CREAF (Centre de Recerca Ecològica i Aplicacions Forestals)


Unitat d'Ecologia

Departament de Biologia Animal, Biologia Vegetal i Ecologia

Facultat de Ciències

Universitat Autònoma de Barcelona


**DISTRIBUCIÓN Y DINÁMICA DE UN *QUERCUS* CADUCIFOLIO (*Q. CERRIOIDES* WILLK. & COSTA) Y UNO PERENNIFOLIO (*Q. ILEX* L.) EN CATALUNYA. ANÁLISIS DE LA ECOLOGÍA DE LA REPRODUCCIÓN, LA RESPUESTA DE LAS PLÁNTULAS A FACTORES AMBIENTALES Y LA RESPUESTA A LAS PERTURBACIONES**


Memoria presentada por


**Pilar Cortés Gimeno**

para optar al grado de Doctor en Biología


Los directores del trabajo de tesis


Josep Maria Espelta                                              Javier Retana

Investigador del CREAF                              Profesor Titular de Ecología


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# GENERAL INTRODUCTION

**VEGETATION PATTERNS: DETERMINANTS OF THE DISTRIBUTION AND ABUNDANCE OF SPECIES**

The study of the factors explaining the change of species abundance is one main topics covered by plant ecology (Harper 1977). Species abundance changes along environmental gradients that, for some authors, are mainly driven at global scale by macroclimate (Box et al. 1993; Neilson 1995; Iverson and Prasad 1998; Motzkin et al. 1999), while others highlight the importance local factors as geomorphology, topography, site disturbance and historical events (Reed et al. 1993; Iverson et al. 1997). Conciliating these contrasted views, some studies have demonstrated that vegetation patterns would be the result of both regional and local scale processes (Ohmann and Spies 1998; Gracia 2000). Macroclimate influences communities, directly because it determines the availability of energy and water influencing the physiology of organisms and limiting the growth of populations, and indirectly, by modifying the importance of the abovementioned local-scale factors and by favouring certain growth forms in interspecific competition (Stephenson 1990; Ohmann and Spies 1998). At a local scale, the range of climatic conditions is small, falling within species physiological tolerances and thus, the local-scale factors achieve larger importance on the fine-tuning vegetation distribution over the landscape. Moreover, amplifying the zoom until a smaller scale, within a given habitat, plants are constrained by the availability of some resources and by mortality caused by disturbances. Thus, within an habitat, the physiognomy of the vegetation is strongly influenced by the forces that control the vertical light gradient and the levels of limiting soil resources (Tilman 1988).

**EVERGREENNESS VS. DECIDUOUSNESS**

A clear example of all this is summarised by the case of the geographic patterns of evergreen and deciduous plant growth forms. This subject has interested naturalists since the fifth century BC, when Menestor recorded that he was clearly aware of the correlation between the evergreen and deciduous habits of vegetation and climate (Morton 1981). Evergreen species retain leaves throughout the year and thus, the evergreen leaf habit is found mainly in areas where plants can conduct photosynthesis all year long. At the world scale, the relative frequency of evergreens has a bimodal latitudinal distribution or puzzling pattern (Chabot and Hicks 1982), as a result of the annual patterns of water availability and temperature. Evergreens predominate in tropical and subtropical regions and Mediterranean woodlands where rainfall is highly variable or the soils infertile, usually decrease in abundance with increasing latitude, accompanied by a corresponding increase of deciduous species, and finally evergreens abundance increases again at higher latitudes. In the other hand, deciduous plants shed all of their leaves either in response to summer drought (summer deciduous) or winter cold (winter deciduous) and therefore spend a portion of the year without foliage. Deciduous species are

found mainly in the temperate regions because the deciduous habit is considered to be associated with seasonality of climatic conditions.

The regional and local-scale processes that control the distribution of evergreen and deciduous vegetation are related to time to amortise the construction cost of leaves, resource conservation (carbohydrates and/or nutrients), control of nutrient recycling and drought and freezing resistance (Chabot and Hicks 1982; Kikuzawa 1991; Aerts 1995). Most studies have found that deciduous woody species show higher specific leaf area (SLA) and higher photosynthetic rates and thus higher potential growth rates than evergreen species (Reich et al. 1992; Cornelissen et al. 1998; Reich 1998). As a result, evergreens tend to dominate in low-nutrient sites where they maintain tissues with a long lifespan and with low nutrient concentrations (Aerts and van der Peijl 1993; Berendse 1994), and deciduous are more abundant in productive habitats (i.e. with high availability of nutrients and water) through a greater competitive ability (Aerts 1990; Reich et al. 1991; Reich et al. 1992; Cornelissen et al. 1996).

## THE LEAF HABIT IN MEDITERRANEAN ECOSYSTEMS: THE CASE OF OAKS

Mediterranean-type ecosystems are characterised by a distinctive annual climatic sequence with hot and dry summers and cold and wet winters. In general there is scarce rainfall with great interannual variability (Aschmann 1973; Specht et al. 1983). Thus, in Mediterranean-type ecosystems, plants have to cope with a selective pressure resulting from a double stress: winter cold and summer drought. Soils present high heterogeneity and the frequent disturbances (i.e. fire, grazing, wood cutting…) may alter light intensity and water and nutrient availability. Within the Mediterranean-type regions, the structure of woody plant communities changes in response to water balance, nutrient availability and human impact (Specht et al. 1983).  In Mediterranean communities, evergreen species are more abundant than deciduous ones (Cody and Mooney 1978; Di Castri 1981). It has been suggested that the winter-deciduous habit presents an important disadvantage because the active period coincides with the most important constraint, that is summer drought., while evergreenness can be advantageous because, under appropriate conditions, it permits carbon fixation at any season. In spite of this, the co-occurrence of winter-deciduous and evergreen species (both shrubs and trees) is frequent, specially in California and the Mediterranean Basin (Gill and Mahall 1986; Hollinger 1992; Tretiach 1993; Damesin et al. 1998).

According to Amaral (1990), in the Iberian Peninsula there are ten native *Quercus* species, the evergreens *Q. ilex* L., *Q. suber* L., and *Q. coccifera* L. and the deciduous *Q. canariensis* Willd.*, Q. petraea* (Matt.) Liebl.*, Q. robur* L.*, Q. pyrenaica* Willd.*, Q. humilis* Miller (=*Quercus pubescens* Willd.), *Q. faginea* Lam. and *Q. lusitanica* Lam. Two of these species, *Quercus ilex* and Quercus humilis are abundant in the north-eastern Iberian Peninsula

*Quercus ilex* is widely distributed in the Mediterranean Basin. Its distribution range goes from the Iberian Peninsula and the Magreb (Morocco and Tunisia) to Italy until Anatolia with its northern limit in the French Central Massif and Piamonte Valleys (Barbero et al. 1992). *Quercus humilis* is distributed through centre and south Europe, south-west of Asia, from Spain to Turkey. In the Iberian Peninsula it is more abundant in the north-east quadrant (Ceballos and Ruiz de la Torre 1971; Amaral 1990). This species usually hybridises with *Quercus faginea* Lam. forming the hybrid *Quercus cerrioides* Willk. & Costa. which is found in the north-western of Spain (Amaral 1990).

These species provide an interesting example of co-occurrence of evergreen and deciduous species in Catalonia (NE Spain), where both species are extensively present as monospecific of mixed forests (Gracia et al. 2000). *Quercus ilex* has been considered a paradigm of Mediterranean plants partly because of its evergreen habit and its sclerophyllous leaves. Some authors have inferred from palinological records that 5000 B.P. *Q. humilis* dominated in areas that are now occupied by *Q. ilex*, but after 5000 BP there was an inversion of this dominance (Pons and Quezel 1985; Riera-Mora 1995). The causes of this shift are attributed to an increase of the aridity and to the long history of land use of Mediterranean-Basin ecosystems by humans (Barbero et al. 1992; Riera-Mora 1995). Men, consciously or unconsciously, favoured *Q. ilex* expansion because it was more valuable than *Q. humilis* for obtaining charcoal and fire wood. And humans also altered the disturbance regime of the Mediterranean basin ecosystems resulting in a high recurrence of disturbances (i.e. fire, coppicing, livestock grazing, etc) that is supposed to favour *Q. ilex* expansion. Both species are able to recover after disturbances due to their resprouting ability. However, the regeneration of deciduous species may be more compromised than that of evergreens because the former are higher resource-demanding species, and the reduction of resource availability by the effect of disturbances, may impede the uptake of enough resources to compensate the large mobilization and consumption of below-ground reserves that the destruction of the aboveground biomass implies.

**OBJECTIVES AND STRUCTURE OF THE THESIS**

The main objective of this thesis is to study the key factors that can determine the co-existence or substitution of these two *Quercus* species with contrasting leaf habit present in the north-western of the Mediterranean Basin, the evergreen *Q. ilex* and the deciduous *Q. humilis/Q. cerrioides*. An approach to investigate the mechanisms and processes that control the distribution of species is to split the life cycle into a different number of stages, considering each of them as a link in the survival chain. If two species differ in a stage in the life cycle this difference might be the key to understand their dynamics. Thus, in order to answer the main

question of this thesis we have compare the performance of *Q. ilex* and *Q. humilis* in different points of the biological cycle, in sites where both are living at present.

Chapter 1

In this chapter we study the determinants of the distribution, abundance and growth of *Q. ilex* and *Q. humilis/Q. cerrioides* in Catalonia. In the first part, we study the distribution patterns of adults and seedlings (regeneration phase) and we analyse how macroclimate (including variables such as temperature or rainfall) and local factors (such as topography or geological substratum) influence these patterns. To achieve this objective, we use data available from the Ecological Forestry Inventory of Catalonia (IEFC). The second main objective of this chapter is to study the dynamics of the species in their distribution area. Thus, we analyse the relative growth rate of both species, testing the hypothesis that the deciduous species has higher growth rates than the evergreen one. To test this hypothesis, we estimate the relative growth rate in basal area of trees measured in both the second and third National Forestry Inventories (IFN2 and IFN3). We relate the climatic, geological substratum and topographic conditions to these different growth rates. Comparing these two inventories we also estimate the mortality rate of adult trees and the recruitment rate of saplings into populations.

Chapter 2

This chapter is focused on the biology of reproduction of *Q. ilex* and *Q. cerrioides*. We analyse the main processes that comprise the seed ecology of these species: potential production and real production of acorns, post-dispersal acorn predation and acorn germination. We compare all processes between both species and we analyse their spatial variability among forests with different structure. All this information is integrated in a simple demographic model that lead us to evaluate the reproductive success of both species.

Chapter 3

Seedlings have to face environments highly heterogeneous in resource availability. In this chapter we study the ability of seedlings to modify their morphology and nutrient content in front of co-variation of resources availability. The extend of these adjustments gives an idea of the individual plasticity. Seedlings can show two different strategies: phenotypic plasticity or phenotypic stability. To evaluate which strategy uses each species we have carried out an experiment on controlled conditions. Seedlings of *Q. ilex* and *Q. cerrioides*, placed in plastics pots, grow under three levels of light intensity, two levels of water availability and two levels of nutrients availability. We monitored survivorship during all the experiment and measured relevant morphological and resource allocation variables.

Chapter 4

In this chapter we study the response of *Q. ilex* and *Q. humilis* individuals to the reiteration of disturbances. Since long time ago, Mediterranean forests have been subjected to very frequent and reiterated disturbances due to the high human pressure. Although both species are able to resprout after disturbances, possible differences in their resprouting response after recurrent disturbances could condition the specific composition of forests. We carry out a field experiment where we study the effect of different fire histories (defined by different periods of fire recurrence), type of experimental disturbance applied and season when the disturbance is applied in survival, growth and architecture of sprouts of both species after disturbance.

**REFERENCES**

Aerts, R. 1990. Nutrient use efficiency in evergreen and deciduous species from heathlands. Oecologia. Vol. 84, pp. 391-397.

Aerts, R. 1995. The advantages of being evergreen. Trends in Ecology and Evolution, 10: 402-407.

Aerts, R. and van der Peijl, M.J. 1993. A simple model to explain the dominance of low-productive perennials in nutrient-poor habitats. Oikos. Vol. 66, pp. 144-147.

Amaral Franco, J. 1990. Quercus. In: Castroviejo, S; Laínz, M; López G; Montserrat, P; Muñoz, F; Paiva, J and Villar, L (eds) Flora Ibérica, Vol. II. Consejo Superior de Investigaciones Científicas. Madrid.

