Pirineos, **131**: 25 a 42, JACA, 1988

STRUCTURE OF MOUNTAIN PINE (*PINUS UNCINATA* RAMOND) POPULATION AT TIS UPPER LIMIT IN CENTRAL PYRENEES [1]

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SUMMARY.— The structure of forest-alpine tundra ecotone is studied, by means of the analysis of data taken along five slopes in Central Pyrenees.

Four growth forms are typified on Mountain Pine (Pinus uncinata *Ramond): pyramidal-trees, flagged-trees, open-mats and closed mats. Pyramidal-trees and closed-mats are zonal phenomena, being the extremes of the altitudinal-sequence; nevertheless, flagged-trees and open-mats are local phenomena not subjected to a clear zonality.*

The stunted growth forms (closed and open-mats) show differences in ecology and structure among themselves. The name "elfin wood" is proposed for former and the term "krummholz" for the latter.

RESUMEN.— Se estudia la estructura del límite superior del bosque en el Pirineo mediante el análisis de los datos obtenidos a lo largo de cinco laderas del Pirineo Central.

Cuatro formas de crecimiento en el pino negro (Pinus uncinata *Ramond): árboles piramidales, árboles bandera, matas abiertas y matas cerradas. Arboles piramidales y matas cerradas se manifiestan como fenómenos zonales, marcando los extremos de la serie altitudinal. Arboles bandera y matas abiertas son, sin embargo, fenómenos locales, no sometidos a una zonalidad clara. Entre las formas achaparradas (matas cerradas y abiertas) se aprecian diferencias de ecología y estructura. Se propone el nombre de "elfin wood" para las primeras y el de "krummholz" para las segundas.*

RÉSUMÉ.— Nous étudions la structure de la limite supérieure de la forêt sur la base de l'analyse des données obtenues dans cinq parcelles del Pyrénées Centrales. Le pin à crochets (Pinus uncinata *Ramond), unique essence présente, nous montre quatre formes de croissance: arbre pyramidal, arbre en drapeu, arbre*

1 Received November, 1988.
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rampant ouvert et arbre rampant fermé. La première et dernière classes se montrent comme un phénomen "zonal", marquant les deux extrêmes de la série altitudinale. Au contraire, les arbres en drapeau et rampants ouverts nous paraissent phénomenes locaux, non soumises a une claire zonalité. Aussi nous apprécions entre les deux types d'arbres rampants une certaine différence écologique et structurale. Pour les arbres rampants fermés nous proposons la qualification d'"elfin wood", tandis que pour les ouverts il est plus convenable le concept de "krummholz".

The transition between forest, which is dominant in montane and sub-alpine zones, and alpine tundra is one of the most conspicuous biological boundaries.

Environmental factors that determine the tree survival limit do not perform equally in all mountain ranges. This fact does not depend on climatic conditions only, but also on the physiological response of the plant.

Sometimes, the change of limiting environmental variables is constant along an altitudinal axis before reaching a critical value. This happens, as WALTER & MEDINA (1969) explains, at the upper forest limit of the tropical mountains in Venezuela, where soil temperature is close and negatively correlated to altitude. This parameter is not subjected there to seasonal variations because of proximity to the Equator. The trees ability to form roots becomes diminished when soil temperature reaches the critical value of 7-8° C, and tree growth is not possible in such conditions.

On the other hand, freezing during spring nights is the reason for the upper limit of *Eucalyptus pauciflora* in the Snowy Mountains of Southwestern Australia (SLATYER, 1976).

In both situations the survival of *mature* trees may depend on a *single* factor, and their upper location may be predicted by means of an isotherm.

Under other circumstances, environment does not restrict directly the survival posibilities of mature trees but those of seedlings, as occurs with *Pinus canariensis* on Teide's slopes (Canary Island) (HÖLLERMANN, 1978). The high thermal variation of the soil surface (abs. diary range of 40° C and abs. annual range of 60° C) limits the regeneration capacity to shadowy places, under the large specimens, where contrast is deadened and dryness is not so extreme. Recruitment is sufficient to ensure a low population density, so, the upper forest border looks like an open pinery formed by large trees with no deformation signals.

In temperate regions, limit does not obey a single factor but various, which have as negative influence on the regenerative capacity of populations as on the survival of mature trees. This fact conditions the kind of upper forest boundary described in the Rocky Mountains (WARDLE, 1968; MARR, 1977) and in the Alps (TRANQUILLINI, 1979).

