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DISTURBANCE, AGE AND SIZE STRUCTURE IN STANDS OF *PINUS UNCINATA* RAM[1]

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ABSTRACT.- The size and age structure of two subalpine conifer pure stands of Pinus uncinata *were examined and interpreted using a simple classification of trees by crown exposure to direct sunlight. Both populations show irregular reverse-J shaped diameter distributions having an uncertain interpretation. However, peaks in the age distribution of both stands and the crown exposure of the youngest ones clearly reveal that regeneration occurs in forest clearings.*

Tree-ring width series from each stand were used to reconstruct their recent disturbance history through the identification of growth releases. Disturbance regimes in the analysed stands are different, but they show an analoguos shaping effect on the age structure in both cases.

Finally, it is concluded that P. uncinata *behaves as a shade-intolerant species that can develop steady-state or multicohort stands under several slight disturbance regimes. This is due to its ability to start regeneration in relatively smal clearings, a process that takes place a short time after the occurrence of disturbance.*

RESUMEN.- Las estructuras de tamaño y edad de dos bosques monoespecíficos subalpinos de Pinus uncinata *en el Pirineo, fueron estudiadas e interpretadas introduciendo una clasificación sencilla de los árboles según la exposición de su copa a la radiación solar directa. Ambas poblaciones muestran distribuciones de diámetro de J invertida irregulares, cuya interpretación es incierta. Por el contrario, la estructura de edad en ambos bosques muestra picos visibles, los cuales, si se tienen en cuenta la exposición de la copa, indican que la regeneración se produce en claros del bosque.*

Se analizaron las series de anillos de crecimiento de los árboles de cada sitio para reconstruir su historia reciente de perturbaciones identificando los incrementos bruscos del crecimiento. El régimen de perturbaciones en los dos bosques es diferente, y en ambos casos muestra un efecto madelador análogo sobre la estructura de edad.

Se concluye que P. uncinata *se comporta como una especie heliófila que puede formar bosques maduros o multicohorte bajo determinados regímenes de perturbaciones suaves, gracias a su capacidad para iniciar la regeneración en claros pequeños. Este proceso tiene lugar en un lapso de tiempo corto después de la incidencia de las perturbaciones.*

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RÉSUMÉ.-Les structures de taille et d'âge de deux forêts monospécifiques subalpines de Pinus uncinata, *dans les Pyrénées, ont été étudiées et interprétées en introduisant un classement simple des arbres selon l'exposition du houppier à la radiation solaire directe. Ces deux peuplements ont montré des distributions irrégulières du diamètre en J inversé, dont l'inteprétation est incertaine. Au contraire, la structure d'âge chez les deux forêts montre des pics visibles qui, si l'on tient compte de l'exposition du houppier, indiquent que la régénération a lieu dans les clairières de la forêt.*

On a analysé les séries d'anneaux de croissance des arbres de chaque lieu afin de reconstruire l'histoire récente de leurs perturbations en identifiant les augmentations brusques de croissance. Le régime de perturbations des deux forêts était différent, et dans les deux cas on voyait un effect analogue de configuration en ce qui concerne la structure d'âge.

On en a conclu que P. uncinata *se comporte en tant qu'espèce héliophile pouvant former des forêts adultes on multicohorte sous des régimes donnés de légères perturbations, grâce à sa capacité pour entamer la régénération dans de petites clairières. Ce processus se déroule peu de temps après l'incidence des perturbations.*

Key-words: *Regeneration,* Pinus uncinata, *disturbance, age and size structure.*

During the last two decades a different, innovative view of ecological succession has been developed, with one distinctive feature: The recognition of the importance of the disturbance regimen of any given site in shaping the landscape, as well as the species composition of each ecosystem and the demographic structure of their populations (WHITE, 1979; RUNKLE, 1985; PICKETT & WHITE, eds., 1985; LORIMER, 1980, 1985; OLIVER & LARSON, 1990). This new approach gives less importance to the traditional concepts of succession (CONNELL & SLATYER, 1977), and it has thrived in forest ecology due to the possibilities of carrying out long-term studies, mainly through reconstruction from tree-ring.

