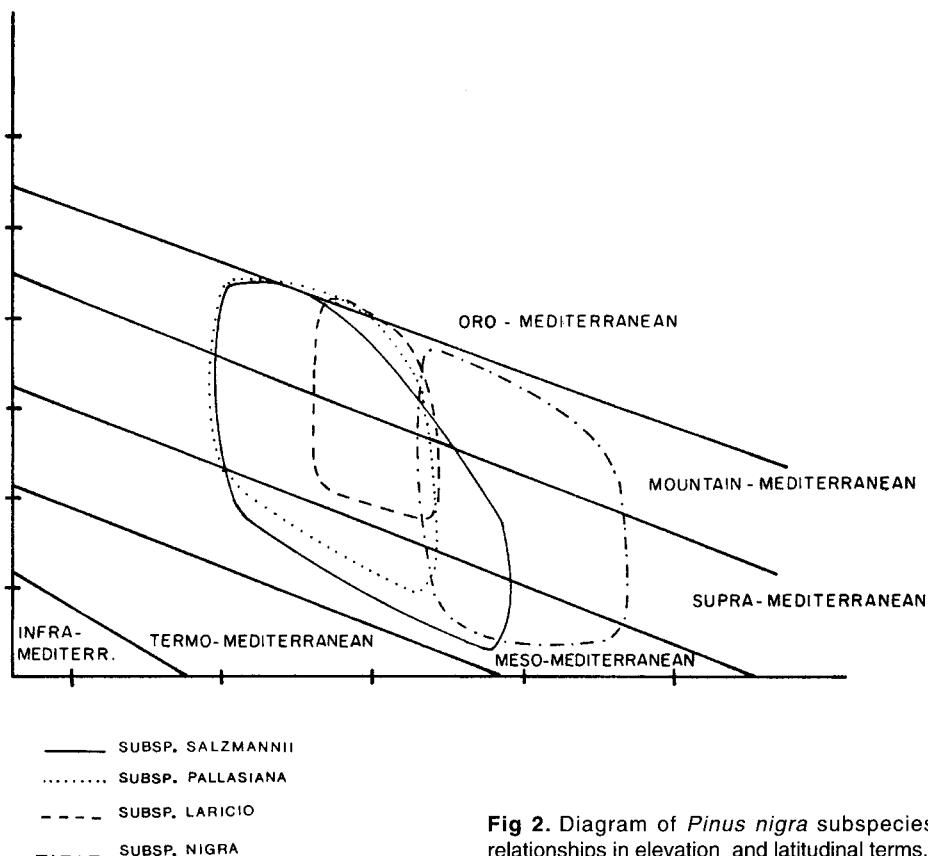


Fig 2. Diagram of *Pinus nigra* subspecies relationships in elevation and latitudinal terms.

southernmost mountains, Sierra de Javalambre, the species reaches the timberline at 1 700–1 800 m.

While most Spanish ranges have a west to east orientation, the Iberic Mountains cross the eastern part of the peninsula from north to south, representing a barrier to the main northwestern rain fronts. As a consequence, the climate becomes highly continental to the core of this mountainous region and results in different characteristics of the water regime between the Mediterranean and the inner face of these mountains.

The physiography of these mountains is particularly affected by the alternance of different lithological types. Karstic elevations prevail, and doline fields, lapiaces and river canyons are frequent. Gravity slopes, upland rocky plains and ridges are mainly made of more or less pure dolomites, while slopes and the floor of the valley are of different lithologic types (limestone, dolomites, marls, sandstone and gypsum), which influence the slope profile.

Soils are poorly developed and mostly superficial, with a prevalence of the rendzina-type (Sánchez-Palomares *et al.*, 1990). According to these authors, in spite of the degree of soil evolution of the black pine woods area, these should be considered as mainly mature, as they represent the edaphic potentiality of such mountains. The abundance of dolomites, which typically have a difficult chemical weathering, makes soil evolution even more difficult.

From the climatic point of view (Regato, 1992), the areas where these pine woods are mainly found have humid and subhumid types of bioclimates, in their "cold" and "very cold" variations (according to Emberger's classification in Daget, 1977) (fig 3). Exceptionally, they can also be found in a semi-arid superior cold bioclimate, corresponding to the lower and more continental areas of its distribution range. According to Allue-Andrade's classification (1990), black pine woods are to be found mainly in the

nemoro-Mediterranean humid (VI(IV)2) and substeppic nemoral (VI(VII)) phytoclimatic types. The most xeric nemoro-Mediterranean type (VI(IV)1) would roughly correspond with the semi-arid bioclimate typical of the lower and most continental areas.

Continentality is remarkable, with winter mean minima temperature as low as -7°C and absolute minima reaching values of -25°C. The frost-free season can be as short as 1 mid-summer month, which also tends to be characterized by a more or less acute hydric deficiency. Under such extreme conditions, the vegetative period is considerably short and, as stated by Walter (1968), evergreen coniferous species take the place of broad-leaf marcescent species.

MATERIALS AND METHODS

Data from 355 forest sites were collected over the full geographic range of *Pinus nigra* in the Sistema Ibérico (Regato, 1992). The sampling method used, that is, preferential sampling (Gauch, 1982), subjectively selects sample sites that appear to be homogeneous and distributes them equitably throughout the black pine study area according to the altitudinal range and to the geomorphological variability. The phytosociological relevés were made using the Braun-Blanquet method (1951). Each relevé represented a comparatively homogeneous area, generally from 200–400 m². Species' cover-abundance values were transformed according to Van der Maarel (1981). Elevation, slope, aspect and proportion of rocks in the surface were calculated for each relevé. Potential solar radiation was calculated using latitude, aspect and slope (Gandullo, 1974).

Polythetic divisive classification was conducted with TWINSPLAN (Hill, 1979) on a data matrix comprising 355 sites x 550 species (Regato, 1992). Subsequently, all final TWINSPLAN dichotomies were explored by detrended correspondence analysis (DCA) (Hill and Gauch, 1980) and canonical correspondence analysis (CCA) (Ter Braak, 1988) to determine to which extent the dichotomies reflected a discontinuity in the site floristic data and their relations with certain variables (Regato, 1992).