Three biological frontiers might be distinguished here:

—An upper limit of forest communities *(timberline),* where the subalpine wood is replaced by an open formation with scarce density. According to FRANKHAUSER (1901) isolated trees receive more light and heat in this way than remaining in a closed stand; this ensures greater productions than those expected at such altitude. Perhaps advancement of the growth period can be considered also, because of faster soil heating.

—An upper limit for well-developed trees *(treeline).* Isolated trees suffer more intensely the abrasive effect of ice particles carried by wind during winter (HADLEY & SMITH, 1983, 1986) and this deforms them, giving them a flagged appearence.

—An upper *species limit* (HUSTICH, 1966) or *krummholz limit* (TRANQUILLINI, 1976), where the survival capacity of specimens that reach higher altitudes is conditioned by the high "frost-drought" incidence (ELLENBERG, 1966; TRANQUILLINI, 1967, WARDLE, 1971), that causes death by desiccation of shoots projected above the snow (GOLDSMITH & SMITH, 1926, MICHAELIS, 1934). Unfavourable hydric balance is related to low soil temperature, which impedes water absorption by roots (AULITZKI, 1961), and to an excessive cuticular transpiration (BAIG et al., 1974) conditioned by an inadequate development of the cuticle in the *short and cool sub-alpine summer* (BAIG & TRANQUILLINI, 1976); so, at this moment, vegetative period duration is considered the reason for the limitation of species. Trees subjected to a continuous pruning of parts not covered by snow develop a stunted growth form, denomitated by the German term "krummholz" or the English "elfin wood" (HOLTMEIER, 1981).

The lack of studies related to the structure of the upper forest limit in the Pyrenees (formed, in natural conditions by a single species, the mountain pine, *Pinus uncinata* Ramond) has motivated this work. Correspondence between the boundary structure and environmental factors is so narrow that the knowledge of its physiognomy will be useful to understand its functioning.

1. Materials and methods

1.1. *Description of the study areas*

We selected five study areas over the sub-alpine and oro-mediterranean levels of the Central Pyrenees, by means of aerial photography and succesive field prospections. Three of the slopes studied belong to the calcareous massifs (Sayerri, basic sandstones scattered by limestone; Collarada and Las Cutas, karstic) and two (Respumoso and Néouvielle) are granite mountains. Most of them are exposed to the south, so experience considerable exposure to the sun, out of the montane atlantic level with its frequent clouds.

As we said the only tree we find in the high Pyrenees is the mountain pine, *Pinus uncinata,* showing a different undergrowth on the oro-mediterranean and sub-alpine areas. The first group (Sayerri, Collarada and Las Cutas) exhibits a very open forest, together with some shrubs as *Juniperus communis, J. sabina* and *Arctostaphylos uva-ursi,* not far from the paches of *Buxus sempervirens* or the spiny coussinets of *Echinospartum horridum* bellow; in addition, dry and stony pastures of *Festuca gautieri* cover the 50 % of the surface.

On the other hand, the sub-alpine sites (Respumoso and Néouvielle) may develop a more dense wood and there we also find a close undergrowth formed by *Rhododendron ferrugineum, Vaccinium myrtillus, V. uliginosum, Empetrum hermaphroditum, Sorbus chamaemespilus* and so on; now the snow cover is longer, especially on the concave places and *Arctostaphylos uva-ursi* becomes rare and is situated only in convexities. Pastures on these slopes are formed by the prickly endemic *Festuca eskia.*

With regard to their conservation state, only the upper limit in Respumoso, Néouvielle and Las Cutas can be considered as unaffected by human activities. The ecotone in Sayerri is the most influenced; the upper forest limit was downed to favour grass development and trees are now recolonizing it. The interest in studying this area was to compare the structure in such a situation with that of natural conditions.

1.2. *Data collection*

Slopes were traversed to examine altitudinal changes presented in the structure of mountain-pine populations, and 200 m^2 plots were established along transects starting above the timberline.