Aschmann, H. 1973. Distribution and Peculiarity of Mediterranean Ecosystems. In: F. di Castri and H.A. Mooney (eds.) Mediterranean-type ecosystems. Origin and structure. Pp. 11-19. Springer-Verlag. Berlin.

Barbero, M; Loisel, R. and Quézel, P. 1992. Biogeography, ecology and history of Mediterranean Quercus ilex ecosystems. Vegetatio, 99-100: 19-34.

Berendse, F. 1994. Competition between plant populations at low and high nutrient supplies. Oikos. Vol. 71, pp. 253-260.

Box, E.O.; Crumpacker, D.W. and Hardin, E.D. 1993. A climatic model for location of plant species in Florida, U.S.A. Journal of Biogeography, 20: 629-644.

Ceballos L, and Ruiz de la Torre J. 1971. Arboles y arbustos. IFIE-Escuela Técnica Superior de Ingenieros de Montes , Madrid.

Chabot, B.F. and Hicks, D.J. 1982. The ecology of leaf life spans. Annual Review of Ecology and Systematics, 13: 229-259.

Cody, M.L. and Mooney, H.A. 1978. Convergence versus non convergence in Mediterranean-climate ecosystems. Annual Review of Ecology and Systematics, 9: 265-321.

Cornelissen, J.H.C; Castro Diez, P. and Hunt, R. 1996. Seedling growth, allocation and leaf attributes in a wide range of woody plant species and types. Journal of Ecology. Vol. 84, pp. 755-765.

Cornelissen, J.H.C.; Castro-Diez, P. and Carnelli, A.C. 1998. Variation in relative growth rate among woody species: scaling up. In: Lambers, H.; Poorter, H. and Vuuren, M van (eds.) Inherent variation in plant growth: physiological mechanisms and ecological consequences. Backhuys, Leiden.

Damesin, C.; Rambal, S. and Joffre, R. 1998. Co-occurrence of trees with different leaf habit: a functional approach on Mediterranean oaks. Acta Oecologica, 19: 195-204.

Di Castri, F. 1981. Mediterranean-type shrubland of the world. In: di Castri, F.; Goodall, D.W. and Specht, R.L. (eds.) Mediterranean-type Shrublands. Ecosystems of the World, Vol. 11. Amsterdam, The Netherlands. Elsevier.

Gill, D.S. and Mahall, B.E. 1986. Quantitative phenology and water relations of an evergreen and a deciduous chaparral shrub. Ecological Monographs, 56: 127-143.

Gracia, M. 2000. La encina y los encinares en Catalunya. Aproximación a su distribución, dinámica y gestión. Tesis Doctoral. Bellaterra. Barcelona.

Gracia, C.; Burriel, J.A.; Ibáñez, J.J.; Mata, T. and Vayreda, J. (2000) Inventari ecològic i forestal de Catalunya. Regió forestal IV. Centre de Recerca Ecològica i Aplicacions Forestals, Barcelona.

Harper, J.L. 1977. Population biology of plants. Academic Press, London, UK.

Hollinger, D. Y. 1992. Leaf and simulated whole-canopy photosynthesis in two co-occurring tree species. Ecology, 73: 1-14.

Iverson, L.R.; Dale, M.E.; Scott, C.T and Prasad, A. 1997. A GIS-derived integrated moisture index to predict forest composition and productivity in Ohio forests. Landscape Ecology, 12: 331-348.

Iverson, L.R. and Prasad, A.M. 1998. Predicting abundance of 80 tree species following climate change in the eastern United States. Ecological Monographs, 68: 465-485.

Kikuzawa, K. 1991. A cost-benefit analysis of leaf habit and leaf longevity of trees and their geographical pattern. The American Naturalist, 138: 1250-1263.

Morton, A.G. 1981. History of Botanical Science. London. Academic Press.

Motzkin, G.; Wilson, P.; Foster, D.R. and Allen, A. 1999. Vegetation patterns in heterogeneous landscapes: The importance of history and environment. Journal of Vegetation Science, 10: 903-920.

Neilson, R.P. 1995. A model for predicting continental-scale vegetation distribution and water balance. Ecological Applications, 5: 362-385.

Ohmann, J.L. and Spies, T.A. 1998. Regional gradient analysis and spatial pattern of woody plant communities of Oregon forests. Ecological Monographs, 68: 151-182.

Pons, A. and Quézel, P. 1985. The history of the flora and vegetation and past and present human disturbance in the Mediterranean area. In: Gomez-Campo, C. (ed) Plant Conservation in the Mediterranean area. Geobotany 7. Junk, Dordrecht.

Reed, R.A.; Peet, R.K; Palmer, M.W. and White, P.S. 1993. Scale dependence of vegetation-environment correlation: a case study of a North Carolina piedmont woodland. Journal of Vegetation Science, 4: 329-340.

Reich, P.B. 1998. Variation among plant species in leaf turnover rates and associated traits: implications for growth at all life stages. In: Lambers, H.; Poorter, H. and Vuuren, M van (eds.) Inherent variation in plant growth: physiological mechanisms and ecological consequences. Backhuys, Leiden.

Reich, P.B; Uhl, C.; Walters, M.B and Ellsworth, D.S. 1991. Leaf lifespan as a determinant of leaf structure and function among 23 amazonian tree species. Oecologia. Vol. 86, pp. 16-24.

Reich, P.B; Walters, M.B. and Ellsworth, D.S. 1992. Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. Ecological Monographs. Vol. 62, pp. 365-392.

Riera i Mora, S. 1995. Evolució del paisatge vegetal holocè al Pla de Barcelona a partir de les dades pol.líniques. Tesi doctoral U.B. Barcelona.

Specht, R.L.; Moll, E. J.; Pressinger, F. and Sommerville, J. 1983. Moisture regime and nutrient control of seasonal growth in Mediterranean ecosystems. In: F. J. Kruger; D.T. Mitchell and J.U.M. Jarvis (eds.) Mediterranean-type ecosystems. The role of nutrients. Pp. 120-132. Springer-Verlag, Berlin.

Stephenson, N.L. 1990. Climatic control of vegetation distribution: the role of the water balance. The American Naturalist, 135: 649-670.

Tretiach, M. 1993. Photosynthesis and transpiration of evergreen Mediterranean and deciduous trees in an ecotone during a growing season. Acta Oecologia, 14: 341-360.

Tilman, D. 1988. Plant strategies and the dynamics of plant communities. Princeton University Press, Princeton, N.J.

# DETERMINANTS OF *QUERCUS ILEX* AND *QUERCUS HUMILIS* CO-OCCURRENCE: A REGIONAL AND LANDSCAPE-SCALE APPROACH TO THEIR DISTRIBUTION

**INTRODUCTION**

One of the paradigmatic topics concerning the study of vegetation distribution is that of evergreen and deciduous species. The distribution of both types of species at a global scale follows a bimodal pattern, mainly driven by macroclimate conditions, such as temperature and thermal range (Chabot and Hicks 1982). On the one hand, broadleaf-evergreen species predominate at sites with high mean annual temperature and low annual thermal variability, while evergreen coniferous forests dominate sites with low mean temperature and high thermal range. On the other hand, the deciduous habit is usually more associated with seasonality, and these species prevail at intermediate values of the abovementioned parameters. In spite of these general trends, coexistence of evergreen and deciduous trees is frequent in the transition between biomes, as in the boreo-nemoral zone, where temperate deciduous forests and boreal forests merge (Fulton and Prentice 1997), and in Mediterranean-type ecosystems, in the transition zone between temperate forests and the scrublands typical of tropical regions (Terradas 1999). At these more regional and local scales, other factors such as microclimate, aspect, topography, geomorphology, disturbance or historical events may overlay the macroclimatic conditions and influence the vegetation patterns (Ohmann and Spies 1998; Clark et al. 1999; Motzkin et al. 1999, Gracia 2000). These factors may condition the existence of suitable "niches of regeneration" for the different species (Grubb 1977) as well as affect keystone life-history traits during the adult stage, such as variation in leaf life-span, growth, survivorship, size or fecundity (Oliver and Larson 1990; Lertzman 1995; Lusk and Smith 1998).

A great number of studies have tried to elucidate the relative importance of macroclimate in front of other characteristics (e.g. substrate, microclimate and topography) in the community composition and local distribution of tree species in temperate and tropical forests (Brzeziecki et al. 1995; Bongers et al. 1999; Minnick and Coffin 1999; Shafer et al. 2001), while some of them focus on Mediterranean-type ecosystems (Piggot and Piggot 1993; Frankin 1998; Rouget et al. 2001). In the Mediterranean basin, the presumed role of climate, topography, soil composition and perturbations on the distribution of evergreen and deciduous oaks is suggested in different studies (Pons and Vernet 1971; Debazac 1983; Pons and Quezel 1985; Barbero et al. 1992; Terradas 1999). However, few studies specifically try to prove these assumptions and thus obtain comprehensible patterns of the distribution of these species, as well as clues to understand the mechanisms that promote their co-existence or segregation.

The genus *Quercus* comprises various species in the Mediterranean basin, both deciduous and evergreens (Blondel & Aronson 1999). The general trend is that evergreen oaks are situated in warmer and drier zones, while deciduous oaks are more common in cooler areas, and thus are usually found at higher altitudes within the same latitude (Barbero et al. 1992). Edaphic variables may also control vegetation distribution, as evergreens have been presumed to dominate nutrient-poorer habitats, while deciduous species would be more competitive in high

nutrient habitats (Aerts and van der Peijl 1993; Berendse 1994). Where deciduous trees become dominant, refuges of evergreens are usually on calcareous, non-oligotrophic soils with relatively low water availability (Terradas 1999). Moreover, the ancient human occupation in the Mediterranean-Basin has been claimed to play also an important role in determining the vegetation structure and the distribution of oaks. Similar proportions of evergreen and deciduous oaks were found in NE Spain 5000 B.P. (Barbero et al. 1992; Riera-Mora 1995), and it is supposed that the former spread more recently into the area of deciduous species due to increasing aridity and higher anthropic impact (Riera-Mora 1995). Thus, it is frequently considered that the occurrence of disturbances has favoured the evergreen sclerophyllous oaks versus the deciduous broadleaved ones (Pons and Vernet 1971; Pons and Quezel 1985). Therefore, it has also been suggested that the abandonment of some forest management practices, such as coppicing, would cause the gradual invasion by deciduous oaks of part of the forests dominated by evergreen species (Bacilieri et al. 1993).

In the northwest of the Mediterranean basin, *Quercus ilex* L. and *Quercus humilis* L. form monospecific or mixed stands (Terradas, 1999). These two species have similar characteristics, such as resprouting ability after disturbances, slow growth, and establishment mainly occurring in stands under a closed canopy and deep litter layer (Gracia et al., 2001). However, they differ markedly in their leaf habit: *Q. humilis* is a winter deciduous oak, while *Q. ilex* is an evergreen one. The first goal of this study is to analyse the patterns of occurrence of *Q. ilex* and *Q. humilis* in Catalonia as a function of different environmental variables, such as climate (precipitation and temperature), topography (altitude, slope and aspect) and geological substrate. To carry out this study we have used tree regression analysis, a method that has been employed in several studies to analyse vegetation distribution (Reichard and Hamilton 1997; Iverson and Prasad 1998; Rouget et al. 2001). The second objective is to study the importance of the abovementioned environmental variables in growth, mortality and recruitment patterns of the two species. We expect that the results obtained will help to elucidate which factors, or combinations of factors, control either the segregation/co-occurrence of evergreen and deciduous oaks in Mediterranean-type ecosystems.

**METHODS**

**Determinants of the distribution of *Q. ilex* and *Q. humilis* adults and regeneration**

*Sampling*

The information of species distribution and abundance was obtained from the Ecological Forestry Inventory of Catalonia (IEFC), carried out between 1988 and 1994 (Gracia et al. 1997). In this inventory, 10626 circular sampling plots of 10 m radius were randomly distributed throughout the whole forested area in Catalonia (NE Spain). The sampling was at a density of

one plot per km$^2$ of natural or managed forest. In each plot, all trees with diameter at breast height (DBH) > 7.5 cm were measured and recorded as adult trees, those with DBH between 2.5 and 7.5 cm were recorded as saplings, and those with DBH < 2.5 cm were recorded as seedlings. From this information we summarized the data on the total basal area of the plot, the percentage of *Q. ilex* and *Q. humilis* basal area in the plot, and the density of seedling and sapling regeneration. Topographical data of each plot (aspect, slope and elevation) was also recorded in the field during the forest inventory and thus used in the analyses.