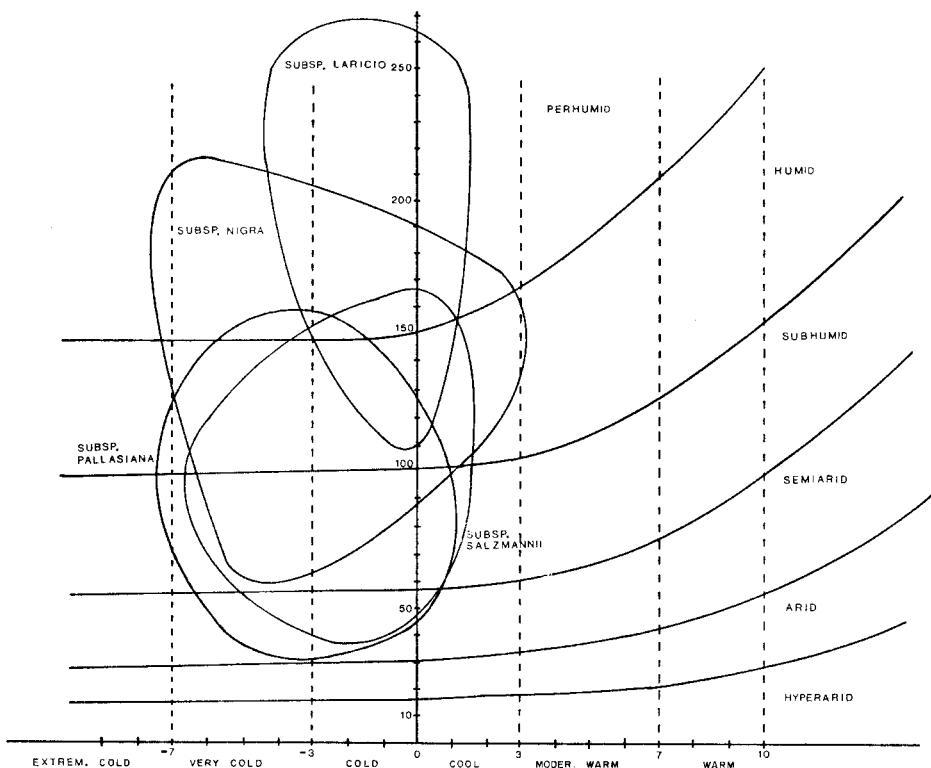


Fig 3. Emberger diagram showing the bioclimatical level ranges of the different subspecies of *Pinus nigra*.

RESULTS

The TWINSPAN classification analysis resulted in 27 different floristic groups. Subsequently, all final TWINSPAN dichotomies were explored using DCA and CCA. On the basis of these ordination analyses, 13 floristic groups were definitively established. The reduction from the initial 27 group classification to the final 13 group classification is represented in figure 4.

The resulting 13 groups are ranked in the dendrogram according to a xerothermic gradient. The first dichotomy in TWINSPAN classification hierarchy distinguishes between black pine forests associated with

sites of mesophilous conditions (cooler and wetter), and generally located at the highest altitude (ranging between 1 100 to 1 500 m), and black pine forest associated with more xerothermic sites (ranging between 900 to 1 100 m).

Some typical species of the bushy formations of the area, *Thymus vulgaris*, *Lavandula latifolia* and *Koeleria vallesiana*, appear as nonindicative of the 2 groups that result in the first division (fig 4). This suggests a certain degradation of the under-story in most black pine woods, particularly those that are subject to heavy timber exploitation. Furthermore, the subrupiculous nature of many of these woods also

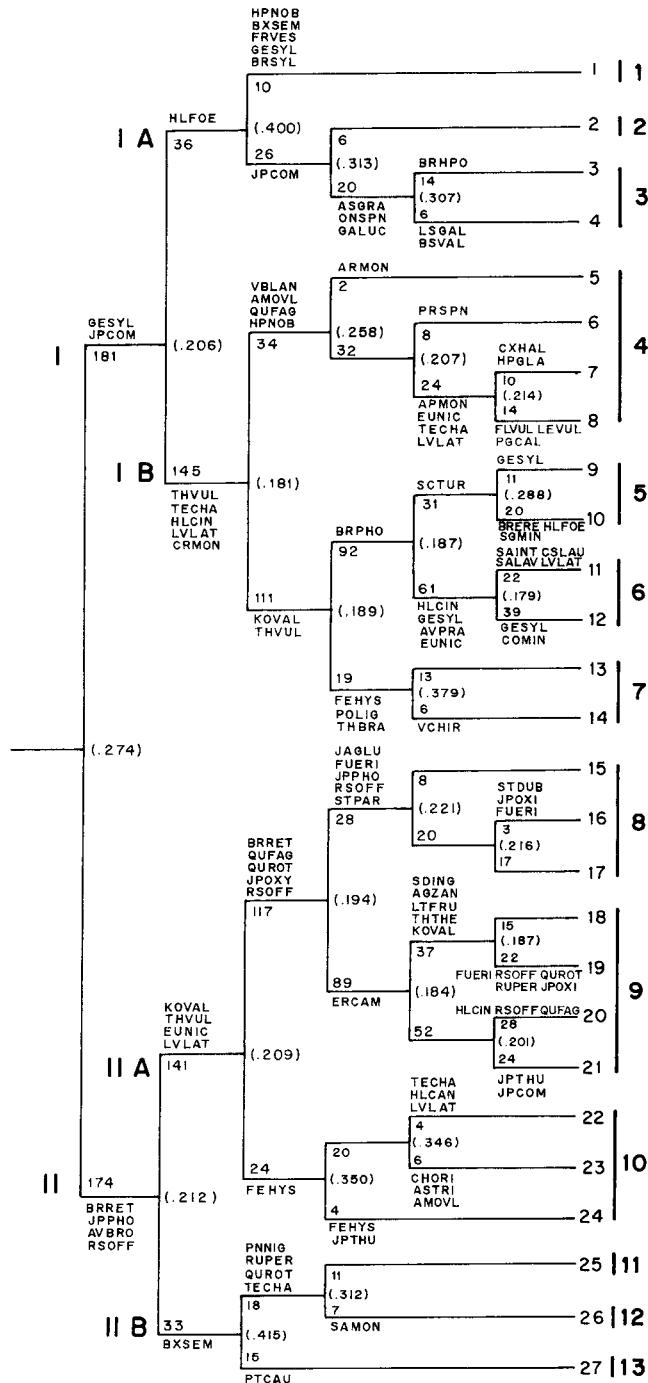


Fig 4. TWINSPAN analysis diagram with indicator species for each division. Codes for the indicator species appear in each dichotomy branch.

contributes to the presence of these species characteristic of open scrub communities.