Several similar models proposed for forest dynamics (OLIVER, 1981; SHUGART, 1984; PEET & CHRISTENSEN, 1987; OLIVER & LARSON, 1990) join the autogenic and allogenic components of succession in a flexible manner, combinig the disturbance regime affecting a given forested region (type of disturbances, their intensity and frequencies) and the autoecology of each species.

The present study was carried out in two mature forest stands of *Pinus uncinata* Ram. located in the Pyrenees. The two aims are: (1) to determine the pattern of regeneration of *P. uncinata,* in relation to its autoecology, and thus place it in the range of pioneer to climax species (WHITMORE, 1989; MARTÍNEZ-RAMOS *et al.,* 1989). And (2) to determine the importance of canopy clearing openings to the stand structure, its seral stage and, therefore, its persistence. Clearing openings are understood to be disturbances of low intensity but with high frequency.

It is convenient to clarify here that the term mature forest stand is used in the sense of multicohort stand (OLIVER & LARSON, 1990) and steady state (PEET & CHRISTENSEN, 1987).

1. Study Sites and Methods

Two stands of *P. uncinata* were sampled in the Catalan Pyrenees. The first, located near the village of Erill la Vall (central Pyrenees, 42° 32'N, 0° 48'E), is established a 1990 m. a.s.l. on a steep (32° inclination), northeast-facing slope with schistous substratum. The second is located near Lles de Cerdanya (eastern Pyrenees, 42° 27'N, 1° 41'E), on a southwest-facing slope of only 12° inclination with schistous and granitic substratum. Conditions for these stands are quite different regarding slope and solar radiation, which will be taken into account for the discussion and interpretation of the results.

Both stands show sings of past disturbances. In the first one most of the dead trees observed were killed by natural agents such as wind, snow overload and others, though some stumps were also observed. In the second one, in contrast, most dead trees had in fact been cut. However, in both cases dead trees or remains are scattered over the entire stand, or clumped only in small groups of a few individuals.

Each stand was sampled by means of a transect using a modified version of the point-center quarter method (COTTAM & CURTIS, 1956). Transect number six, T6, was performed in Erill la Vall, and number twuelve, T12, in Lles de Cerdanya. Each transect consisted of fifteen points aligned according to the contour line and evenly spaced: 25 m for T6 and 20 m in T12. From every sampling point four quadrants (A, B, C, and D) were delimited using the transect line and its perpendicular, and in each of them the nearest tree greater than or equal to 7.5 cm DBH (considered here adults as trees) was sampled.

For each adult tree, DBH (diameter at 1.30 m from ground) was recorded and an increment core was taken at ground level for age determination. Another core was taken at 1.30 m level only from trees A anc C for radial growth pattern analysis. Furthermore, a rectangle was outlined from tree A to tree C, by 1 m wide. For all saplings (trees of DBH < 7.5 cm and height > 0.5 m) present within the rectangle, age was determined by counting annual bud scars, and size (DBH and/or basal diameter) was recorded. Age and size of all seedligns (height < 0.5 cm) were recorded within a square of 1 m² placed systematically in the same position in relation to sampling point.

The exposure to direct sunlight of the crown of every tree, sapling and seedling was rated from 1 to 3. Thus, **1** means that the individual is completely shaded by other individuals. This is the category of, for example, suppressed adults, understory saplings and seedlings or those overtopped by other taller saplings in a gap. **2**, intermediate, means that the individual is receiving direct sunlight on a relatively small portion of its crown or only during a fraction of the day because some near, larger individuals shade it partly or temporarily. Some overstory trees relatively overtopped by their neighbors may be in this situation, as well as saplings and seedlings growing in small gaps or near the edge of larger gaps. So, in general, the number two was given to any tree, sapling or seedling receiving more sunlight than understory individuals, but notably less than canopy or open-grown individuals. And finally, number **3** denotes absence of shading, and is given to canopy trees and saplings or seedlings within relatively large, well-lighted clearings.