*Environmental variables*

Different environmental variables for the plots sampled in the two inventories (IEFC, IFN) were obtained from data sets available for Catalonia, after placing all plots in a Geographical Information System. The digital climate model (Ninyerola et al. 2000) provided information about mean annual rainfall (mm) and mean annual temperature (ºC). Other climate variables were rejected because they were obtained from regressions and spatial interpolation of the dates of meteorological stations and they were highly correlated among them. The geological substratum of plots was obtained from the geological map of Catalonia (Institut Cartogràfic de Catalunya 1989).

*Statistical analyses*

The relationships between environmental and biotic variables and species distribution and regeneration were described using the Formal-based Inference Recursive Modelling (FIRM), a recursive partitioning technique or tree regression analysis (Hawkins 1999). This type of modelling technique does not rely on assumptions of linearity, and it is able to analyse both continuous and categorical data types. FIRM splits the data set into smaller subsets, based on the values of the predictor variables. To test the significance of the new grouping of classes, a $\chi^2$ test is performed between each pair, and the overall significance of the split is assessed by a Bonferroni analysis. Following this recursive method, each subset (node) is split successively into a set of successor nodes that are maximally homogeneous, until no splitting is possible (according to the *p* threshold defined). Finally, the output of FIRM is a dendrogram or tree diagram that describes the structure of the problem analysed and that can be used for interpreting the effects of the different predictors on the dependent variable (see Rouget et al. 2001 for a more detailed explanation of the use of FIRM as a recursive partitioning technique).

To analyse the distribution and regeneration of *Q. ilex* and *Q. humilis* in Catalonia*,* regression trees were generated using Firm 2.3 (Hawkings 1999). In the analysis of tree distribution, we classified all the 10626 plots inventoried in the IEFC as: ABSENT (neither Q. humilis nor Q: ilex were present in the tree layer), *Q. ilex* (*Q. ilex* was present but not *Q. humilis*), *Q. humilis* (*Q. humilis* was present but not *Q. ilex*) or MIXED (both *Q. ilex* and *Q. humilis* were present). The distribution areas of *Q. ilex* and *Q. humilis* and the areas where both coexist are shown in Figure 1. Since biotic factors did not significantly improve the model performance, only environmental variables were included in the model. Predictor variables used in these analyses

were: altitude (m), aspect (N, E, S, W), slope (in °), mean accumulated annual rainfall (< 600, 600-700, 700-800, 800-900, 900-1000 and > 1000 l m$^2$ yr$^{-1}$), mean annual temperature (<7, 7-9, 9-11, 11-13, 13-15 and > 15° C) and geological substrate (consolidate alluvial rocks – conglomerates-, non consolidate alluvial rocks –gravels-, clays, limestones, sandstones, marls, siliceous rocks and basal-volcanic basic rocks).
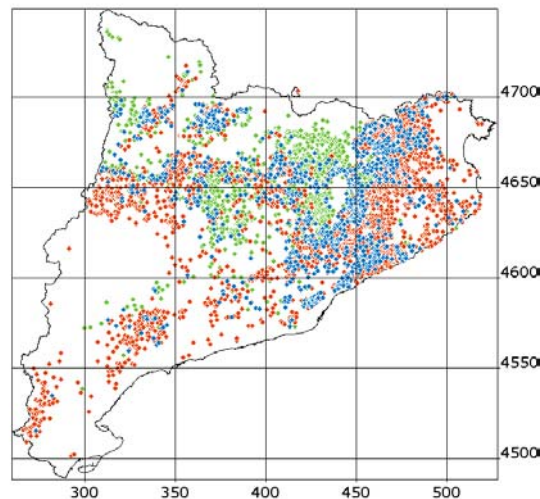


**Figure 1**. Distribution de *Quercus ilex* and *Quercus humilis* in Catalonia. Plots where only *Q. ilex* trees are present are represented by red dots. Plots where only *Q. humilis* trees are present are represented by green dots and plots where both species are present are represented by blue dots.

Regeneration patterns were analysed separately for *Q. ilex* and *Q. humilis*. For each species, we built separated models for the presence of seedlings and the presence of saplings, as effects of environmental factors may have a distinct importance in the different juvenile stages (Grubb 1977). Thus, in each species and for seedlings and saplings regeneration we classified the 10626 plots inventoried in the IEFC dicotomically as: ABSENT (no regeneration) or PRESENT (presence of regeneration). Predictor variables used in these analyses included the same environmental variables previously used in the analysis of distribution of the two species (see above) but we also included three biotic variables: total basal area of the plot (m$^2$ ha$^{-1}$), presence of the studied species in the tree layer (absent = 0% of the total basal area, present = more than 0 but less than 66% of the total basal area, and dominant = more than 66% of the total basal area), and basal area of the studied species (m$^2$ ha$^{-1}$).

In all FIRM models performed, to avoid very large dendrograms containing spurious splits, we parameterised the model with very stringent *p* values (*p*=0.01). Moreover, as the chi-squared approximation to Pearson's $\chi^2$ deteriorates when frequencies in the contingency table get small, leading to unremarkable splits with huge $\chi^2$ values, we established a restrictive size of 250 plots, as the minimum size a node should have to be considered for further splitting (see, Hawkins 1999 for details on parameterisation of FIRM models). Finally, to check the validity of the FIRM methodology we randomly split the entire data set (10626 plots) into two parts, the "calibration" and the "validation" data sets (containing 5313 plots each one). We first calibrated the models, above referred, in the calibration data set, and then applied them to the validation data set. If the splits that are found to be highly significant in the calibration data set tend also to be highly significant in the validation data set it can be concluded that the model is highly accurate and credible (Hawkins 1999).

Regeneration patterns of *Q. ilex* and *Q. humilis* in mixed forests were also compared considering separately seedlings and saplings. On the one hand, we classified mixed forests in two categories, either dominated by *Q. ilex* (density of *Q. ilex* in the plot > 1.5 density of *Q. humilis*) or dominated by *Q. humilis* (*Q. humilis* in the plot > 1.5 * density of *Q. ilex*). On the other hand, we classified the regeneration in four classes: no regeneration at all, dominance of the regeneration of the dominant species in the canopy (density of the regeneration of dominant species at canopy > 1.5 * density of the regeneration of the secondary species in the canopy), dominance of the regeneration of the non-dominant species in the canopy (density of the regeneration of the secondary species in the canopy > 1.5 * density of the regeneration of dominant species at canopy), and similar regeneration of the two species.

**Quercus ilex and Q. humilis dynamics: growth and survival of adult trees and recruitment to the tree layer**

*Sampling*

Data used in this section were obtained from the Spanish National Forestry Inventory (IFN) in the region of Catalonia, where it comprises ca. 11000 fixed sampling plots. These plots were sampled at a density of one plot per $km^2$ of natural or managed forest. The maximum size of plots was 25 m of radius. Plots were sampled between 1990 and 1992 in the second IFN (IFN2 hereafter), and re-sampled again ten years later, in 2000-2002 (IFN3 hereafter). DBH of trees was carefully measured in two perpendicular directions allowing the comparison among inventories. We selected those plots that (i) were sampled in both inventories, and (ii) contained at least one *Q. ilex* and/or one *Q. humilis* tree. In both inventories, the number and DBH of *Q. ilex* and *Q. humilis* adult trees, and the plot basal area were measured. Data of plot aspect, slope and elevation were also available. The basal area of *Q. ilex* and *Q. humilis* per plot calculated in both inventories was compared to obtain the relative growth rate in basal area ($RGR_{ba}$ = *($ba_{IFN3}$ − $ba_{IFN2}$)/ $ba_{IFN2}$*, measured in percentage). The rate of individual mortality

(individuals found dead in the IFN3 except those burned or thinned) was calculated comparing the trees present in the IFN2 and IFN3 inventories. The rate of incorporation of saplings to the tree layer (i.e., those individuals with a DBH < 7.5 cm in the IFN2, and > 7.5 cm in the IFN3) in each plot was also obtained comparing the data of both inventories.

*Statistical analysis*

In the plots where both species co-occur (a total of 532 plots), we analysed the effects of species (*Q. ilex, Q. humilis*), mean annual temperature (<11ºC, 11-13ºC, >13ºC), mean accumulated annual rainfall (<700 mm, 700-900 mm, >900 mm) and aspect (northern, eastern, southern and western) on the $RGR_{ba}$ on tree growth. We tested these effects with a four-way ANCOVA model, using as a covariate the total basal area of the plot recorded in the first inventory (IFN2).

The mortality rate of adult trees was analysed with a log-linear model, using data of plots where both species co-occur. We selected those plots with trees recorded as alive or death in the IFN3, and alive in the IFN2. A multi-way frequency table was constructed with the variables species (*Q. ilex*, *Q. humilis*), state (alive, death) and size (7.5-12.5 cm, 12.5-22.5 cm, 22.5-42.5 cm, >42.5 cm)

Finally, multiple regressions were constructed for each species to analyse the effect of environmental and plot variables on the number of saplings recruited to the tree layer. We chose those plots where *Q. ilex* and *Q. humilis* co-occurred and that were sampled in both inventories, IFN2 and IFN3 (a total of 703 plots). The independent variables used in the regressions were: slope, altitude, mean accumulated annual rainfall, mean annual temperature, tree density and basal area in the plot.

**RESULTS**

**Determinants of the distribution of *Q. ilex* and *Q. humilis* adults and regeneration**

Figure 2 shows the most relevant variables determining the distribution of *Q. ilex* and *Q. humilis* adult trees in Catalonia. Mean annual temperature was the first factor incorporated in the tree regression analysis and, thus, the most important one to predict the presence or absence of the two species. In a secondary term, aspect and total annual precipitation are included in the model: i.e. aspect is highly significant at lower temperatures, while annual rain is highly significant at higher temperatures. Ultimately, geological substrate, altitude and slope appear in lower levels of the dendrogram. According to the comparison of the *p* values obtained with the model applied to the calibration data set and those obtained with the validation data set, the model obtained is highly accurate and credible, with the only exception of slope (a tertiary-level