In the second division level of the classification, both mesophytic and xerothermic sites are divided into 2 groups: a more continental group typical of the inner mountains (western sector), and another group with subcontinental character typical of the ranges closer to the Mediterranean Sea (eastern sector) (fig 4).

These 4 groups resulting from the second tier are separately located in the 4 quarters of the DCA diagram, defined by the first 2 axes. Axis 1 represents a xerothermic gradient, while axis 2 represents a continentality gradient. Therefore, those black pine forests which have good mesophyllous conditions and are typical of the most advanced

phases appear towards the negative values of the axis 1, while those forests which have a more sparse structure appear towards the positive values of the axis (fig 5), being typical of lowest xerothermic areas, where *P. nigra* is found at the limits of its distribution, or of degraded areas where more xerophytic species colonize the sub-canopy.

In the CCA ordination analysis, groups resulting from subsequent divisions of the TWINSPAN classification analysis are the best defined. Such groups are associated to sites with a high proportion of rocky substrates and steep slopes, both factors strongly associated with axis 2. An altitudinal gradient becomes apparent along the axis 1 (fig 6).

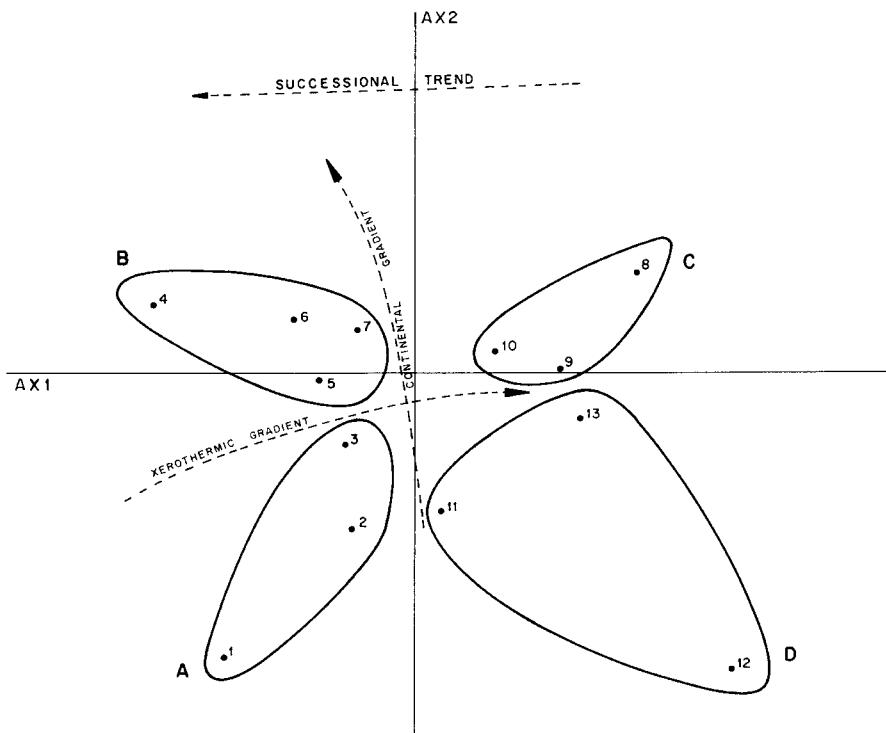


Fig 5. DCA analysis diagram. Numbers indicate the situation of the 13 TWINSPAN site groups. Arrows show the underlying ecological factors. Capital letters indicate the 4 site groups established at the TWINSPAN second level.

Mesophytic black pine woods of the eastern sector: groups 1–3

This grouping includes 40 sites associated to the highest altitude zones of the eastern mountains characterized by the lowest continentality. Frequently, its sites are located in the ubacs, where the comparatively higher air relative moisture attenuates their thermal continentality. Their phytoclimatic type, located between 1 000 and 1 700 m of altitude, is humid nemoro-Mediterranean (VI(IV)2) or substeppic nemoral (VI(VII)). Dolomite substrates are predominant. Sites in groups 1–3 are located mostly in the lower left quarter of the DCA diagram.

Group 1: includes forest formations well vertical-structured and developed, with nemoral understorey, that can be considered as climax vegetation of the high supra- and low mountain-Mediterranean level of the

dolomite-limestone mountains of the western Iberian system (Puertos de Beceite, Maestrazgo and western stations of Gudar and Javalambre sierras). A group of sub-Mediterranean and eurosiberian species characterizes both the scrub and the herbaceous layers, belonging to *Quercetalia pubescantis*, or in a wider scope, to *Querco-Fagetea*. Indicator and preferential species are *Primula veris* subsp. *columnae*, *Hepatica nobilis*, *Brachypodium sylvaticum*, *Fragaria vesca*, *Pteridium aquilinum*, *Acer opalus* subsp. *granatense*, *Sorbus aria*, *Buxus sempervirens*, *Ilex aquifolium*, among others. Mixed forest formations with *Pinus sylvestris*, characteristic of the upper forest level, are very often defined. Due to floristic similarities of black pine woods in this zone with the woods described in the Pyrenees (Gamisans and Gruber, 1988), it can be considered that both belong to the same association, *Lonicero xylostei*-*Pinetum salz-*