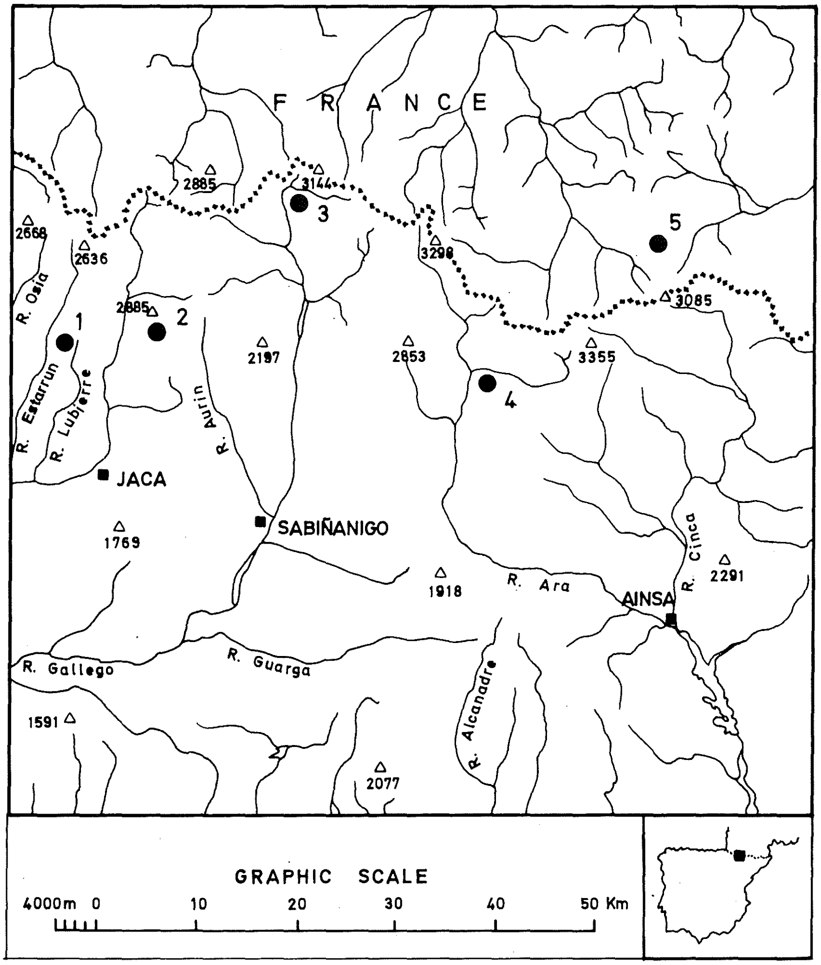

Figure 1. Study areas: 1) Sayerri (Valle de Aísa), Spain. 2) Collarada (Villanúa), Spain. 3) Respumoso (Sallent de Gállego), Spain. 4) Las Cutas (Torla), Spain. 5) Néouvielle (Aragnouet), Hautes Pyrénées, France.

Position and number of transects depend on the wideness of the transition-zone (band of slope between forest —and species— limit), according to structural changes of the mountain pine populations.

The following information was taken in each of those sampling plots:

—Altitude, aspect and bedrock type.

—Structure of the population: density, by counting stems; maximum and minimum tree height (estimated with relascope or ruler); presence or absence of contagious distribution of trees. This observation was made taking into account the main pattern of the altitudinal band in which the sampling plots were situated.

—Pine geometry: The number of specimens belonging to the different forms were registered. The types used in this classification were as follows:

* *Pyramidal-trees,* those which show a well-developed form, with no signs of lesion.

* *Flagged-trees,* having a monopodial growth form and showing a clear asymmetry, with branches bearing live needles only on one side.

* *Open-mats,* stunted trees with large dimensions (more than 200 cm of main crown axis). They have various prostrate stems that become vertical at their distal end.

* *Closed-mats,* smaller and more solid than the open ones with a lot of short branches densely grouped. This kind of growth form coincides with that named "elfin wood" in literature.

—Direction of pine asymmetry, relating it to the maximum slope gradient.

—Presence of dead wood and aborted summits in pines.

—Presence of seedlings in the plot (all specimens less than 10 years old were included).

1.3. *Data organization before analysis*

Some of the information, taken as explained above, was organized as a matrix with 26 observations and 12 qualitative or semiquantitative type variables (see table 1). The meaning of each variable is explained in table 2. Moreover, as additional information, we offer, in table 3, other data related to every plot, no used in the analysis.