The number of individuals of each class was converted to numbers per hectare so that they could be joined for data analysis. Table 1 shows raw data of sampled individuals and areas, as well as density of each forest. These data were used to obtain the age and size (DBH) distributions of both stands, differentiating the individuals by their degree of shading.

TABLE 1.
Basic parameters of sampling and density of both stands.
(Parámetros básicos de muestreo y densidad de ambos pies).

	Transect 6	Transect 12
Adult trees		
Sampled area (m^2)	1023.0	875.2
Number	60	60
Density (Ind/Ha)	586.5	685.6
Saplings		
Sampled area (m^2)	104.2	117.3
Number	3	33
Density (Ind/Ha)	287.9	2813.3
Seedlings		
Sampled area (m^2)	15	15
Number	1	17
Density (Ind/Ha)	666.7	11333.3

1.1. *Radial Growth Pattern Analysis*

Annual growth rings of cores taken at a height of 1.30 from trees A and C (30 cores per transect) were measured using Aniol ring measuring equipment. The resulting growth series were analysed to identify years in which a growth release occurred.

Abrupt changes in growth rate are quite usual in tree-ring width series. These changes may be caused by many factors such as the individual growth trend of each tree, climatic variability, disease, defoliation by insects, or changes in resource availability. However, it is generally possible to distinguish between the latter situation and the former ones, since the increase in resource availability due to disturbances which destroy part of the overstory in a forest is usually recorded by the surviving individuals as a growth release during several years after a relatively long period of low growth rate. So, an arbitrary criterion is needed to set the cutoff point and threshold between a growth release and any other kind of variation in the growth rate. Here we have considered as significant any growth increase for a given year in which the mean width of the five following annual rings was at least twice the mean of the preceding five rings. We assume that such a change cannot have any explanation other than the occurrence of a disturbance in that year. Two examples of this are shown in Fig. 1.

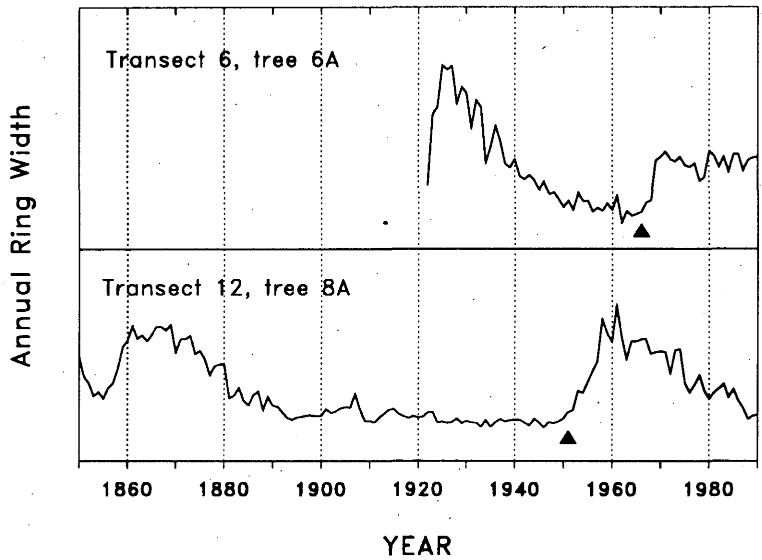

Fig. 1. Ring-width series obtained from two sampled trees. Years in which an increase in growth was found to be significant according to the criterion explained in the text are marked with and arrowhead. *(Series dendrocronológicas de dos árboles. Los años en los que se encontró un crecimiento significativo de acuerdo con el criterio explicado en el texto están marcados con una flecha).*

Then, according to the criterion just explained and using the individual ring-width series, the number of trees per decade showing a release of growth were counted for each transect. The number of releases divided by the number of sample trees having rings in that decade (labelled as 'sample size' in Fig. 2, and represented by a line), was used as an indix of the intensity of disturbances occurring during that time interval ('Intensity of disturbances' in Fig. 2, represented by bars).

This method of assessing the intensity of disturbances in forests, which equals it to the proportion of canopy area removed, seems to be more suitable in forests in which there is always advance understory regeneration that quickly increases its growth rate after the removal of the overstory, and also in which the surviving overstory trees do not show such a stroung growth response (LORIMER, 1985; FREELICH, 1986). The overstory removed is totally replaced by younger individuals that all show a growth release in the same year.