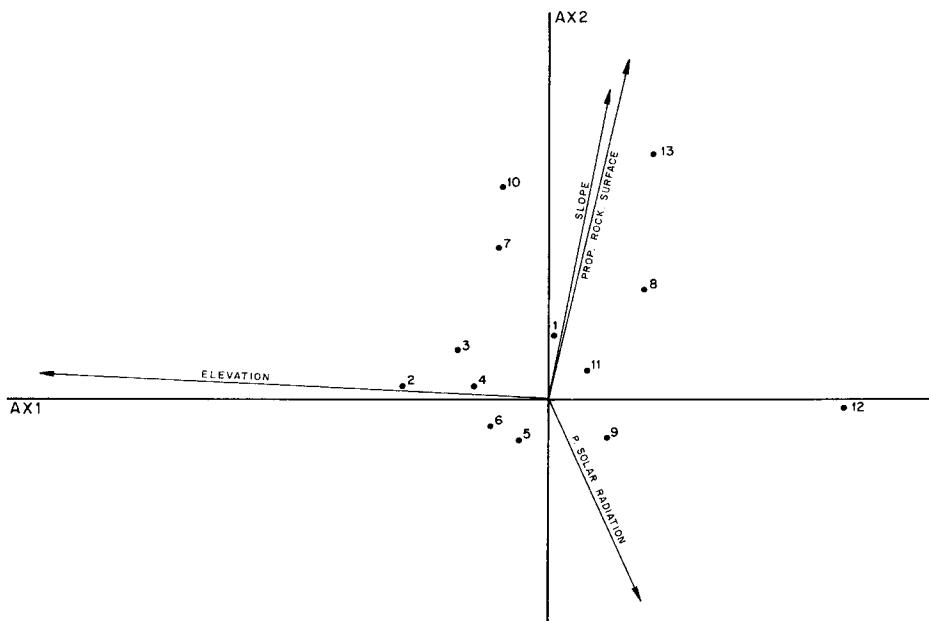


Fig 6. CCA analysis diagram. The situation of the 13 TWINSPAN site groups is indicated by a number. Arrows indicate environmental physical gradients. The isolines suggest 3 groups of site quality: good (I); medium (II); and poor (III).

mannii (table I). Therefore, black pine woods in this group may be a southern expansion from the Pyrenees formations, and represent a transition from these to the more continental ones. Furthermore, some typically Pyrenean species are found in the under-story, and they are representative of their southern limit (*Lavandula angustifolia* and *Teucrium pyrenaicum*).

Group 2: comprises forest formations with an open structure that define the timberline of the western slopes of Javalambre and Camarena sierras, towards Teruel, with cold

and xeric continental climate. These sites are located in the transitional zone from the forest of the more continental western sector to the eastern sector, and therefore their characterization is sometimes difficult. Furthermore, the lack of floristic elements in the under-story makes it difficult to determine their phytosociology. Indicator and differential species show the orophyloous character of such forest formations: *Juniperus sabina*, *Astragalus granatensis*, *Thymus leptophyllus*, etc. High mountain pastures, favored by human intervention, clearly have

Table I. *Lonicero xylostei–Pinetum salzmannii* (Gamisans and Gruber, 1988) (subassociation *genistetosum patentis*; Regato, 1992).

Character- and differential species of the association:

<i>Pinus nigra</i> subsp <i>salzmanni</i>	V	<i>Tanacetum corumbosum</i>	II
<i>Lonicera xylosteum</i>	II	<i>Genista hispanica</i>	II
<i>Helleborus foetidus</i>	V	<i>Cephalanthera rubra</i>	II

Differential species of subas *genistetosum patentis*:

<i>Genista patens</i>	IV	Character-species of <i>Querco-Fagetea</i> :	
<i>Lathyrus filiformis</i>	III	<i>Hedera helix</i>	IV
<i>Juniperus oxycedrus</i>	III	<i>Hepatic nobilis</i>	III
<i>Juniperus phoenicea</i>	III	<i>Pinus sylvestris</i>	III
<i>Thalictrum tuberosum</i>	II	<i>Hieracium aggreg murorum</i>	IV
		<i>Euphorbia amygdaloides</i>	IV
		<i>Cruciata glabra</i>	III
		<i>Brachypodium sylvaticum</i>	III

Differential species vs *Violio-Quercetum fagineae*:

<i>Avenula pratensis</i>	IV	<i>Aquilegia vulgaris</i>	II
<i>Valeriana montana</i>	III	<i>Sanicula europaea</i>	II
<i>Juniperus communis</i>	III	<i>Fragaria vesca</i>	II
<i>Prunella grandiflora</i>	II	<i>Corylus avellana</i>	I
<i>Pteridium aquilinum</i>	III	<i>Ilex aquifolium</i>	I
		<i>Geum sylvaticum</i>	III

Character-species of *Aceri-Quercion*:

<i>Acer opalus</i> subsp <i>granatensi</i>	V	Species of <i>Querceta ilicis</i> :	
<i>Paeonia officinalis</i> subsp <i>humil</i>	III	<i>Quercus ilex</i> subsp <i>ballota</i>	IV
<i>Viola willkommii</i>	III	<i>Rubia peregrina</i>	III
		<i>Rhamnus alaternus</i>	I

Character-species of *Quercetalia pubescantis*:

<i>Buxus sempervirens</i>	V	Other species:	
<i>Amelanchier ovalis</i>	V	<i>Brachypodium retusum</i>	III
<i>Vicia tenuifolia</i>	III	<i>Rosmarinus officinalis</i>	II
<i>Primula veris</i> subsp <i>columnae</i>	II	<i>Bupleurum fruticosens</i>	II
<i>Sorbus aria</i>	II	<i>Euphorbia characias</i>	II
<i>Coronilla emerus</i>	II	<i>Polygala calcarea</i>	III
<i>Sorbus domestica</i>	II		

contributed to the open-structure characteristic of forests of this group.

Group 3: forests located on steepy sites with unstable substrates, and superficial rocks and boulder fields. These conditions favor the establishment of certain subrupiculous taxa, with the subsequent impoverishment of the more sciophilous species. Preferential species are *Festuca gauthieri*, *Amelanchier ovalis*, *Thalictrum tuberosum*, *Sorbus domestica*, *Paeonia officinalis* and *Lonicera xylosteum*. This community has been defined as *festucetosum gauthieri* (Regato, 1992) subassociation of the climax type *Lonicero-Pinetum* (table II).

Mesophytic black pine woods of the western sector: groups 4–7

This grouping comprises 145 sites associated with the most mesophilous conditions of the supra-Mediterranean and Mediterranean mountain belts, between 900 and 1 500 m. The main phytoclimatic type is humid nemoro-Mediterranean (VI(IV)2), with high values of thermic continentality (seasonal extremes of temperature). The characteristic substrate is dolomite-limestone, with an abundant appearance of massive dolomite covering the surface of a high plateau or flat-topped mountain. In the DCA diagram, sites

Table II. *Lonicero xylostei–Pinetum salzmannii* (Gamisans and Gruber, 1988) *festucetosum gauthieri* (Regato, 1992).