factor). *Quercus sp.* forests were predominantly predicted to occur at mean annual temperatures ranging from 9 to 15º. At 9-11º, the two main factors conditioning their presence
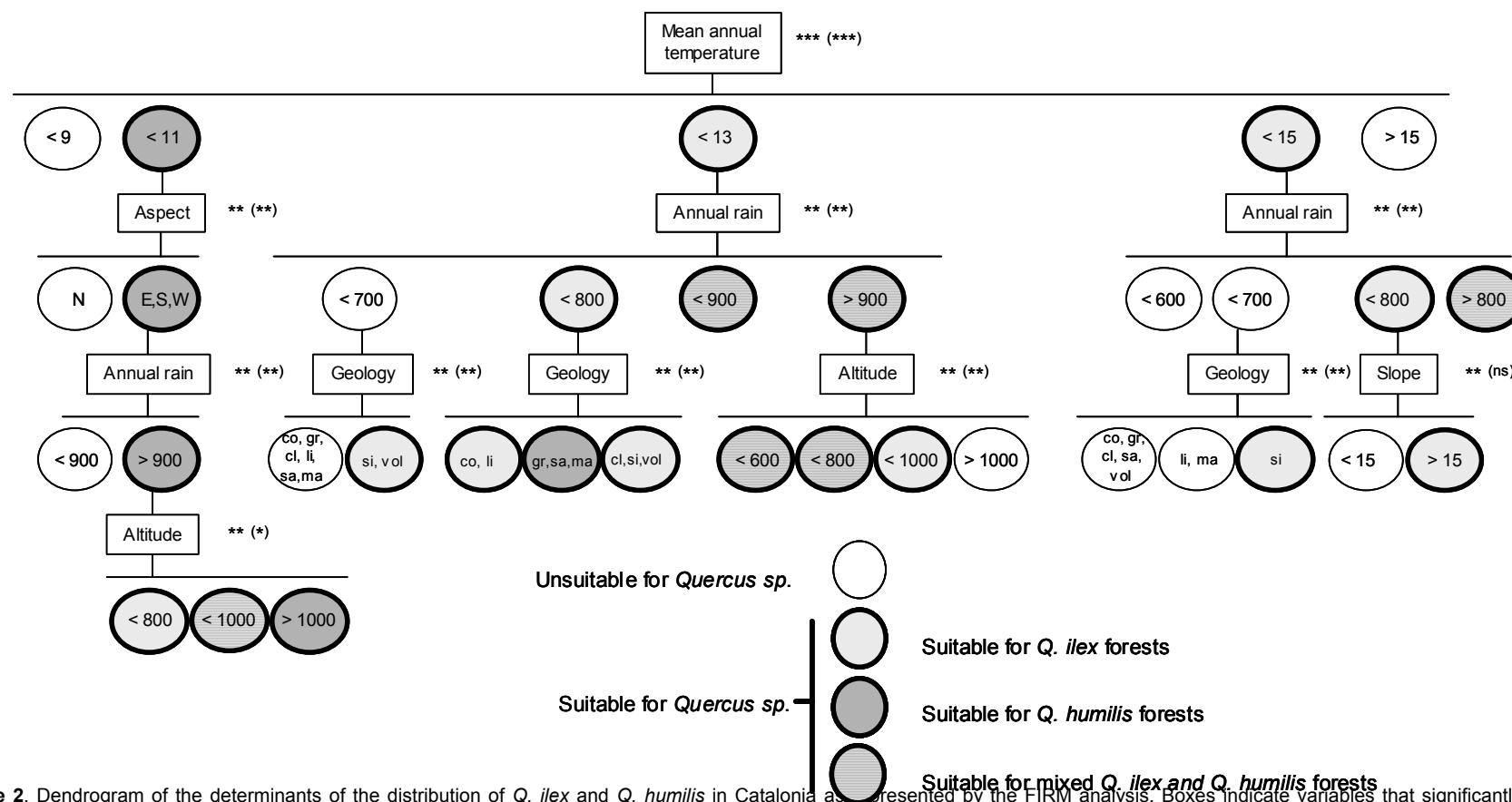
**Figure 2**. Dendrogram of the determinants of the distribution of *Q. ilex* and *Q. humilis* in Catalonia as presented by the FIRM analysis. Boxes indicate variables that significantly influence the presence of these species. Importance of the different variables decreases from top to down. Plain ellipsoids indicate combination of variables where the occurrence of *Quercus sp.* plots is lower than 50% Bold ellipsoids indicate combination of variables where the occurrence of *Quercus sp.* plots is higher than 50%. Bold and light-grey filled ellipsoids indicate combination of variables suitable for the occurrence of *Q. ilex* forests (s.e. *Q. ilex* plots are the most represented among those where *Quercus sp.* are present). Bold and dark-grey filled ellipsoids indicate combination of variables suitable for the occurrence of *Q. humilis* forests (s.e. *Q. humilis* plots are the most represented among those where *Quercus sp.* are present). Bold and vertically-dashed ellipsoids indicate combination of variables suitable for the occurrence of mixed *Q. ilex* and *Q. humilis* forests (s.e. mixed forest represents at least 30% of plots among those where *Quercus sp.* are present). Values are indicated in the ellipsoids (Temperature in °, annual rain in l m$^2$ yr$^{-1}$ and altitude in m). Significance of the variables used by the FIRM model in the calibration and in the validation (between parenthesis) data sets are indicated. ns = not significant, * < 0.05, ** < 0.0001.

were aspect and annual rain, being eastern, southern or western areas with a total annual rain higher than 900 l m$^2$ yr$^{-1}$ the most favourable conditions. At higher temperatures (11-13º), annual rain becomes the most important variable and *Quercus* forests are mostly expected to occur when annual rain is higher than 700 l m$^2$ yr$^{-1}$. At even warmer temperatures (13-15º), annual rain still remains the most important environmental variable and *Quercus sp.* forests are predicted to be located mainly in places when annual rain is higher than 800 l m$^2$ yr$^{-1}$ and slope is higher than 15º.

Concerning the distribution of each species separately, the comparison of the most suitable conditions for the presence of *Q. humilis* and *Q. ilex* forests reveals that temperature is the first and most important discriminator factor. *Quercus humilis* is absent at temperatures lower than 7º, while the probability of occurrence of this species is highest at temperatures of 9-11º (Figure 3).



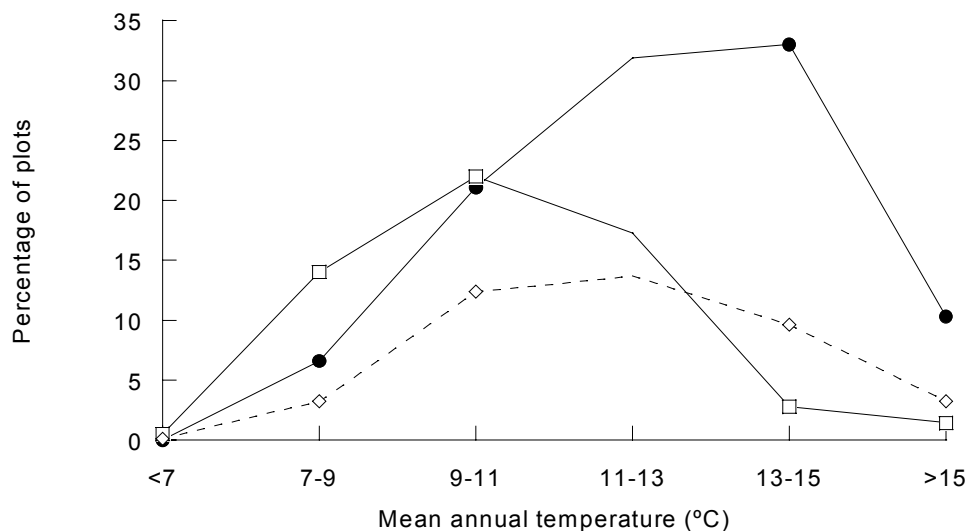**Figure 3.** Percentage of plots where adult trees of *Q. humilis* or *Q. ilex* are present in function of the mean annual temperature (ºC). *Quercus ilex* is represented by black dots and continue line, *Q. humilis* is represented by white squares and continue line and co-occurrence of both species (mixed forests) is represented by white diamonds and discontinue line.

According to Figure 2, *Q. humilis* forests are mostly predicted to occur in areas with a mean annual temperature between 9-11º, located in eastern, southern and western aspects that receive an annual rain higher than 900 l m$^2$ yr$^{-1}$ and that are situated in higher altitudes (> 1000 m). At mean annual temperatures between 11-13º *Q. humilis* forests are still well represented (Figure 3), they are expected to occur in areas with an annual rainfall between 700 l m$^2$ yr$^{-1}$ and 800 l m$^2$ yr$^{-1}$ either located in gravels, sandstone or marble substrates (Figure 2). The presence

of *Q. ilex* also increases with temperature until a mean annual temperature of 15º (Figure 3). At colder temperatures (9-11º), the occurrence of *Q. ilex* is very low and it would be restricted to eastern, southern and western aspects receiving an annual rainfall higher than 900 l m$^2$ yr$^{-1}$ and situated at lower altitudes than *Q. humilis* (< 1000 m) (Figure 2). At higher temperatures (11-13º), *Q. ilex* is expected to occur mostly in areas with an annual rainfall higher than 700 l m$^2$ yr$^{-1}$ but, in the rainiest areas (900 l m$^2$ yr$^{-1}$), *Q. ilex* is mainly present at an altitude lower than 1000 m (Figure 2). In the temperature interval of 13-15º, *Q. ilex* forests are mainly restricted to areas with annual rainfall higher than 700 l m$^2$ yr$^{-1}$, except in siliceous substrates receiving 600-700 l m$^2$ yr$^{-1}$ (Figure 2). The presence of mixed forests of *Q. ilex* and *Q. humilis* never surpass the percentage of presence of monospecific *Q. ilex* and *Q. humilis* forests (Figure 3). Mixed forests have a higher probability to occur (more than 1/3 of all the plots where oaks are present) in mild temperatures (11-13º) (Figure 3), with an annual rainfall higher than 800 l m$^2$ yr$^{-1}$ and at altitudes lower than 800 m (Figure 2). Moreover, mixed forests are also predicted to be present at warmer temperatures (13-15) with annual rainfall higher than 800 l m$^2$ yr$^{-1}$.

The regeneration of *Q. ilex* and *Q. humilis* is primarily driven by the presence of these species in the overstory, because this is the first factor incorporated in the tree regression models (Figures 4, 5). Total basal area of the plot and environmental variables such as temperature, rain or altitude appear in a secondary term. Notwithstanding the referred importance of the presence of adult trees in the overstory, seedlings and saplings of both species were found in a small percentage of plots where *Q. humilis* and *Q. ilex* were absent in the tree layer (respectively, 7% and 6% for *Q. ilex* seedlings and saplings, and 6% and 5% for *Q. humilis* ones). Concerning the presence of seedlings in plots where *Q. humilis* and *Q. ilex* were present as adults, it is important to remark that: i) it was considerably low (less than 20% of plots presented seedling regeneration) and ii) no difference existed between plots where the species were present in the overstory (>0 but les than 66% in basal area) and those where they dominated the forest stand (more than 66% in basal area) (Figures 4A and 5A). The comparison of the *p* values obtained with the models indicates that the models were, in all cases, highly accurate and credible (see *p* values in Figures 4 and 5). The number of plots with regeneration of *Q. ilex* seedlings in *Q. ilex* forests increased with the basal area of the plot, while the presence of *Q. ilex* seedlings in absence of *Q. ilex* in the canopy mainly occurred in areas receiving between 600 and 1000 l m$^2$ yr$^{-1}$ and with a mean annual temperature between 11-13º (Figure 4A). The presence of saplings in *Q. ilex* forests followed a more complex model: it increased with the total basal area of the stands where this species was present, while in plots where it dominated, was higher in the areas located in a temperature interval between 9 and 15º (Figure 4B). According to Figure 5A, the presence of *Q. humilis* seedlings in other forest types increased in stands with higher basal area and, in a second term, in places with an annual rainfall of 700-800 l m$^2$ yr$^{-1}$ and a temperature over 7º. In this species, the presence of sapling regeneration increased with the dominance of *Q. humilis* in the overstory. In stands

where *Q. humilis* was present but not dominant, occurrence of saplings was higher in places with a mean annual temperature over 9º and a basal area higher than 10 m$^2$ ha (Figure 5B).

**(A) Seedlings**

Q. ilex presence in the canopy   ** (**)

0          > 0

Annual rain   ** (**)          Total BA   ** (**)

< 600   < 1000   > 1000          < 15   > 15

Mean annual temperature   * (*)

< 11   < 15   > 15

**(B) Saplings**

Q. ilex presence in the canopy   ** (**)

0          < 66          > 66

Annual rain   ** (**)          Total BA   ** (**)          Mean annual temperature   ** (**)