Criteria chosen to express the semiquantitative variables as classes, are the following:

—The absolute altitude (m. a.s.l.) at each plot was assigned to one of the six following classes:

1.900 - 2.000 m. a.s.l.	class 1
2.001 - 2.100 m. a.s.l.	class 2
2.101 - 2.200 m. a.s.l.	class 3
2.201 - 2.300 m. a.s.l.	class 4
2.301 - 2.400 m. a.s.l.	class 5
2.401 - 2.500 m. a.s.l.	class 6

Table 1:

Data matrix for analysis

Location	*Las Cutas*				*Respumoso*							*Collarada*				*Sayerri*				*Néouvielle*						
Plot number	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*17*	*18*	*19*	*20*	*21*	*22*	*23*	*24*	*25*	*26*
Var. 1	3	3	3	3	3	4	4	4	5	6	6	2	1	1	1	2	2	1	1	1	3	4	4	5	5	6
Var. 2	4	3	3	1	2	2	2	3	4	4	4	4	3	3	1	4	4	2	1	1	2	2	3	3	3	4
Var. 3	0	1	1	1	1	1	1	1	1	1	0	0	1	1	1	0	1	0	1	1	1	1	1	1	0	0
Var. 4	0	0	1	3	2	0	0	0	0	0	0	0	0	4	5	0	3	2	5	2	0	0	2	5	0	0
Var. 5	0	2	3	2	3	2	2	0	0	0	0	0	2	0	0	0	4	1	0	0	0	2	0	0	2	0
Var. 6	0	0	0	0	2	5	5	5	5	5	2	0	0	0	0	0	0	0	0	5	5	5	5	0	0	0
Var. 7	5	5	4	0	0	0	0	0	0	5	5	5	5	3	0	5	0	4	0	0	0	0	0	0	5	5
Var. 8	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0	1	1	1	0	0	0	1	0	0	1	1
Var. 9	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0
Var. 10	1	1	1	1	1	1	1	1	1	0	1	0	1	0	0	1	1	1	0	1	0	1	1	0	1	1
Var. 11	1	1	1	0	1	1	1	1	1	1	1	1	1	1	0	1	0	1	0	1	1	1	1	0	1	1
Var. 12	0	0	1	1	0	1	1	0	1	0	0	0	0	1	1	1	1	1	1	1	0	0	0	1	0	0

TABLE 2.

Meaning of variables used in the analysis

Variable 1:	Absolute altitude (m. a.s.l. expresed as classes from 1 to 6).
Variable 2:	Relative altitude. It locates each sampling plot into the altitudinal range of the transition-zone.
Variable 3:	Presence or absence of contagious distribution of trees.
Variable 4:	Pyramidal-trees.
Variable 5:	Flagged-trees.
Variable 6:	Open-mats.
Variable 7:	Closed-mats.
Variable 8:	Presence of asymmetry in pines not coinciding with the maximun slope gradient.
Variable 9:	Presence of asymmetry in pines coinciding with the maximun slope gradient.
Variable 10:	Presence of dead wood in pines.
Variable 11:	Presence of aborted summits in pines.
Variable 12:	Presence of seedlings into the plot.

—The relative altitude code, that aims to locate each samplig site in the altitudinal range of the transition-zone, was obtained as follows:

$$\frac{\text{Plot abs. alt.} - \text{Timberline alt.}}{\text{Species limit alt.} - \text{Timberline alt.}} \times 100$$

This relation reaches a value close to 1 when the plot is near the species limit, and close to 0 when it is near the timberline. The value obtained as a percentage was grouped in four classes with 25 % amplitude.

—Variables related to tree growth form expressed as classes too, by grouping the frecuency values (as percents of the population total) in 6 categories.