Character- and differential species of the association:			
<i>Pinus nigra</i> subsp <i>salzmannii</i>	V	<i>Cruciata glabra</i>	III
<i>Lonicera xylosteum</i>	II	<i>Hepatica nobilis</i>	II
<i>Helleborus foetidus</i>	V	<i>Prunus spinosa</i>	II
		<i>Hedera helix</i>	II
Differential species vs <i>Violo-Quercetum valentiae</i> :			
<i>Juniperus communis</i>	IV	Species of <i>Ononido-Rosmarinetea</i> :	
<i>Avenula pratensis</i>	IV	<i>Euphorbia nicaensis</i>	IV
<i>Knautia arvensis</i>	III	<i>Lavandula latifolia</i>	III
Differential species of subas <i>festucetosum</i> :		<i>Genista scorpius</i>	III
<i>Festuca gautieri</i>	IV	<i>Aphyllantes monspeliensis</i>	II
<i>Lavandula angustifolia</i>	II	<i>Koeleria vallesiana</i>	III
<i>Teucrium pyrenaicum</i>	I	<i>Helianthemum organifolium</i>	II
<i>Thalictrum tuberosum</i>	II	<i>Leuzea conifera</i>	II
Character-species of <i>Quercetalia pubescens</i> :		<i>Potentilla tabernaemontani</i>	II
<i>Amelanchier ovalis</i>	V	<i>Lotus corniculatus</i>	I
<i>Ononis aragonensis</i>	II	<i>Medicago suffruticosa</i>	I
<i>Quercus faginea</i>	II	<i>Galium pumilum</i> subsp <i>pinetorum</i>	III
<i>Tanacetum corymbosum</i>	III		
<i>Berberis vulgaris</i> subsp <i>seroi</i>	II	Other species:	
<i>Buxus sempervirens</i>	I	<i>Quercus ilex</i> subsp <i>ballota</i>	III
<i>Paeonia officinalis</i> subsp <i>humili</i>	II	<i>Brachypodium phoenicoides</i>	
<i>Acer opalus</i>	II	<i>Arrhenatherum elatius</i>	III
<i>Lathyrus filiformis</i>	I	<i>Bromus erectus</i>	II
Character-species of <i>Querco-Fagetea</i> :		<i>Crepis albida</i>	III
<i>Pinus sylvestris</i>	III	<i>Epipactis atrorubens</i>	III
<i>Hieracium aggr murorum</i>	IV	<i>Galium maritimum</i>	II
		<i>Biscutella valentina</i>	III
		<i>Sedum sediforme</i>	II
		<i>Laserpitium gallicum</i>	II
		<i>Centranthus lecoqii</i>	II

included within these groups are located in both higher and lower left quarters.

Group 4: includes all those black pine forests in the western sector which have the best structure and development and can thus be considered the climax or mature vegetation under these specific ecological conditions. These are mainly located in ubacs, although it should be considered that this might depend on the fact that adrets tend to be managed by humans for cattle-raising and agricultural purposes. The understory is characterized by the abundance of sub-Mediterranean and central-European scrub and herbaceous species. Among indicator and preferential species are *Viburnum lantana*, *Ligustrum vulgare*, *Buxus sempervirens*, *Rosa pimpinellifolia*, *Thalictrum tuberosum*, *Lathyrus filiformis*, *Geranium sanguineum* and *Phyteuma orbiculare*. Such pine forests have been described as a new association, *Thalictrum tuberosi – Pinetum salzmannii* (Regato, 1992), which is considered as the potential vegetation type of the high supra- and low mountain-Mediterranean levels on the mountains of the western Iberian Range (Serranía de Cuenca, Montes Universales and western side of Sierra de Gúdar), (table III). The main phytoclimatic type is the nemoro-Mediterranean humid, VI(IV)2.

Group 5: includes those mesophytic black pine forests of a more steppic nature, which are typical of the transitional mountains between the western and eastern sectors. These are situated around the very cold and xeric depression of Teruel. Substeppic nemoral, VI(VII), is the main phytoclimatic type and limestone-marl substrates prevail. In several sites, the sparse structure of the forest is due to intensive human management. The understory is poorer in sub-Mediterranean species, while species of the bushy formations are more frequently found. Among indicator and preferential species are *Astragalus granatensis*, *Avenula pratensis*, *Festuca rubra*, *Scabiosa turolensis*, *Brachypodium phoenicoides* and *Avenula bromoides*. This can well be considered as a

variation of group 4 climatic wood, which has been defined as the subassociation *astragletosum granatensis* (Regato, 1992) of the climax type *Thalicstro-Pinetum* (table IV).

Group 6: includes mesophytic black pine forests adapted to steppic conditions. These are typical of the highest areas of plateaus and hilly uplands, which share with the steppic *Juniperus thurifera* forests. Pine woods are mainly placed on dolomite substrates, while Juniper formations tend to develop in limestone-marl areas. *Juniperus thurifera* is quite common in the pine wood subcanopy tree layer, where the sub-Mediterranean bushy element becomes rare. Among their indicator and preferential species are *Brachypodium sylvaticum*, *Geum sylvaticum*, *Lathyrus filiformis*, *Prunus spinosa*, *Rosa pimpinellifolia*, *Hepatica nobilis*, *Berberis vulgaris*, *Buxus sempervirens*, *Thymus bracteatus*, etc. This can be considered as a geomorphological variation of the typical mature pine woods of group 4, to more extreme climatic conditions in the upland plains and flat-topped mountains. This formation has been defined as *juniperetosum thuriferae* (Regato, 1992) subassociation of the climax type *Thalicstro-Pinetum* (table V).

Group 7: includes subrupicolous black pine forests of dolomitic gravity slopes and rocky plains, with abundant dolomite-limestone indicator taxa. This is clearly differentiated in the CCA diagram. The black pine has a very irregular development, and hardly ever constitutes a proper canopy. Indicator and preferential species are *Jasonia glutinosa*, *Juniperus phoenicea*, *Stipa offneri*, *Fumana ericoides*, *Alyssum lapeyrouesianum*, etc.