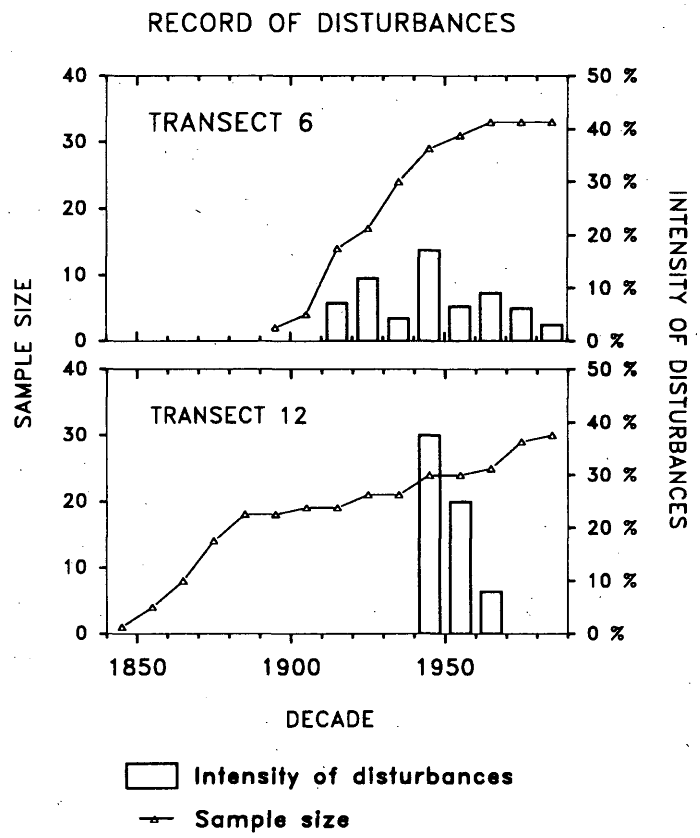

Fig. 2. Dendrocronological record of the disturbances occurring in Erill, T6, and Lles, T12, during the life span of trees currently alive (see explanation in text). In T6, 33 % of trees showed the effect of at least one disturbance, whereas this proportion was 55 % in T12. *(Registro dendrocronológico de las perturbaciones ocurridas en Erill, T6, y Lles, T12, durante el lapso de vida de tres árboles actualmente vivos. Ver explicación en el texto. En T6 el 33 % de los árboles mostraron el efecto de al menos una perturbación, mientras que esa proporción fue del 55 % en T12).*

Although the pattern of regeneration in the stands is completely different, as will be discussed later, we considered the use of this indicator, as a first approach, to be reasonable, since adult *P. uncinata* trees do show strong growth responses. However, it is clear that in this case the indicator does not have the same meaning (disturbed area), but now it may be the sum of several minor disturbances (clearing openings) occurring during the same decade. Therefore, the information given by this number is a mixture of disturbance intensity and frequency of disturbances per decade, rather than an estimation of only disturbance intensity.

2. Results and Discussion

The diameter distributions of both stands (Fig. 3) are quite irregular, with a wide range of values and several small peaks which are difficult to interpret. They also show that the highest frequency of individuals appears in the smallest size classes. These include saplings and seedlings. Although these