< 700   > 700          < 5   < 15   < 20   > 20          < 9   > 9

>0 - 5% plots containing *Q. ilex* seedlings or saplings

5 - 10% plots containing *Q. ilex* seedlings or saplings

10 - 15% plots containing *Q. ilex* seedlings or saplings

15 - 20% plots containing *Q. ilex* seedlings or saplings

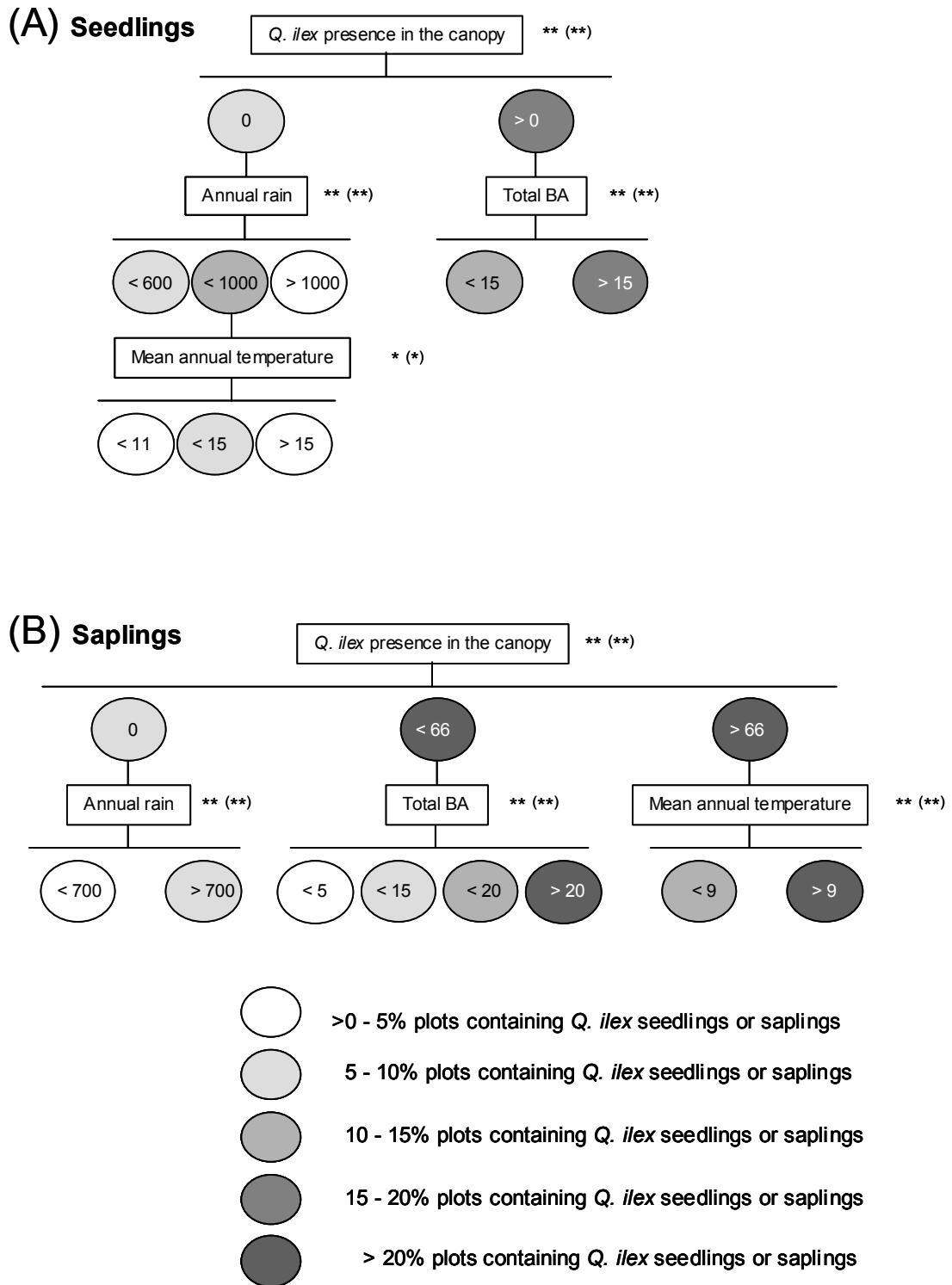> 20% plots containing *Q. ilex* seedlings or saplings

**Figure 4**. Dendrogram of the determinants of the presence of *Q. ilex* seedlings (A) and saplings (B) in Catalonia as represented by the FIRM analysis. Boxes indicate variables that significantly influence the presence of plots with regeneration of *Q. ilex*. Importance of the different variables decreases from top to down. Colours of the ellipsoids indicate different percentages of occurrence of plots with seedlings or saplings of *Q. ilex* present. Values are indicated in the ellipsoids: Q. ilex presence in the canopy (0= absent, >0 and <66% = present, > 66% dominant), total basal area of the plot in $m^2$, temperature in °, annual rain in $l\ m^2\ yr^{-1}$ and altitude in m). Significance of the variables used by the FIRM model in the calibration and in the validation (between parenthesis) data sets are indicated. ns = not significant, * < 0.05, ** < 0.0001.
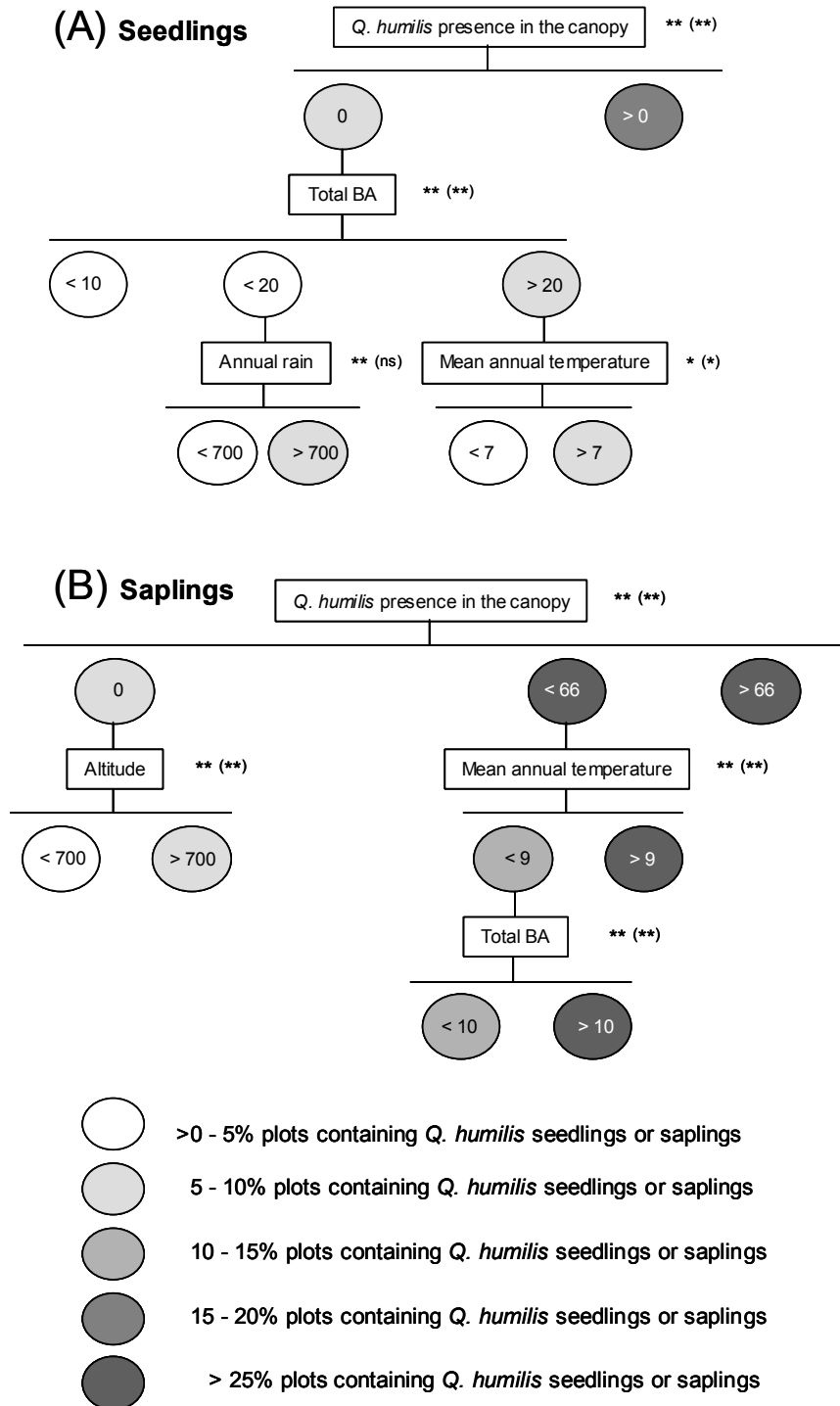
**Figure 5.** Dendrogram of the determinants of the presence of *Q. humilis* seedlings (A) and saplings (B) in Catalonia as represented by the FIRM analysis. Boxes indicate variables that significantly influence the presence of plots with regeneration of *Q. humilis*. Importance of the different variables decreases from top to down. Colours of the ellipsoids indicate different percentages of occurrence of plots with seedlings or saplings of *Q. humilis* present. Values are indicated in the ellipsoids: *Q. humilis* presence in the canopy (0= absent, >0 and <66% = present, > 66% dominant), total basal area of the plot in $m^2$, temperature in °, annual rain in $l\ m^2\ yr^{-1}$ and altitude in m). Significance of the variables used by the FIRM model in the calibration and in the validation (between parenthesis) data sets are indicated. ns = not significant, * < 0.05, ** < 0.0001.

The regeneration patterns of mixed *Q. ilex - Q. humilis* forests varied depending on which species was dominant in the mixture ($\chi^2 = 66.97$, *p*<0.0001). In mixed forests dominated by *Q. ilex* in the overstory, the percentage of plots where seedlings of this species dominated the regeneration were more frequent than plots dominated by seedlings of *Q. humilis* (19.9 % and 0.9 % of plots respectively), while in forests dominated by *Q. humilis*, the regeneration of the two species was very similar (7.5 % of plots dominated by seedlings of *Q. humilis* and 10.4% of plots dominated by those of *Q. ilex*). The presence of saplings coincided with the dominant species in the canopy: under *Q. ilex* canopy, in 82.0 % of the plots dominate *Q. ilex* saplings and under *Q. humilis* canopy in 52.3 % of the plots dominate *Q. humilis*. The number of *Q. ilex* saplings regenerating in forests dominated by *Q. humilis* (24.0 % of the plots) was higher than the proportion of *Q. humilis* saplings regenerating in *Q. ilex* forests (4.3% of the plots) ($\chi^2 = 110.14$, *p*<0.0001).

**Quercus ilex and *Q. humilis* dynamics: growth, survival of adult trees and recruitment in the tree layer**

The results of the ANOVA for the $RGR_{ba}$ are summarized in Table 1. All main factors except aspect had a significant effect on $RGR_{ba}$. Thus, *Q. humilis* had higher $RGR_{ba}$ than *Q. ilex* (46.2±1.7% and 37.1±1.3%, respectively). The two species performed similarly under the different levels of mean annual temperature, with higher values of $RGR_{ba}$ in the temperature classes 11-13°C (44.1 ± 1.8%) and > 13°C (42.6 ± 1.6%) than in temperatures < 11°C (32.4 ± 2.2%).

**Table 1.** F values of the analysis of variance for the effects of species, mean annual temperature, annual precipitation and aspect on the RGR in area basal of trees during a ten-yr period. Statistical significance: n.s., not significant; *, *p*<0.05; **, *p*<0.01; ***, *p*<0.001.

| Source of variation | df | F |
|---|---|---|
| Species (Sp) | 1 | 6.2* |
| Mean annual temperature (AT) | 2 | 5.4** |
| Annual precipitation (AP) | 2 | 6.5** |
| Aspect (As) | 3 | n.s. |
| Sp x AT | 2 | n.s. |
| Sp x AP | 2 | n.s. |
| Sp x As | 3 | n.s. |
| AT x AP | 4 | 3.1* |
| AT x As | 6 | n.s. |
| AP x As | 6 | n.s. |
| Residual | 491 | |

Finally, trees achieved higher $RGR_{ba}$ values in the level of rainfall > 900mm (50.4 ± 2.6%) than in the other two levels (700 mm: 38.4± 1.9%; 700-900 mm: 38.2 ± 1.3%). The only significant interaction was mean annual temperature x annual rainfall, with $RGR_{ba}$ clearly favoured by an

increase of rainfall in the temperature level 11-13ºC, but not in the other levels (Figure 6). The basal area of plots, introduced in the analysis as a covariate, was negatively correlated with the $RGR_{ba}$, similarly for both species.
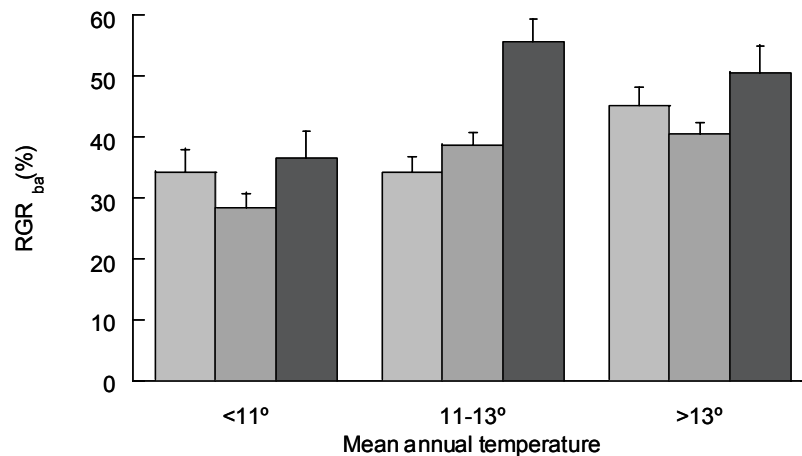


**Figure 6.** Mean and + S.E. of the $RGR_{ba}$ (%) of *Quercus ilex* and *Quercus humilis* trees under the three categories of mean annual temperature and the three categories of precipitation. Light grey bars represent the annual precipitation level <700 mm, dark grey bars represent the precipitation level 700-900 mm and black bars are the precipitation level >900.