Xerophytic pine forests of the western area: groups 8–10

This grouping comprises 140 sites found in the lowest altitude ranges of the southern and western portion of the Serranía de Cuenca, where the xeric nemoro-Mediterranean

ranean type (VI(IV)1) is the main phytoclimatic. Under such climatic conditions, *Pinus nigra* finds its ecological limit and gives origin to moderately developed formations. These tend to have a sparse structure, mainly due to anthropic action as well as to the subrupicolous features of several sites. Such structure favors a xerothermic nature of the wood understory. *Quercus faginea*

and *Quercus ilex* subsp *ballota* are frequently present in the tree layer, as the zone is ecotonal with the woods of such oak species. Among indicator and preferential species, only xerothermic taxa of bushy formations, such as *Rosmarinus officinalis*, *Brachypodium retusum*, *Juniperus phoenicea*, *Salvia lavandulifolia*, *Satureja intricata* and *Erinacea anthyllis* can be found.

Table III. *Thalictro tuberosi–Pinetum salzmannii* (Regato, 1992).

Character and differential species of the association:		Character-species of Querco-Fagetea:
<i>Pinus nigra</i> subsp <i>salzmannii</i>	V	<i>Crataegus monogyna</i>
<i>Thalictrum tuberosum</i>	IV	<i>Hepatica nobilis</i>
<i>Lathyrus filiformis</i>	IV	<i>Geum sylvaticum</i>
<i>Sorbus aria</i>	IV	<i>Polygonatum odoratum</i>
		<i>Cornus sanguinea</i>
Differential species vs <i>Cephalanthero-Quercetum fagineae</i> :		<i>Viola reichenbachiana</i>
<i>Rosa pimpinellifolia</i>	IV	<i>Lonicera xylosteum</i>
<i>Juniperus communis</i>	IV	<i>Aquilegia vulgaris</i>
<i>Ononis aragonensis</i>	II	<i>Corylus avellana</i>
<i>Filipendula vulgaris</i>	III	<i>Brachypodium sylvaticum</i>
<i>Avenula pratensis</i>	III	<i>Sanicula europaea</i>
		<i>Hedera helix</i>
Character-species of Aceri-Quercenion:		<i>Cephalanthera rubra</i>
<i>Acer monspessulanum</i>	IV	<i>Lonicera peryclimenum</i>
<i>Quercus faginea</i>	III	<i>Clematis vitalba</i>
<i>Bupleurum rigidum</i>	II	<i>Ulmus glabra</i>
<i>Paeonia officinalis</i> subsp <i>humilis</i>	III	<i>Tilia platyphyllos</i>
		<i>Vicia tenuifolia</i>
Character-species of Quercion pubescenti-petraeae:		<i>Silene nutans</i>
<i>Phyteuma orbiculare</i>	III	
<i>Leucanthemum vulgare</i>	IV	Species of Aphyllantion:
<i>Rhamnus saxatilis</i>	III	<i>Catananche coerulea</i>
<i>Campanula rapunculoides</i>	II	<i>Aphyllantes monspelliensis</i>
<i>Saponaria ocymoides</i>	I	<i>Lotus corniculatus</i>
<i>Lonicera etrusca</i>	I	<i>Potentilla tabernaemontani</i>
<i>Buxus sempervirens</i>	II	<i>Anthyllis montana</i>
<i>Sorbus domestica</i>	II	
<i>Helleborus foetidus</i>	I	Other species:
Character-species of Quercetalia pubescenti-petraeae:		<i>Arrhenatherum elatius</i>
<i>Amelanchier ovalis</i>	V	<i>Brachypodium phoenicoides</i>
<i>Viburnum lantana</i>	IV	<i>Euphorbia nicaensis</i>
<i>Ligustrum vulgare</i>	IV	<i>Teucrium chamaedrys</i>
<i>Primula veris</i> subsp <i>columnae</i>	IV	<i>Rubia peregrina</i>
<i>Geranium sanguineum</i>	III	<i>Hippocratea glauca</i>
<i>Berberis vulgaris</i> subsp <i>seroi</i>	III	<i>Lavandula latifolia</i>
<i>Tanacetum corymbosum</i>	III	<i>Genista scorpius</i>
<i>Vicia onobrycioidea</i>	II	<i>Bromus erectus</i>
<i>Prunus mahaleb</i>	II	<i>Koeleria vallesiana</i>

The almost complete absence of nemoral species in the understory and the frequent appearance of *Quercus* species make it very difficult to characterize these ecotonal sites, where *Pinus/Quercus* mixed forest is most likely their foreseeable forest type.

Xeromesophytic pine forests of the eastern section: groups 11–13

This grouping includes 33 sites found in the lower elevation areas of the dolomitic ranges

Table IV. *Thalictrum tuberosi–Pinetum salzmannii astragaletosum granatensis* (Regato, 1992).

Character-species of the association:			
<i>Pinus nigra</i> subsp. <i>salzmannii</i>	V	<i>Thymus leptophyllus</i>	II
<i>Thalictrum tuberosum</i>	III	<i>Potentilla cinerea</i>	II
<i>Lathyrus filiformis</i>	II	<i>Polygala calcarea</i>	II
		<i>Festuca hystrix</i>	II
		<i>Juniperus sabina</i>	I
Differential species of subas <i>astragaletosum</i> :			
<i>Astragalus granatensis</i>	IV	Character-species of <i>Ononido-Rosmarinetea</i> :	
<i>Festuca gautieri</i>	II	<i>Lavandula latifolia</i>	V
<i>Astragalus hypoglottis</i>	III	<i>Koeleria vallesiana</i>	IV
<i>Juniperus thurifera</i>	III	<i>Euphorbia nicaensis</i>	IV
		<i>Potentilla tabernaemontani</i>	IV
Diff species vs <i>Cephalanthero-Quercetum fagineae</i> :			
<i>Juniperus communis</i>	V	<i>Aphyllantes monspeliensis</i>	III
<i>Rosa pimpinellifolia</i>	III	<i>Sanguisorba minor</i>	IV
<i>Avenula pratensis</i>	IV	<i>Thymus vulgaris</i>	IV
<i>Knautia arvensis</i>	III	<i>Genista scorpius</i>	II
		<i>Scabiosa turolensis</i>	IV
		<i>Santolina chamaecyparissus</i>	III
Character-species of <i>Quercetalia pubescens</i> :			
<i>Amelanchier ovalis</i>	IV	<i>Salvia lavandulifolia</i>	II
<i>Helleborus foetidus</i>	V	<i>Avenula bromoides</i>	II
<i>Tanacetum corymbosum</i>	III	<i>Leuzea conifera</i>	III
<i>Ononis aragonensis</i>	III	<i>Catananche coerulea</i>	II
<i>Leucanthemum vulgare</i>	II	<i>Medicago suffruticosa</i>	II
<i>Silene nutans</i>	III	<i>Digitalis obscura</i>	II
<i>Acer opalus</i>	I	<i>Galium verum</i>	II
<i>Vicia tenuifolia</i>	II	Other species:	
<i>Teucrium chamaedrys</i>	V	<i>Arrhenatherum elatius</i>	V
		<i>Bromus erectus</i>	IV
Character-species of <i>Querco-Fagetea</i> :			
<i>Pinus sylvestris</i>	III	<i>Brachypodium phoenicoides</i>	IV
<i>Crataegus monogyna</i>	III	<i>Ononis spinosa</i>	II
<i>Hieracium aggr. murorum</i>	II	<i>Carex humilis</i>	II
<i>Cruciata glabra</i>	II	<i>Hieracium pilosella</i>	II
<i>Viola reichenbachiana</i>	III	<i>Campanula hispanica</i>	II
<i>Rosa nitidula</i>	II	<i>Dactylis glomerata</i>	II
<i>Hepatica nobilis</i>	I	<i>Brachypodium retusum</i>	II
		<i>Festuca rubra</i>	II
Species of <i>Erinacetalia</i> :			
<i>Thymus bracteatus</i>	III	<i>Asperula cynanchica</i>	III
<i>Festuca hystrix</i>	III	<i>Hieracium pilosella</i>	II
<i>Centaurea pinæ</i>	II	<i>Ononis tridentata</i>	I
<i>Erinacea anthyllis</i>	II	<i>Biscutella valentina</i>	II
		<i>Erysimum grandifolium</i>	II