Absence 0
To 15 % 1
15-25 % 2
25-50 % 3
50-75 % 4
75-100 % 5

TABLE 3

Information not presented in Data Matrix

Plot	*Bedrock*	*m. a.s.l.*	*aspect*	*density (200 m ^{2})*	*max/min tree high*	*Observations*
1	limestone	2.170	S-SW	5	80/45	species limit
2	limestone	2.160	S-SW	9	220/50	transition between treeline and species-limit
3	limestone	2.160	S	22	600/30	treeline
4	limestone	2.150	S	10	500/40	between timberline and treeline
5	granite	2.170	S-SW	17	550/120	near treeline; pyramidal and flagged-trees with some open mats.
6	granite	2.220	SW	5	260/40	open-mats with some flagged-trees.
7	granite	2.220	SW	9	400/180	open-mats on glacier shoulder. Presence of a flagged-tree.
8	granite	2.300	SW	2	220/90	open-mats on glacier shoulder.
9	granite	2.360	SW	5	140/30	open-mats on glacier shoulder.
10	granite	2.420	SW	1	80/80	closed-mat. Near species-limit.
11	granite	2.480	SW	3	270/50	closed-mat and a flagged-tree. Near species-limit.
12	limestone	2.030	S-SW	3	120/50	at species-limit.
13	limestone	2.000	SW	3	400/60	closed-mat and flagged-trees. Near species-limit.
14	limestone	2.000	SW	6	700/40	pyramidal-trees with tendence to become flagged.
15	limestone	1.940	S-SW	11	700/90	open stand of pyramidal-trees.
16	flysch	2.050	W-NW	14	90/15	species-limit.
17	flysch	2.050	NW	26	200/15	pyramidal-and flagged-trees.
18	flysch	2.000	W	6	100/15	pyramidal-and flagged-trees and closed mats.
19	flysch	1.990	W-NW	17	700/25	only pyramidal-trees. Treeline
20	granite	1.940	NW	22	500/150	open-mats in avalanche channel.
21	granite	2.130	E-NE	5	250/120	open-mats on glacier cirque bottom.
22	granite	2.230	E-NE	2	190/100	open-mats. Convexity in glacier cirque bottom
23	granite	2.280	E-SE	3	320/110	cliffs of glacier cirque.
24	granite	2.320	E-NE	9	550/80	pyramidal-trees. Treeline.
25	granite	2.350	E-NE	3	260/60	flagged-trees and closed-mats near species-limit.
26	granite	2.500	NE	7	180/100	closed-mats. Species-limit.

TABLE 4

Results of Contingence Analysis

	contingence type	*degree of freedom*	*G value*	*square Chi value (a = 0,025)*
Var. 4 - Var. 1	2 × 6	5	9,06	12.832
Var. 5 - Var. 1	2 × 6	5	7,78	12.832
Var. 6 - Var. 1	2 × 6	5	13,94	12.832
Var. 7 - Var. 1	2 × 6	5	11,61	12.832
Var. 4 - Var. 2	2 × 4	3	10,70	9.348
Var. 5 - Var. 2	2 × 4	3	8,42	9.348
Var. 6 - Var. 2	2 × 4	3	6,78	9.348
Var. 7 - Var. 2	2 × 4	4	10,91	9.348
Var. 6 - Var. 7	2 × 2	1	15,40	5.024
Var. 6 - Var. 9	2 × 2	1	27,06	5.024
Var. 6 - Var. 12	2 × 2	1	0,02	5.024
Var. 7 - Var. 9	2 × 2	1	17,90	5.024
Var. 7 - Var. 4	2 × 2	1	2,80	5.024
Var. 4 - Var. 12	2 × 2	1	8,02	5.024
Var. 4 - Var. 5	2 × 2	1	0,08	5.024
Var. 5 - Var. 6	2 × 2	1	0,02	5.024
Var. 5 - Var. 7	2 × 2	1	0	5.024

1.4. *Data Analysis*

Three different statistic procedures were used for data analysis. The first was a correspondence factorial analysis. This procedure aimed to detecting tendences in data by ordering both plots and variables in the same axis. The second was a binary cluster, to define which variables of those analyzed are more important to group plots. The last was a contingence analysis, to define the dependence degree among those outlined variables.

A correspondence factorial analysis was done from data in table 1. Observations and variables were ordered by means of axis 1 and 2 obtained from this procedure (see fig. 2).

A 2 × 2 binary cluster (association analysis) was done to classify the plots in similarity groups (see fig. 3). A new and simplified matrix, where all variables were qualitative, was also prepared. So, the semiquantitative variables were transformed by means of the following criteria:

—Absolute altitude.
less than 2.200 m. a.s.l. 0
more than 2.200 m. a.s.l. 1

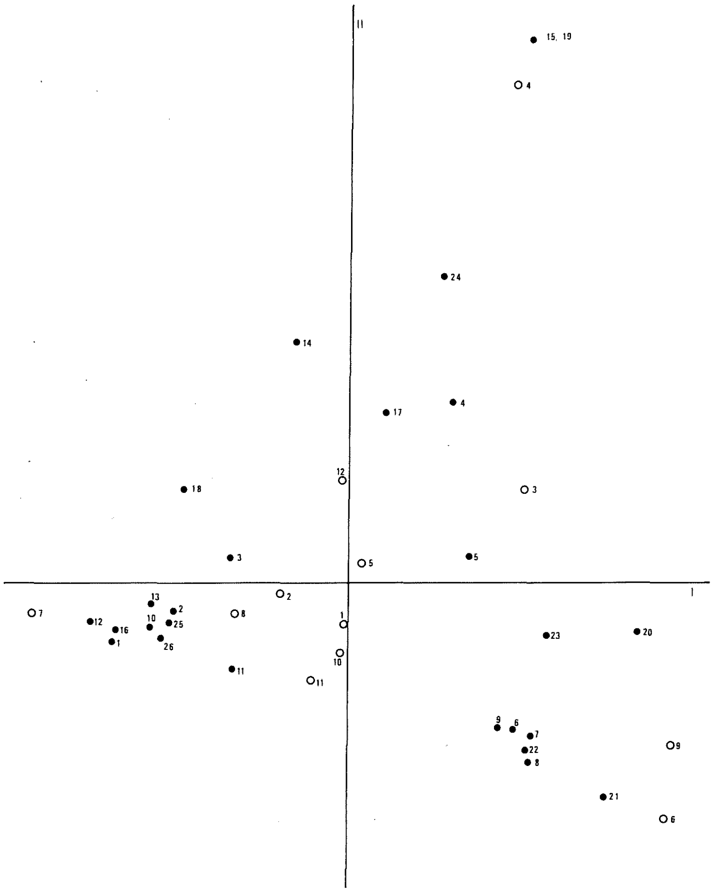

Figure 2. Representation of axis 1 and 2 from correspondence factorial analysis. Points are plots, circles are variables. *(Representación de los ejes 1 y 2 del análisis factorial de correspondencias. Los puntos representan observaciones, los círculos representan variables).*

The limit chosen coincides with the altitude of 10° C isotherm in the hottest month. This is a classic criteria to situate the upper forest limit in temperate mountains.

—Relative altitude.

The limit chosen gives value 0 to those plots situated below the 3/4 of transition zone.

—Tree growth form.

All values in the original matrix different from 0 were considered as "presence" (1 in the binarious matrix).

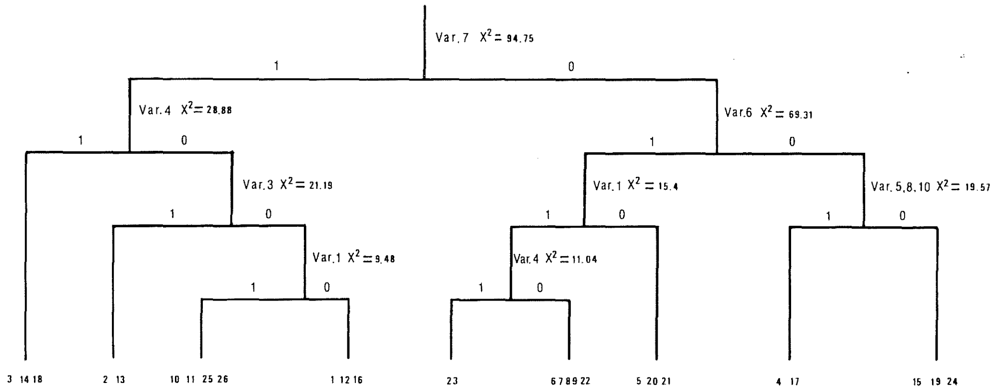

Figure 3. Dendrogram from association analysis. Groups of plots are presented at the end of each branch. *(Dengrograma procedente del análisis de asociación. Los grupos de parcelas se presentan al extremo de cada rama).*

The statistical independence among some outlined variables selected, regarding to their importance in the factorial ordination, was valorated by means of contingence analysis. Variable 1 (absolute altitude) and 2 (relative altitude) were related with the qualitative ones as 2 × 6 type contingence. Relations between qualitative variables were established employing 2 × 2 type contingence.

2. Results

2.1. *Correspondence factorial analysis*

Variables 7 (closed-mat), 4 (pyramidal-trees) and 6 (open-mat) organize the space defined by the first two axis. The first one, opposes var. 7 (with negative values) to the rest. The second axis define the opposition between var. 4 (with positive values) and 6. Var. 7 has little importance in the organization of this second tendency. So, three main groups can be defined:

—In the negative pole of axis 1 are grouped plots having only closed-mats. Here are also situated variables 1 and 2 (both related to altitude), 8 (pine asymmetry direction not coincident with the maximum slope gradient), 10 (presence of dead wood on trees) and 11 (presence of aborted summits).