The log-linear analysis of the frequency of death trees for the variables species, state and size reported a best model with the interactions state x size and species x size (goodness-of-fit: $\chi^2$= 2.20 and *p* value of the model = 0.70). The highest percentage of live trees (56.2 % of alive trees) was of the size between 12.5-22.5 cm of DBH, while the highest percentage of death trees (52.0% of death trees) was found in the size category between 7.5-12.5 cm of DBH.

The multiple regressions for the number of saplings recruited in the tree layer as dependent variable were significant for both species: $R^2_{(Q. ilex)}$ = 0.332, *p* < 0.0001, and $R^2_{(Q.humilis)}$ = 0.055, *p* < 0.0001. According to the results shown in Table 2, the recruitment of *Q. ilex* saplings was affected positively by mean annual temperature and tree density in the plot, and negatively by basal area of the plot. On the other hand, tree density improved the recruitment of *Q. humilis* saplings, while basal area had a negative effect (Table 2).

**Table 2.** Significant variables in the backward multiple regression for *Q. ilex* and for *Q. humilis* in the area where both species co-occur. The dependent variable was the number of saplings recruited in the tree layer and the independent variables tested were: slope, altitude, mean accumulated annual rainfall, mean annual temperature, plot tree density and plot basal area.

| Species | *Variables* | Beta | *S.E. of Beta* | *B* | *S.E. of B* | *t* | *p-level* |
|---|---|---|---|---|---|---|---|
| | Mean annual temperature | 0.109 | 0.032 | 0.116 | 0.034 | 3.460 | <0.0001 |
| *Q. ilex* | Tree density | 0.774 | 0.042 | 0.002 | 0.000 | 18.363 | <0.0001 |
| | Basal Area | -0.427 | 0.042 | -0.087 | 0.009 | -10.140 | <0.0001 |
| | Density | 0.304 | 0.049 | 0.000 | 0.000 | 6.190 | <0.0001 |
| *Q. humilis* | Basal Area | -0.260 | 0.049 | -0.025 | 0.005 | -5.283 | <0.0001 |

**DISCUSSION**

**Determinants of the distribution of *Q. ilex* and *Q. humilis* adults and regeneration**

This study points out that the distribution of *Q. ilex* or *Q. humilis* in Catalonia follows a temperature gradient, with an optimal for *Q. humilis* at temperatures between 9-11ºC, while temperatures between 11-15ºC are more favourable for *Q. ilex*. Aspect and annual rainfall fine-tune both species distribution at smaller scales, being aspect more important in the colder range of temperatures and, as temperature increases, annual rainfall achieves more relevance. At these small scales, where aspect controls species distribution, *Q. humilis* presented a large tolerance (excepting northern faces in the lower temperature). Thus, similar to other studies (Ohmann and Spies 1998, Gracia 2000), our results point out a multiscaled control of vegetation distribution, with climate as a main determinant of *Q. ilex* and *Q. humilis* distribution patterns, and topography (altitude and slope) and geology fine tuning these patterns over the landscape. Mean annual temperature and annual precipitation have been extensively used to describe climatic requirements of communities (Ozenda 1985; Sun and Feoli 1992; Brzeziecki et al. 1995), in part because these averaged climate characteristics are more appropriate for climatological characterization of communities (Breziecki et al. 1995). Global distribution of evergreen and deciduous species has been related to temperature (Chabot and Hicks 1982), with evergreen broadleaf species dominating in warm areas and deciduous broadleaf species in more temperate areas. This pattern is repeated at the regional scale of this study and may be associated with differences in the physiology of the species in front of climate variables. In areas with lower mean annual temperature, where winter severity is high, carbon balance of evergreens during the unfavourable season becomes increasingly negative, whereas that of deciduous trees do not (Kozlowski 1991; Waring 1991). Moreover, evergreens may undergo extensive water stress due to frost-drought (Savé et al. 1988). In these cold areas, slope aspect, which is related to solar insolation and hence potential evapotranspiration seems to improve the effect of low temperatures, enabling *Q. ilex* to be present at least in southern aspects. In the opposite end of the gradient, elevated temperatures condition trigger a great evaporative demand that may be matched by *Q. ilex* in high rainfall areas. Although the different tendencies of *Q. ilex* and *Q. humilis* optima, the distribution of both species is widely overlapped, as is shown in Figure 1. Moreover, mixed forests exist in a broad range of environmental conditions, representing 21.4 % of the plots where *Quercus* trees are present: in the colder extreme mixed forests appear in all aspects except in the northern one, but only under levels of rainfall higher than 900 l m$^2$ yr$^{-1}$ and altitudes between 800-1000 m. At increasing temperatures, they are well represented in areas with mean annual rainfall over 800 l m$^2$ yr$^{-1}$.

The patterns of distribution of the regeneration are the result of a complex set of processes that integrate the effect of biotic and abiotic environments on seed dispersal, germination and

emergence, and growth, survival, and establishment of seedlings and juveniles (Grubb 1977; Harper 1977; Herrera et al. 1994). Our results confirm that the regeneration of both species may depend largely on the availability of seeds, because the presence of adults in the canopy is the main factor that describes the presence of seedlings and saplings of both species. Oaks recover after disturbances due to their resprouting ability. However, in the large periods between disturbances, when sexual reproduction takes place, seedling regeneration of oak species is rare (Crow 1988, 1992; Callaway and Davis 1998; Retana et al. 1999). In this study, the number of plots with *Q. ilex* or *Q. humilis* seedling regeneration is also very low, with less than 20% of plots with *Q. ilex* or *Q. humilis* on the canopy with saplings or seedlings. Very few plots had oak regeneration when *Q. ilex* or *Q. humilis* were absent in the canopy, a phenomenon that has been related to the long distance dispersal of acorns by animals (Bossema 1977). The two species were favoured by a large total basal area in the plots, a characteristic that is associated to the positive effect of the canopy vegetation on the water balance of seedlings (Bran 1990; Broncano 1995). However the positive effect of the plot basal area was exerted in two different situations for both species: in plots with *Q. ilex* canopy for seedlings of this species, and in plots without *Q. humilis* in the canopy for seedlings of this species. This fact may imply that both species are favoured by different overstory composition that, in turn, may trigger different microenvironmental conditions. Moreover, the probability of occurrence of saplings is related to variables different than those that condition seedling occurrence. These differences between seedlings and sapling suggest the existence of a conflict seedling-sapling (sensu Schupp 1995). A profound study of the response of seedlings of both species to the environmental variables (i.e. light, water and nutrients) is required to understand their patterns of regeneration and distribution.

In the case of mixed forests, the regeneration showed a different pattern depending on the two size categories of regeneration: the frequency of *Q. ilex* seedlings was higher than the frequency of *Q. humilis*, but in the phase of saplings both species presented the same frequency of individuals. Differences in the abundance of seedlings between both oaks seem to be due to the close relationship between adults' presence and regeneration under adults canopy. Thus, as has been found in other studies (Rusch and Fernández-Palacios 1995; Wester 1995), the differences in seedlings abundance may be more related to variability in available space, resource patchiness, seed production rather than the effect climate or local factors.

**Quercus ilex and Q. humilis dynamics: growth and survival of adult trees and recruitment of saplings to the tree layer**

The highest RGR$_{ba}$ obtained for *Q. humilis* coincides with the results found in numerous studies showing deciduous species having higher potential growth rates than evergreen ones (Reich et

al. 1992, 1997; Cornelissen et al. 1996, 1998; Reich 1998). However, the general assumption that deciduous species are relegated to moist and nutrient-rich environments with high resources availability (i.e. low rainfall levels) (Aerts 1995) does not agree with our data, becauase *Q. humilis* also has higher $RGR_{ba}$ than *Q. ilex* under the lower rainfall conditions where mixed forest are distributed. Evergreenness has been related to the resistance to desiccation and drought injury (Mitrakos 1980), thus, until a certain point, it is surprisingly that the deciduous *Q. humilis* maintains a higher $RGR_{ba}$ than *Q. ilex* under all conditions. This may be explained by the fact that leaves of the two species respond similarly to water-limiting conditions and have similar intrinsic water use efficiency (Damesin et al 1997, 1998). The highest RGR of deciduous species confers them more competitive advantage over the evergreen species (Cornelissen et al. 1996, 1998), but it remains unclear how *Q. humilis* performs in the poor end of the resources gradient, and why *Q. ilex*, with its lower RGR ratio, is able to occur in rich areas where it should be outcompeted by the deciduous oak.

Annual mortality rates for *Q. ilex* (0.13%) and *Q. humilis* (0.09%) were very low but comparable with the mortality rates of some shade tolerant species in second-growth stands (Lorimer et al. 2001). The highest mortality rates of both species were concentrated on the smaller size class (7.5-12.5 cm DBH), that usually are the suppressed individuals that remain in the understory until the appearance of an opportunity to reach the canopy. The lack of differences in mortality rates between pure forest and mixed forests was expected because these formations are placed in suitable areas for the performance of both species.

Finally, in mixed forests recruitment of *Q. ilex* saplings in the tree layer is favoured by high mean annual temperature, while *Q. humilis* saplings seem to be not dependent on temperature conditions. The recruitment of both species is negatively affected by total basal area of the plot (as a surrogate of shade). This negative effect of shade in the recruitment of *Quercus* spp. juveniles has long be described for different authors (Tang et al. 1990; Kolb et al 1990; Crow 1992; Espelta 1995). *Quercus ilex* and *Q. humilis* behave as shade tolerant species, that are able to survive under low light conditions without a positive net growth, but that require higher light conditions than those existing under the oak canopy, to be capable to recruit into the next life state (Retana et al. 1999).

**CONCLUSIONS**

At the regional scale of the study, the results of the distribution of the evergreen *Q. ilex* and the deciduous *Q. humilis* show that both species co-occur in a wide intermediate range of annual temperatures. The colder end is more advantageous for *Q. humilis*, while the warmer end is more favourable for *Q. ilex*. However the analysis of the distribution of the mixed forests show that the probability of occurrence of these formations is lower than the probability of occurrence

of pure forests. Due to the common range of distribution of both species, it will be expected to find higher occurrence of mixed forests. Moreover, species dynamics in areas where both species co-occur show *Q. humilis* having the highest RGR values under all temperature and rainfall conditions, no differences in mortality between both species, and a lack of effect of environmental variables on the recruitment of *Q. humilis* saplings in the tree layer. All these results suggest that pure *Q. humilis* and mixed forests of both species could be more abundant and that a large proportion of pure *Q. ilex* forests may be the result of the action of factors other than climate, topography or soil. Thus, it seems more feasible that human action, directly or indirectly, has favoured the spread of *Q. ilex* in the past (Barbero et al. 1992; Riera-Mora 1995) because it was more valuable than *Q. humilis* for obtaining charcoal and firewood. Humans have also altered the disturbance regime in the Mediterranean basin, resulting in a high recurrence of disturbances (i.e. fire, coppicing, livestock grazing, etc) that is supposed to favour *Q. ilex* expansion (Barbero et al. 1992; Riera-Mora 1995). The abandonment of coppicing practices in some Mediterranean regions opens the question of how may change pure and mixed forests of both species, because oak regeneration values under oak canopies are very low, and there is no enough information on the factors that limit seedling abundance and establishment. Moreover, it is clear that the environment perceived by a seedling is different by that perceived by an adult. It makes essential to perform a more detailed study on the regeneration niche of these species to understand the factors and processes that limit their regeneration, because the patterns of relative abundance of different species at the seedling stage may further persist in the community composition of adult trees (Denslow 1987; Latham 1992).

**REFERENCES**

Aerts, R. 1995. The advantages of being evergreen. Trends in ecology and evolution, 10: 402-407.

Aerts, R. and van der Peijl, M.J. 1993. A simple model to explain the dominance of low-productive perennials in nutrient-poor habitats. Oikos. 66: 144-147.

Bacilieri R., Bouchet M. A., Bran D., Grandjanny M., Maistre M., Perret P. & Romane F.. Germination and regeneration mechanisms in Mediterranean degenerate forests. Journal of Vegetation Science 4: 241-246

Barbero, M; Loisel, R. and Quézel, P. 1992. Biogeography, ecology and history of Mediterranean Quercus ilex ecosystems. Vegetatio, 99-100: 19-34.

Berendse, F. 1994. Competition between plant populations at low and high nutrient supplies. Oikos: 71: 253-260.