Table V. *Thalictrum buterosi–Pinetum salzmannii juniperetosum thuriferae* (Regato, 1992).

Character-species of the association:			
<i>Pinus nigra</i> subsp. <i>salzmannii</i>	V	<i>Poa ligulata</i>	I
<i>Thalictrum tuberosum</i>	III	<i>Ranunculus gramineus</i>	I
<i>Lathyrus filiformis</i>	III	<i>Stipa officinalis</i>	+
		<i>Dianthus hispanicus</i>	I
		<i>Erinacea anthyllis</i>	I
Differential species of the subas <i>juniperetosum</i> :			
<i>Juniperus thurifera</i>	III	Species of <i>Ononio-Rosmarinetea</i> :	
<i>Thymus bracteatus</i>	IV	<i>Genista scorpius</i>	III
<i>Berberis vulgaris</i> subsp. <i>seroi</i>	IV	<i>Lavandula latifolia</i>	V
<i>Prunus spinosa</i>	III	<i>Euphorbia nicaensis</i>	V
		<i>Potentilla tabernaemontani</i>	IV
Differential species vs <i>Cephalanthero-Quercetum fagineae</i> :			
<i>Juniperus communis</i>	V	<i>Helianthemum cinereum</i>	IV
<i>Avenula pratensis</i>	II	<i>Coronilla minima</i>	III
<i>Filipendula vulgaris</i>	III	<i>Koelleria vallesiana</i>	IV
<i>Rosa pimpinellifolia</i>	III	<i>Medicago suffruticosa</i>	II
		<i>Aphyllantes monspelliensis</i>	III
		<i>Lotus corniculatus</i>	II
Character-species of <i>Quercetalia pubescens</i> :			
<i>Amelanchier ovalis</i>	III	<i>Helianthemum apenninum</i>	II
<i>Buxus sempervirens</i>	II	<i>Sanguisorba minor</i>	II
<i>Paeonia officinalis</i> subsp. <i>humilis</i>	II	Other species:	
<i>Quercus faginea</i>	II	<i>Arrhenatherum elatius</i>	V
<i>Cephalanthera damasonium</i>	I	<i>Thymus vulgaris</i>	IV
<i>Cephalanthera longifolia</i>	I	<i>Anthyllis vulneraria</i>	I
<i>Limodorum abortivum</i>	II	<i>Hippocratea glauca</i>	II
<i>Rhamnus saxatilis</i>	II	<i>Teucrium chamaedrys</i>	III
<i>Acer monspessulanum</i>	I	<i>Polygala calcarea</i>	II
<i>Vicia onobrychoides</i>	I	<i>Trifolium campestre</i>	II
<i>Leucanthemum vulgare</i>	II	<i>Achillea odorata</i>	III
<i>Orchis mascula</i>	I	<i>Erysimum grandiflorum</i>	II
		<i>Bromus erectus</i>	I
Character-species of <i>Querco-Fagetea</i> :			
<i>Geum sylvaticum</i>	IV	<i>Brachypodium phoenicoides</i>	I
<i>Crataegus monogyna</i>	IV	<i>Dactylis glomerata</i>	II
<i>Rosa sicula</i>	V	<i>Thapsia villosa</i>	III
<i>Brachypodium sylvaticum</i>	III	<i>Acinos alpinus</i>	II
<i>Pinus sylvestris</i>	I	<i>Biscutella valentina</i>	I
<i>Hieracium aggr. murorum</i>	IV	<i>Carex hallerana</i>	II
<i>Viola reichenbachiana</i>	II	<i>Hieracium pilosella</i>	I
<i>Hepatica nobilis</i>	I	<i>Globularia vulgaris</i>	I
<i>Sanicula europaea</i>	+	<i>Asphodelus cerasifer</i>	II
<i>Fragaria vesca</i>	I	<i>Phlomis lychnitis</i>	II
		<i>Marrubium supinum</i>	I
Differential species of the com with <i>G mugronensis</i> :			
<i>Festuca hystrix</i>	II	<i>Carduus assoi</i>	I
<i>Genista mugronensis</i>	I	<i>Eryngium campestre</i>	II
<i>Arenaria obtusiflora</i>	II	<i>Lithodora fruticosa</i>	I
<i>Cerastium brachypetalum</i>	II	<i>Santolina chamaecyparissus</i>	I
		<i>Vicia pyrenaica</i>	+

in the proximity of the coast. Escarpments and canyons are common, producing very heterogeneous site conditions. Group 11 has the most nemoral conditions, and can be considered as a xerothermic variation of the mature black pine woods of the eastern sector, *Lonicero–Pinetum* subassociation *genistetosum patentis* (Regato, 1992) (table I). There is a considerable amount of mesophytic taxa in the understory, but with a lower abundance index. The presence of species such as *Juniperus oxycedrus*, *Juniperus phoenicea*, *Bupleurum fruticosens* and *Brachypodium retusum* indicates their xeromesophytic character.