In the positive pole of axis 1 are situated the last two main groups, that are separated along axis 2:

—One of them, in the positive pole of axis 2, is formed by plots having only pyramidal-trees.

—The other, in the negative pole of said axis, is constituted by plots having only open-mats. Here we also find var. 9, relating the asymetry of this kind of growth form to the direction of maximun slope gradient.

The rest of the plots are situated among these groups, being intermediate situation.

Flagged-trees are not a useful variable to analyse the tendences in plots because of their position, near to the coordenates origin.

2.2. *Association analysis*

The first division is established based upon the presence or absence of closed-mat as occurs with the first axis of factorial analysis.

The second division in each group is defined by var. 4 (pyramidal-trees) and var. 6 (open-mats) respectively, coinciding with the tendency of the second correspondence axis.

So, both binary clustering and factorial ordination show the same resulting groups.

2.3. *Contingence analysis*

According to the results of the analysis (see table 4), there is statistical independence (a = 0,025) among the presence of pyramidal-trees, flagged-trees and closed-mats with absolute altitude. However, closed-mats, usually situated in an altitudinal band between 2.100-2.300 m. a.s.l., show a dependence with that variable.

Statistical relations are very different when the position of growth forms along the transition-zone is considered. Now, pyramidal-trees and closed-mats are respectively dependent on the lower and upper levels of the band. However, flagged-trees and open-mats do not show a clear zonality.

Var. 6 (open-mats) shows a negative contingence (a = 0,025) with var. 7 (closed-mats); they never coincide in the same plot. Nevertheless, var. 6 is positively associated with var. 9, indicating that asymmetrical directions of these growth forms follow maximum sloping. It induce us to consider snow weight as the origin of this kind of deformation. Seedling existence is independent of open-mats presence.

Var. 7 shows a negative contingence with var. 9. Snow weight is probably not the reason for this growth form, but rather the frost-drought processes. The existence of plots where pyramidal trees-and closed-mats coincide, forces the variables to be independent.

Pyramidal-trees and presence of seedlings are positively associated indicating that germinative regeneration is still important at lower ecotonal levels.

The occurrence of flagged-trees is independent of other growth forms, as they appear along the transition-zone following local phenomena more than zonal ones; in fact, wind might have a great influence.

3. Discussion

3.1. *Zonal and local phenomena*

As it was explained in the introduction, the existence of a form-sequence along the slope and from the timberline would characterize the structure of forest-alpine tundra ecotone in the Alps and Colorado Rocky Mountains. We had previously observed stunted growth forms, deformed by environmental factors, in the same areas as are studied here. However, the study of their position along the slope has permited us to know, in greater detail, the structure of their populations compared with the descriptions given for other ranges.

The variables that allude to specimens form are the main ones to organize all the observations done.

The clear separation between plots with abundance in stunted specimens and those where well-formed trees predominate, indicates a difference among populations, specially in the extremes.

After proving that observations could be typified from the specimens form, we migth look for the relation of these structural changes of altitude. Contingence analysis allows us to define the statistical dependence among variables characterizing pine geometry and those which situate plots along the slope. The results of this analysis allow us to state the following conclusions:

—Among typified forms (pyramidal-trees, flagged-trees, open-mats and closed-mats) only the third shows a dependence on absolute altitude; the open mats are always situated along a concrete altitudinal band. The others show a clear independence on this variable. The maximum altitude reached by mountain-pine populations cannot be glibly simplified. At the moment, the 10° C isotherm in the hottest month, situated at 2.200 m. a.s.l., can be used only as an approximation.

—The same did not occur when the variable used in the analysis was relative altitude; as we explained formerly, this variable divides the transition-zone into four homogeneous bands. Now, closed-mats and pyramidal-trees show a clear statistical dependence (a = 0,025); the first ones were mostly located in the upper band while the others clearly appear at the lower levels of the ecotone. These forms, subjected to zonality, are the extremes of the series. The open-mats do not follow this sequence, being considered azonal formations.

Flagged-trees must be considered as transitional elements in the areas studied, because they do not depend clearly on relative altitude, being more dependent on local phenomena. The trees are more intensely subjected to the abrasive effect of ice particles carried by wind when the forest looses its closed structure. Transition from flagged growth forms to stunted ones starts by the development of basal branches, with needles shorter than those of the apical ones, that survive winter under the snow.