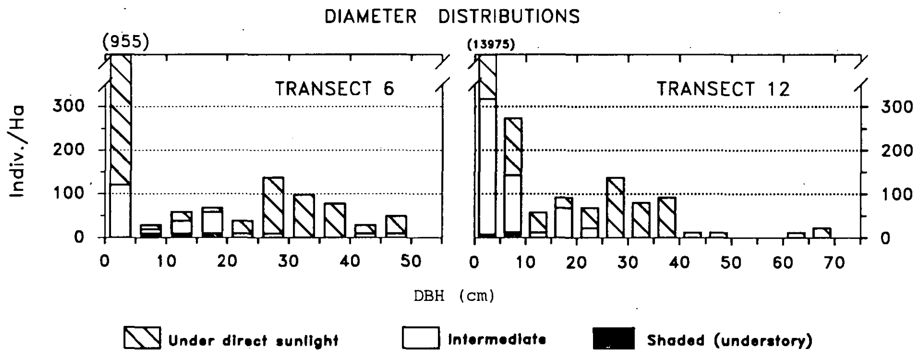

Fig. 3. Size distribution of both stands. For each DBH class, trees are distinguished by their crown exposure to the sunlight. Numbers too large in the smallest size class are shown above the corresponding bar. Although the bar is then cut, the original proportion between crown exposure classes in each bar is kept. Thus, in T6, 70 % of the 955 ind/ha in the smallest DBH class had their crown exposed, and none was found to be shaded. In T12, 1.2 % of the 13975 ind/ha in the first DBH class were in shaded conditions. *(Distribución de tamaño de ambas parcelas. Para cada DBH los árboles se distinguen por la exposición de su copa a la luz de sol. Los números demasiado largos en las clases menores se muestran sobre la barra correspondiente. Aunque la barra está en ese caso cortada, se mantiene la proporción original entre las clases de exposición de la copa en cada barra. Así, en T6, el 70 % de los 955 individuos por Ha tenían su copa expuesta, y ninguna estaba en sombra. En T12, el 1,2 % de los 13.975 indiv./Ha de la primera clase estaban en condiciones de sombra).*

distributions, close to a reverse-J shape, may indicate either the presence of multiple cohorts in the population or continuous recruitment (PARKER, 1986) they can also be found in single-cohort stands (OLIVER *et al.*, 1990). Therefore, each one of these small peaks may not be attributed to a unique cohort, particularly when the correlation between diameter and age is low for both stands (Fig. 4).

Unlike the size distribution, the age structure of both stands (Fig. 5) is much more meaningful and explicit as long as separate age peaks are more evident. These age peaks are useful to identify different cohorts, which were not so evident from Figs. 3 & 4. Besides, we emphasize that it is possible to obtain more information from age distributions: First, they indicate that 100 % of the seedlings and saplings grow under sunlight conditions. In other words, the regeneration always starts in canopy gaps. Although T12 shows many young trees in a intermediate condition of light, this involves higher

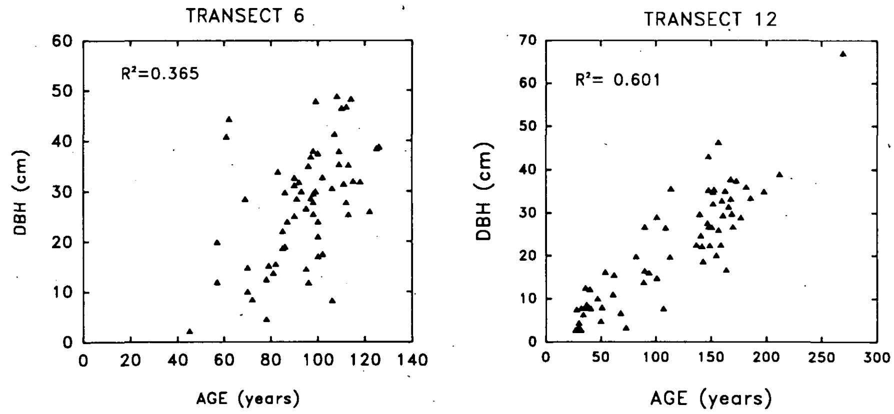

Fig. 4. Relationship between diameter and age in each stand. The correlation R^2 for each population is also shown. *(Relaciones entre el diámetro y la edad de cada estación. Se indica también la correlación R^2 para cada población).*