Groups 12 and 13 are clearly differentiated in the CCA diagram. The former includes the most thermic sites of black pine formations in the Sistema Ibérico, and it should be considered as azonal open communities with the worst growth potential. The latter group comprises the subrupliculous sites, where the canopy hardly exists, and where trees have an irregular distribution over the rocky slopes.

DISCUSSION AND CONCLUSION

Black pine forests have their ecological optimum between the supra- and mountain-Mediterranean levels of these dolomite-limestone ranges, under a very cold humid nemoro-Mediterranean continental phytoclimate. Under these conditions, the potential for growth of *Pinus nigra* is better than that of other species. In the Sistema Ibérico, there are 2 climax communities, the more continental one, *Thalictro–Pinetum salzmannii*, located in the western part (groups 4–6) and the less continental one, *Lonicero–Pinetum salzmannii*, located in the eastern part (groups 1, 3 and 11), similar to the black pine woods of the Pyrenees.

The indicator species group of the best sites is a combination of sub-Mediterranean and central-European taxa. Some of the most common characteristics are:

<i>Sorbus aria</i>
<i>Hepatica nobilis</i>
<i>Rosa pimpinellifolia</i>
<i>Lathyrus filiformis</i>
<i>Juniperus communis</i>
<i>Thalictrum tuberosum</i>
<i>Lonicera xylosteum</i>
<i>Primula veris</i> ssp <i>columnae</i>
<i>Viburnum lantana</i>
<i>Sanicula europaea</i>
<i>Amelanchier ovalis</i>
<i>Geum sylvaticum</i>
<i>Buxus sempervirens</i>
<i>Avenula pratensis</i>
<i>Acer opalus</i> ssp <i>granatensis</i>
<i>Brachypodium sylvaticum</i>

These woods, included in Cl *Querco-Fagetea* (or, *Quercetalia pubescantis*), represent the ecological optimum (with real nemoral understory conditions and well vertical-structured canopy) of extensive areas that were previously established as potential sites of more xerophytic vegetation (*Juniperus thurifera* cold steppic woods and *Quercus ilex* subsp *ballota* thermic woods).

In these climax communities, we can distinguish 2 site types:

- 1) Those stands associated with the hilly uplands, where the subcanopy is dominated by the herbaceous layer. The arbustive layer is poor and integrated by the most continental species (*Juniperus communis*, *Rosa pimpinellifolia* and *Berberis vulgaris* subsp *seroi*). This type has the best site quality, particularly over convex reliefs or plains. In the floor of some doline fields, the growth rate of *Pinus nigra* is very high. Nevertheless, soil conditions in these sites have an unstable equilibrium, often broken by overgrazing and clear-cutting practices. Consequently, important soil losses and problems in tree regeneration will arise. The abundance of *Juniperus thurifera* in the tree layer can be considered a good index for determining the worst conditions of these kind of sites. Such bad conditions are frequently related to the concave reliefs.

2) Those stands are associated with the steepy sites on karstic valleys and canyons. The understory is dominated by the arbustive layer. They have a good site quality despite their usually uneven-aged structure. This depends on the heterogeneous conditions of the substrate (rocks, boulder fields, steep slopes). Although the growth potential of black pine is good, the canopy structure may not be uniform. The proportion of subruplicicolous taxa can be used as an indicator value of the potential heterogeneous canopy.

The characteristics landform in the Sistema Ibérico is the "cantil-talud" (gravity slope-pediment) system, where intense geomorphologic dynamics occur (Calvo, 1987). The slope retreat maintains the verticality of the cliff. The mixed pine/oak woods growing in pediments with best edaphic conditions are modified by rock avalanches. These dolomitic blocks remove the soil, increasing dolomites and rock surface proportion. Under such conditions, black pine plays an important role in stabilizing and restoring the site conditions.

At the oro-Mediterranean level of the southern mountains (Sierra Javalambre) (group 2), the characteristic cold climate becomes more xeric, tending to steppic conditions. The indicator taxa are dwarf scrubs (eg *Juniperus sabina*, *J hemisphaerica*, *Prunus prostrata* and *Astragalus granatense*), revealing an open structure of the wood. Nevertheless, these scrubs offer protection to the black pine saplings and to the few nemoral species that only grow below them. Pines have a medium growth potential and, according to Elena-Rosselló and Sánchez-Palomares (1991), their site quality appears to be average.

A high proportion of characteristic species of *Oniondo–Rosmarinetea* bush communities reveal a somewhat extensive understory degradation. In the mountain-Mediterranean level, this usually reveals anthropical degradation (overgrazing; cleaning and thinning processes) and it is difficult to deter-

mine its site quality. Highest degradation is revealed with the appearance of *Festuco-poetalia* species (eg *Festuca hystrix*, *Poa ligulata*, *Arenaria erinacea* and *Globularia repens*), which show strong soil denudation (groups 7 and 10). The black pine usually shows special growth limits with a characteristic table-shaped crown.

The presence of taxa typical of more xerothermic bush communities (*Rosmarino-ericion*) (eg *Rosmarinus officinalis*, *Helianthemum hirtum*, *Coris monspeliensis* and *Brachypodium retusum*) is considered as being evidence of the lowest site quality. This generally corresponds to sites where *Pinus nigra* has its ecological limit on the lowest xerothermic slopes (groups 8 and 9). These species are also typical of sites which correspond to rocky or eroded adrets at a higher elevational level.

In the eastern subcontinental sector, the worst site quality corresponds to the lowest sites, where azonal black pine communities are defined, having an open structure and a predominant *Quercetea ilicis* species under-story (group 12).

This phytoecological classification has made it possible to recognize *Pinus nigra* climax communities, representing the potential vegetation for this mountain region. Once the potential area and ecological optima for *Pinus nigra* are established, a precise basis for determining the quality of its different site types is available.

When analyzing the TWINSPAN dendrogram, several interesting conclusions were obtained. At the first division level, climax *Pinus nigra* sites were separated from the azonal ones. In its second level, both site types were divided into 2 groups according to regional climate reasons: the subcontinental types, located in the eastern sector, and the continental types in the western sector. Lower divisions can only be understood when taken into account physiographic factors, showing the landform patterns of the regional geomorphological typical structure.

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