3.2. *"Elfin wood" versus "krummholz"*

The existence of stunted growth forms is a common phenomena in the upper species-limit of mountain ranges of the temperate region, as was explained in the introduction. In the Alps, nevertheless, two different kinds of mat-like trees can be found:

—Crippled forms of species belonging to the subalpine forest *(Picea abies, Pinus cembra, Larix decidua),* deformed by the "frost-drought" phenomena **(Phenotypic response).**

—Specimens of *Pinus mugo* and *Alnus viridis,* species that show stunted growth forms in all natural conditions **(Genotypic response)**.

The formations of "dwarf mountain pine" and "green alder" are named "krummholz" in German literature. Nevertheless, the convergence phenomenon has motivated the use of that term to refer to both the phenotypic and the genotypic response.

HOLTMEIER (1981) discusses the term based upon the difference mentioned above, referring to the Alps and Colorado Front Range, in the Rocky Mountains. The author proposes to reserve the name "krummholz" for the genetically defined situation, using the name "elfin wood" when environment is the cause of the stunted form.

All the stunted growth forms in the Pyrenees must be considered as phenotypical responses of the arboreous mountain pine. So, with regard to criteria given by Holtmeier, there are not any "krummholz" formation in this mountain range.

However, *closed-mats* in the upper levels of the forest-alpine tundra ecotone correspond to the denominated "elfin wood", because it seems that their growth form is defined by the "elfin wood", because it seems Open-mats, in addition, show certain characteristics that make them very different from the closed-mats, as the multivariate analysis indicates. They are a zonal-type growth form, indicated by the high degree of dependence of this variable on the relative altitude. The direction of asymmetry does not coincide with maximun sloping, but the main axis of the specimen follows the same direction as that of flagged-trees. As the form of those trees depends on eolic abrasion, the growth direction of closed-mats may be conditioned by the same factor. Apical dominance is broken in these specimens because of the pruning effect; so, they show densely grouped, poorly developed shoots. This kind of growth form usually has needles shorter than common to the species and those at the extremes of the shoots look dead when the snow dissipates.

Open-mats, nevertheless, are not subjected to clear zonality; they may be more dependent on topographical phenomena. This kind of growth form always shows its branches prostrated along maximum sloping; this fact may indicate that snow weight is the cause of deformation. Open-mat structure is not so dense as that of closed because, although they have various stems (polycormic development), they all end vertically with greater annual growths; apical dominance is maintained. Needles do not clearly differ in length from those shown by trees growing within the forest. There are no signals of "frost-drought" on leaves after snow melting. Nevertheless, there are signs of *Herpotrichia nigra* attack. This fungus lives on pine needles when shoots remain covered by snow over a long period of time. This type of growth is confined to avalanche channels, cirque bottoms and glacier shoulders. Snow effects, either by movement *(mechanometamorphosis)* or by weight are clear in all of these sites. Both the structure and ecology of open-mats coincide with those reported by Holtmeier for *Pinus mugo.* So, although environment were the reason for the existence of this type of growth form, we propose the adoption of the term "krummholz" to refer to this stunted form of *Pinus uncinata,* also cited in the Septentrional-Prealps by SCHOENENBERGER (1978).

4. Conclusions

The structure of forest-alpine tundra ecotone in the Pyrenees resembles that of other temperate mountain ranges. A sequence of growth forms can be distinguished from timberline to the species-limit as the forest diminishes.

The extremes of this sequence are closed-mats at the upper, and pyramidal trees at the lower. Both growth forms are dependent on zonality.

The presence of flagged-trees and open-mats are an azonal phenomena. The former appear along a transition-zone, related to eolic abrasion. The presence of open-mat depends on topography, appearing in all those sites where snow accumulate.

Closed and open-mats must be considered as strongly different kinds of stunted growth forms of mountain pine because of their structural and ecological peculiarities. Closed-mats might be named "elfin wood", to relate them to crippled trees found in the species-limit of other ranges. "Frost-drought" is probably the cause of their phisiognomy. Open-mats might be named "krummholz", due to their similarity with *Pinus mugo.* Snow weight is probably the cause of their stunted form.

Acknowledgments. We gratefully acknowledge the assistance from Dr. J. P. Martínez Rica in statistical procedure, Dr. J. Puigdefábregas in several commentaries about the original text and Dr. R. Cantegrel, who kindly accompanied us in visiting the Néouvielle Massif.

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