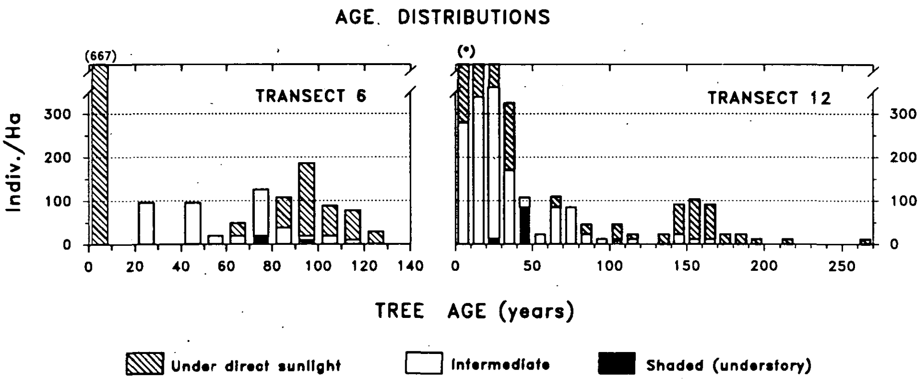

Fig. 5. Age structure of both stands. As in Fig. 3, all individuals are classified by light conditions within every age class. Bars corresponding to classes containing large numbers of individuals are cut, but show original proportion between crown exposure subclasses. No individuals younger than 10 years were found in the shade in T12, while these two first age classes (*) contain 11,000 individuals per hectare. In T6, the youngest shaded tree was 72 years-old whereas nearly 700 seedlings per hectare were growing in sunlight conditions. *(Estructura por edad de ambas estaciones. Como en la Fig. 3, todos los individuos están clasificados por las condiciones de luz dentro de cada clase de edad. Las barras correspondientes a clases que contienen gran número de individuos están cortadas, pero muestran la proporción original entre las subclases de exposición de copa. En T12 no se encontraron individuos de menos de 10 años en sombra, en tanto que las dos primeras clases de edad (*) contienen 11.000 individuos por hectárea. En T6 el árbol más joven en sombra tenía 72 años, cuando casi 700 bunzales por hectárea crecían en condiciones soleadas).*

levels of radiation than those represented by the same condition in T6, due to its different aspect and slope. This result clearly attributes to *P. uncinata* the category of shade-intolerant species, though with some constraints that will be discussed later. The presence of small but old trees with suppressed growth (trees of category number 1, black bars in Figs. 3 & 5) contributes to diminishing the correlation between diameter and age, but it is at the same time evidence of the competition that may occur within every cohort. The age of those individuals prevents us from including them in the regeneration class, which could lead to an erroneous conclusion about the degree of shade-intolerance of *P. uncinata*.

Secondly, if the first result is assumed, it must then be accepted that the different cohorts making up both stands were established after disturbances occurring in the recent past history of these forests. Those age peaks alone are already a sign of the shade-intolerance of *P. uncinata*. In fact, it can be noticed that the disturbance regime affecting the stand of T6 (Fig. 2), characterized by its continuity and low intensity (17.2% is the maximum between decades), led to an age distribution that is also quite continuous, showing a wide range of ages without empty classes during 90 years. In contrast, the disturbance regime in the stand T12 (Fig. 2), with higher frequency of disturbances in a narrower time interval preceded by a quiet period, led to a less continuous age structure, with different and separate cohorts which are shown in Fig. 5.

Moreover, cohorts are established shortly after each disturbance. This is more evident in Lles de Cerdanya, T12, where a cohort with a maximum age of 40 years (Fig. 5) follows the disturbances which occurred 41 to 50 years ago, in the 1940's, although a much greater number of individuals are younger than 30 years-old.

Finally, the quantitative differences in regeneration between the two stands may be due to the conditions of both slope and aspect, which may slow down the establishment of seedlings in Erill la Vall, and also to their disturbance history, which offers more opportunities for regeneration in Lles de Cerdanya, simply because the amount of growing space released is higher.

3. Conclusions

The results of this study confirm the sade-intolerant condition of *P. uncinata* and its dependence on disturbances for regeneration, which always appears in canopy gaps, although some trees may later survive in the shade (understory). In particular, relatively small gaps that are originated by the death of a few trees are colonized shortly after their opening. This introduces a constraint to this condition of pioneer or shade-intolerant species that has an important consequence, since in spite of this condition, *P. uncinata* may form multi-cohort stands under a regime of small disturbances. Disturbances of higher intensity would probably be followed by a slower and less efficient regeneration.

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