Blondel, J. and Aronson, J. 1995. Biodiversity and ecosystem function in the Mediterranean basin: human and non-human determinants.. In:. Davis G. W & Richardson D. M: (eds).Mediterranean-type ecosystems: the function of biodiversity. Springer-Verlag, Berlin. pp. 43-119.

Bongers, F; Poorter, L; Van Rompaey, R.S.A.R. and Parren, M.P.E. 1999. Distribution of twelve moist forest canopy tree spcies in Liberia and Côte d'Ivoire: response curves to a climatic gradient. Journal of Vegetation Science, 10: 371-382.

Bossema, I. 1977. Jays and oaks: an eco-ethological study of a symbiosis. Behaviour, 70: 1-10.

Bran, D.; Lobreaux, O.; Maistre, M.; Perret, P. and Romane, F. 1990. Germination of Quercus ilex and Quercus pubescens in a Q. ilex coppice. Long-term consequences. Vegetatio, 87: 45-50.

Broncano, M.J. 1995. Estudio de la revegetación de zonas potencialmentes ocupadas por bosques mixtos de pino carrasco y encina. Trabajo de master. Universidad Autònoma de Barcelona, Barcelona.

Brzeziecki, B; Kienast, F and Wildi, O. 1995. Modelling potential impacts of climate change on the spatial distribution of zonal forest communities in Switzerland. Journal of Vegetation Science, 6: 257-268.

Chabot, B.F. and Hicks, D.J. 1982. The ecology of leaf life spans. Annual Review of Ecology and Systematics, 13: 229-259.

Clark, D.B; Palmer, M.W. and Clark, D.A. 1999. Edaphic factors and the landscape-scale distributions of tropical rain forest trees. Ecology, 80: 2662-2675.

Cornelissen, J.H.C; Castro Diez, P. and Hunt, R. 1996. Seedling growth, allocation and leaf attributes in a wide range of woody plant species and types. Journal of Ecology, 84: 755-765.

Cornelissen, J.H.C.; Castro-Diez, P. and Carnelli, A.C. 1998. Variation in relative growth rate among woody species: scaling up. In: Lambers, H.; Poorter, H. and Vuuren, M van (eds.)Inherent variation in plant growth: physiological mechanisms and ecological consequences. Backhuys, Leiden.

Crow, T.R. 1988. Reproductive mode and mechanisms for self-replacement of Northern red oak (*Quercus rubra*)- A review. Forest Science, 34: 19-40.

Crow, T.R. 1992. Population dynamics and growth patterns for a cohort of northern red oak (Quercus rubra) seedlings. Oecologia, 91: 192-200.

Damesin, C.; Rambal, S. and Joffre, R. 1997. Between-tree variations in leaf $\delta^{13}$C of *Quercus pubescens* and *Quercus ilex* among Mediterranean habitats with different water availability. Oecologia, 111: 26-35.

Damesin, C.; Rambal, S. and Joffre, R. 1998. Co-occurrence of trees with different leaf habit: a functional approach on Mediterranean oaks. Acta Oecologica, 19: 195-204.

Denslow, J.S. 1987. Tropical rainforest gaps and tree species diversity. Annual Review of Ecology and Systematics, 18: 431-451.

Espelta, J.M. 1996. La regeneració de boscos d'alzina (*Quercus ilex* L.) i pi blanc (*Pinus halepensis* Mill.): Estudi experimental de la resposta de les plàntules a la intensitat de llum i a la disponibilitat d'aigua. Tesi Doctoral. Universitat Autònoma de Barcelona.

Espelta, J.M; Riba, M. and Retana, J. 1995. Patterns of seedling recruitment in West-Mediterranean *Quercus ilex* forests influenced by canopy development. Journal of Vegetation Science, 6:465-472.

Franklin, J. 1998. Predicting the distribution of shrub species in southern California from climate and terrain-derived variables. Journal of Vegetation Science, 9: 733-748.

Fulton, M.R. and Prentice, I.C. 1997. Edaphic controls on the boreonemoral forest mosaic. Oikos, 78: 291-298.

Gracia, C.A; Ibáñez, J.J; Vayreda, J; Pons, X. and Terrradas, J. 1997. A nuevo concepto de inventario forestal. In: Proceedings of the XI World Forestry Congress, Vol I. World Forestry Association, Antalya.

Gracia, M. 2000. La encina y los encinares en Catalunya. Aproximación a su distribución, dinámica y gestión. Tesis Doctoral. Bellaterra. Barcelona.

Gracia, M; Retana, J. and Picó, X. 2001. Seedling bank dynamics in managed holm oak (*Quercus ilex*) forests. Annals of Forest Science, 58: 843-852.

Grubb, P.J. 1977. In plant communities: the importance of the regeneration niche. Biological Reviews, 52: 107-145.

Hawkins, D.M. 1999. Formal inference-based recursive modelling. Department of Applied Statistics, University of Minnesota, St. Paul, MN.

Harper, J.L. 1977. Population biology of plants. Academic Press, London, UK.

Herrera, C.M.; Jordano, P.; López-Soria, L. and Amat, J.A. 1994. Recruitment of a mast-fruiting, bird-dispersed tree: bridging frugivore activity and seedling establishment. Ecological Monographs, 64: 315-344.

Institut Cartogràfic de Catalunya. 1989. Mapa geològic de Catalunya. 1:250000. Barcelona.

Iverson, L.R. and Prasad, A.M. 1998. Predicting abundance of 80 tree species following climate change in the eastern United States. Ecological Monographs, 68: 465-485.

Kolb, T.E.; Steiner, K.C; Mc Cormick, L.H. and Bowersow, T.W. 1990. Growth response of northern red-oak and yellow-poplar seedlings to light, soil moisture and nutrients in relation to ecological strategy. Forest Ecology and Management, 38: 65-78.

Kozlowshi, T.T. 1991. Effects of Environmental Stresses on Deciduous Trees. In: Mooney, H.A.; Winner, W.E. and Pell, E.J. (eds.). Response of Plants to Multiple Stresses. Academic Press, San Diego, California.

Latham, R.E. 1992. Co-occurring tree species change rank in seedling performance with resources varied experimentally. Ecology, 73: 2129-2144.

Lertzman, K.P. 1995. Forest dynamics, differential mortality, and variable recruitment probabilities. Journal of Vegetation Science, 6: 191-204.

Lorimer, C.G; Dahir, S.E and Nordheim, E.V. 2001. Tree mortality rates and longevity in mature and old-growth hemlock-hardwood forests. Journal of Ecology, 89: 960-971.

Lusk, C.H. and Smith, B. 1998. Life history differences and tree species coexistence in an old-growth New Zealand rain forest. Ecology, 79: 795-806.

Mitrakos, K. 1980. A theory for Mediterranean plant life. Acta Oecologica Oecologia Plantarum, 1: 245-252.

Minnick, T.J; Coffin, D.P. 1999. Geographic patterns of simulated establishment of two *Bouteloua* species: implications for distributions of dominants and ecotones. Journal of Vegetation Science, 10: 343-356.

Motzkin, G.; Wilson, P.; Foster, D.R. and Allen, A. 1999. Vegetation patterns in heterogeneous landscapes: The importance of history and environment. Journal of Vegetation Science, 10: 903-920.

Ninyerola, M; Pons, X. and Roure, J.M. 2000. A methodological approach of climatological modelling of air temperature and precipitation through GIS techniques. International Journal of Climatology, 20: 1823-1841.

Ohmann, J.L. and Spies, T.A. 1998. Regional gradient analysis and spatial pattern of woody plant communities of Oregon forests. Ecological Monographs, 68: 151-182.

Oliver, C.D. and Larson, B.C. 1990. Forest Stand Dynamics. McGraw-Hill, New York.

Ozenda, P. 1985. La végétation de la chaîne alpine dans l'espace montagnard européen. Masson, Paris.

Pacala, S.W ; Canham, C.D ; Saponara, J ; Silander, J.A ; Kobe, R.K and Ribbens, E. 1996. Forest models defined by field measurements : II. Estimation, error analysis and dynamics. Ecological Monographs, 66: 1-43.

Pigott, C.D. and Pigott, S. 1993. Water as a determinant of the distribution of trees at the boundary of the Mediterranean zone. Journal of Ecology, 81: 557-566.

Pons, A. and Vernet, J.L. 1971. Une synthèse nouvelle de l'historie du chêne vert. Bull Soc Bot Fr, 118 : 841-850.

Pons, A. and Quézel, P. 1985. The history of the flora and vegetation and past and present human disturbance in the Mediterranean area. In: Gomez-Campo, C. (ed) Plant Conservation in the Mediterranean area. Geobotany 7. Junk, Dordrecht.

Reich, P.B. 1998. Variation among plant species in leaf turnover rates and associated traits: implications for growth at all life stages. In: Lambers, H.; Poorter, H. and Vuuren, M van (eds.) Inherent variation in plant growth: physiological mechanisms and ecological consequences. Backhuys, Leiden.

Reich, P.B; Walters, M.B. and Ellsworth, D.S. 1992. Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. Ecological Monographs, 62: 365-392.

Reich, P.B; Walters, M.B and Ellsworth, D.S. 1997. From tropics to tundra: global convergence in plant functioning. Proc Natl Acad Sci USA, 94: 13730-13734.

Reichard S.H and Hamilton, C.W. 1997. Predicting invasions of woody plants introduced to North America. Conservation Biology, 11: 193-203.

Riera i Mora, S. 1995. Evolució del paisatge vegetal holocè al Pla de Barcelona a partir de les dades pol.líniques. Tesi doctoral U.B. Barcelona.

Rouget, M; Richardson, D.M; Lavorel, S; Vayreda, J; Gracia, C and Milton, S.J. 2001. Determinants of distribution of six Pinus species in Catalonia, Spain. 2001. Journal of Vegetation Science, 12: 491-502.

Rusch, G. and Fernández-Palacios, J.M. 1995. The influence of spatial heterogeneity on regeneration by seed in a limestone grassland. Journal of Vegetation Science, 6: 417-426.

Savé, R; Rabella, R and Terradas, J. 1988. Effects of low temperature on Quercus ilex L. ssp. Ilex water relationships. In: Di Castri, F; Floret, C; Rambal, S and Roy J. (eds.) Time scales and water stress. Proc 5$^{th}$ Int Conf on Mediterranean ecosystems. International Union of Biological Sciences, Parris.

Schupp, E.W. 1995. Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. American Journal of Botany, 82: 399-409.

Shafer, S.L; Bartlein, P.J and Thompson, R.S. 2001. Potential Changes in the Distributions of Western North America Tree and Shrub Taxa under Future Climate Scenarios. Ecosystems, 4: 200-215.

Sun, C.Y. and Feoli, E. 1992. Trajectory analysis of Chinese vegetation types in a multidimensional climatic space. Journal of Vegetation Science, 3: 587-594.

Tang, Y; Washitani, I. and Takayoshi, I. 1990. Growth analysis of Quercus serrata seedlings within Miscanthus sinensis grass canopies differing in light availability. Ecological Research, 5: 367-376.

Terradas, J. 1999. Holm oak and holm oak forests: an introduction. In Ecology of Mediterranean evergreen oak forests. Rodà, F; Retana, J; Gracia, C.A. and Bellot, J. (eds.) Springer-Verlag, Berlin.

Waring, R.H. 1991. Responses of Evergreen Trees to Multiple Stresses. In: Mooney, H.A.; Winner, W.E. and Pell, E.J. (eds.). Response of Plants to Multiple Stresses. Academic Press, San Diego, California.

Wester, D.B. 1995. Seed physiology and germination. In: Bedunah, D.J and Sosebee, R.E. (eds.) Wildland plants: physiological ecology and development morphology. Society for Range Management, Denver, CO.

# CONTRIBUTION OF SEED PRODUCTION, SEED SURVIVAL AND SEEDLINGS EMERGENCE TO THE REPRODUCTIVE OUTPUT OF TWO COEXISTING MEDITERRANEAN OAKS

**INTRODUCTION**

Understanding plant population and community dynamics requires a detailed knowledge of each species recruitment. Differences in seed production, seed survival, seed germination and seedling establishment between co-occurring species may largely determine species coexistence (Louda 1982; Schupp 1988, 1990; Latham 1992; Valverde and Silvertown 1995). Seed production, predation and germination, which depend on inherent plant characteristics (seed size, seed infection and nutritional, energy or water content of seeds), are in turn affected by biotic and abiotic factors such as weather conditions, attack by pathogens, etc. (Tripathi and Khan 1990; Johnson et al. 1993; Reader 1993; Kollmann et al. 1998). And all these processes and relationships, which vary among habitats (Hulme 1994; Holt et al. 1995; Ostfeld et al. 1997), might be fine-tuned by the timing of fruit ripening and dispersion, that determine the length of time that seeds are vulnerable for predators (Blate et al. 1998), for desiccation (Gryj and Dominguez 1996) and the weather conditions that seeds will find during the germination period.

Despite their ubiquitous presence in the northern hemisphere, oaks are difficult to regenerate (Crow 1988, 1992; Callaway and Davis 1998). *Quercus* spp. produce acorns of large size and weight that can improve seedling germination, survival and growth (Ke and Werger 1999; Seiwa 2000; Kirkpatrick and Pekins 2002), but that may have negative effects on seed performance because they are more susceptible to predation (Reader 1993) and desiccation (Sonesson 1994, Germaine and McPherson 1998). Many oaks produce seeds at irregular intervals, a pattern of seed production called masting (Koening et al. 1994; Healy et al. 1999; Greenberg 2000). In Mediterranean ecosystems, all these characteristics interact with a heterogeneous environment, and a seasonal drought. Due to the particular climatic sequence, acorns ripening process coincides with the hot and dry summer whereas acorn dispersion takes place during the wet and mild autumn. Moreover, the high plant diversity of the Mediterranean forest understory increases the variety of fruits available for predators and their particular structure generates a highly heterogeneous mosaic of habitats and resources.

In the Mediterranean Basin, Quercus coppices are characterized by a long history of human exploitation (Barbero et al. 1992). However, the abandonment of the extracting/thinning activities has generated a mosaic of coppices in different successional phases. In this new context, sexual reproduction has acquired greater importance in the regeneration of the forest, because the seed ecology processes might generate the basis for determining community composition (Swaine et al. 1987; Schupp 1990). *Quercus ilex* L. and *Q.* x *cerrioides* Wk. et Costa are two of the most characteristic oak species in the western Mediterranean Basin. *Q. ilex* is a widespread species present over a large area extending 6000 km longitudinally from Portugal to Syria and 1500 km latitudinally from France to Morocco and Algeria (Terradas 1999). *Q. cerrioides* is a deciduous oak, whose distribution is more restricted to the plains of NE

Spain (Ceballos and Ruiz de la Torre 1971). These species are extensively present as monospecific or mixed forests in the northeastern part of the Iberian Peninsula (Gracia et al. 2000). Both share in common similar life-history traits, such as producing flowers in spring, which are fertilised and develop into mature fruit in autumn of the same year, and the large size of acorns. However, they differ markedly in their leaf habit, because *Q. cerrioides* is a deciduous oak, while *Q. ilex* is a broadleaved evergreen species. Despite that some attention has been given to the difficulties or the slow rate of *Q. ilex* seedlings establishment (Espelta et al. 1995, Retana et al. 1999), the dynamics of the regeneration of both species remains still unclear. In this paper, we have studied the seed ecology of *Q. ilex* and *Q. cerrioides*, to compare their performance in the early regeneration phases (from seed production to seed germination). A simple demographic model has been constructed to evaluate the incidence of these different events in an integrate way, in order to be able to make predictions about the reproductive output of the two species in different habitats.

## METHODS

### Site description

Field work was conducted at Collserola Park, a protected area near Barcelona, (NE Spain; 41º 24' N, 2º 6' E) with a total are of 8,466 ha of which 5,225 ha corresponds to forests (Figure 1).
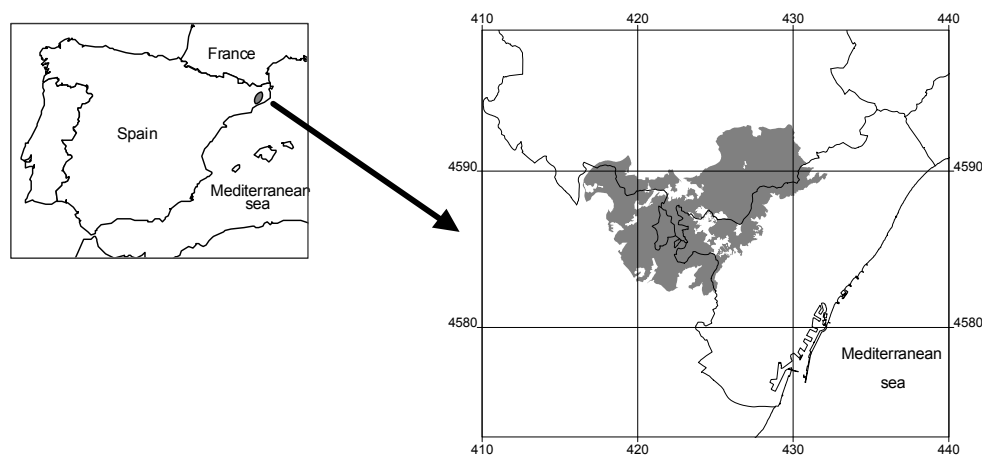


**Figure 1:** Geographical location of the Collserola Park, the area of study.

Climate is typically Mediterranean, with 620 mm of mean annual rainfall, and mean monthly temperatures with a maximum of 23.2ºC in August, and a minimum of 7.8ºC in January. The vegetation of Collserola is a patchwork of forests, woods, scrubland and croplands. The whole

of the mountain range appears as an immense pine forest of *Pinus halepensis* sprinkled with small glades of evergreen (*Q. ilex*) and deciduous (*Q. cerrioides*) oaks. These two oak species form a kind of undergrowth of a good height, above which the pines emerge. Oak forests without pines are also found in Collserola on the least sunny, steepest slopes, which have not been cultivated in recent centuries. *Quercus ilex* is present in the 94.7 percent of the forest area and *Q. cerrioides* is the 75.4 percent. Vegetation grows above lithological strata predominantly of shales and granite but limestone is also present in a few places.

**Sampling and data analysis**

*Acorn production and dispersal*

We monitored acorn production monitored in 17 sites, covering all the forest extension of the Park, during three years. Sites were classified into two main forest types, depending on oak density, mean dbh of each stand, and structure of the canopy: intermediate-canopy forests (9 sites), with low oak density (mean±SE: 1189.7 ± 290.0 shoots/ha) and small trees (mean dbh±SE: 7.9 ± 0.8 cm), and closed-canopy forests (8 sites), with higher oak density (1755.6 ± 307.6 shoots/ha) and larger trees (10.4 ± 0.8 cm). In each or these stands, we randomly selected, tagged and measured (height and dbh) fifteen *Q. ilex* and fifteen *Q. cerrioides* individuals. Trees of both species were of similar dbh (ANOVA, F=0.4, p=0.52) and height (ANOVA, F=0.9, p=0.35). In early September 1998, 1999 and 2000, just prior to acorn dispersion, four branches of similar size (1 cm of diameter, approximately) were randomly chosen in different directions of the canopy of each selected tree, and have been marked with a plastic tag. In each branch, we counted the number of acorns after a careful review of all twigs. Acorns were classified into non developed (fertilised flower but incomplete embryo development or some unidentifiable source of mortality), infested (with signals of beetle infestation -*Curculio* spp.-) and sound (without any signal of insect damage).

Acorn production per tree was estimated as mean number of acorns per branch multiplied by the number of branches of the tree. As the direct measurement of the number of branches per tree was difficult and very time-consuming, we estimated this variable indirectly from the crown surface of each tree. Thus, we selected a sample of 33-38 individuals of each species within the range of tree sizes used in the study and measured the number of branches and the crown projection. Finally regressions between these variables for each species were obtained (*Q. ilex*: $R^2$=0.6, p<0.0001; Number branches = 24.1 + 6.4 * Crown surface; *Q. cerrioides*: $R^2$=0.6, p<0.0001; Number branches = 10.8 + 3.9 * Crown surface), that allowed us to compute the number of branches of all sampled trees.

The following variables were calculated for each tree: 1) *Real Crop,* as the number of fertilised flowers that developed into acorns, 2) *Percent of infestation*, as the proportion of infested acorns of the Real Crop, and 3) *Potential Acorn Production*, that is the sum of Real Crop plus Number of non developed acorns and represents the number of female flowers that potentially would produce acorns. The effects of species (*Q. ilex, Q. cerrioides*), forest type (closed, intermediate), site (nested within forest type) and year (1998, 1999 and 2000) on potential and real crop production were analysed with a three-way repeated-measures ANOVA model. These dependent variables were normalised by a log transformation. As there were few trees that produced acorns every year, there were few complete data in the dataset of percent of infestation. For this reason, the ANOVA for this variable was carried out without repeated-measures. In all cases, the sequential Bonferroni method was employed to avoid Type I error (Rice 1989).

To evaluate differences in dispersal phenology between species and among years, we monitored acorn fall in 1999, 2000 and 2001. The study was carried out in two sites that corresponded with old firebreaks where understory and some pines had been removed and oaks produced large crops. In each site we chose 8-11 trees per species and we marked 50 developed acorns with thin plastic tags in each tree. The monitoring of acorn fall started in September, when acorns start to be mature, and was carried out weekly, until almost 90 % of acorns had fallen. The comparison of acorn ripening between *Q. ilex* and *Q. cerrioides* and among years was carried out using $G^2$ tests.

*Post-dispersal acorn removal*

In order to asses the factors limiting the number of available acorns once they had been dispersed from the mother tree, we carried out an experiment of post-dispersal seed removal (seed removal, hereafter) during autumn/winter 2000. Seed removal was assimilated to seed predation, because the main acorn predators present in the area: Wild Boar (*Sus scrofa*) eats seeds in situ, destroying the great majority of removed acorns and Wood Mice (*Apodemus sylvaticus*) places them in deep larder-hoards from which successful establishment is unlikely (Montgomery and Gurnell 1985) and where seeds are probably consumed (Price and Jenkins 1986). Three forest types where it is feasible to find dispersed acorns were selected: old-abandoned fields surrounded by oaks (open forest), mid-succession forests where pines were the dominant tree species in the canopy and oaks formed a secondary tree layer (intermediate forest), and mature oak forest with large oaks, closed canopy and poor developed understory vegetation (closed forest). Three sites were selected per forest type. In each site we placed two blocks, that consisted in 25 acorns per species distributed in a rectangle of 9x4 m, where acorns were separated 1 m from their neighbours. Seeds were individually glued to a 4x4 cm piece of metallic mesh, which was nailed to the ground. Acorns of both species were distributed alternately to avoid possible grouping effects. The removal experiment was repeated twice per

year, firstly in the dispersal peak of *Q. cerrioides* (when 50% of acorns were dispersed) and afterwards in the dispersal peak of *Q. ilex*. Time-points to start the experiments were calculated from the dispersion curves. Seed removal was checked 3, 9, 21 and 45 days after the placement of acorns in the field. The variables computed were *removal rate* (defined as the number of days required to disappear 50% of the acorns, D50) and *total removal* (defined as the percent of removed seeds at the end of the experiment).

The effects of species (*Q. ilex, Q. cerrioides*), forest type (closed, intermediate, open), site (nested within forest type) and dispersal peak (*Q.ilex*'s peak, *Q.cerrioides*' peak) on the former variables were analysed by a three-way ANOVA model. Inspection of residuals was carried out to check for normality and homoscedasticity. Data of D50 was normalised by a log transformation and % removal was normalised by an arcsin transformation. The different levels of the main factors were compared with the Fisher LSD post-hoc test.

*Acorn germination*

Acorn viability

Loss of viability (i.e., decrease of the percent of germination with time) of acorns due to the effect of ageing, desiccation and other extrinsic factors was tested in a laboratory experiment. Acorns of both species were collected in the field in late September 1998 and maintained in open air to simulate field conditions, avoiding direct full sun and losses by predators. Each month, from October to March, three sub-sets of 10-20 sound acorns of each species were installed and well watered in plates filled with turf. The number of germinated acorns (those whose root had emerged ≥ 2 mm) was recorder one month later.

The effects of species and month (month 1 to 6) on the percent of germination were analysed by a two-way ANOVA model. Inspection of residuals was carried out to check for normality and homoscedasticity. Data of percent of germination was normalised by an arcsin transformation. Fisher LSD post-hoc test was used to compare the viability found in the different months.

Germination of infested acorns

As infested acorns might germinate if the embryo is not damaged, we tested the germination ability of acorns with insect infestation in the laboratory. After a meticulous inspection of the external appearance of the acorns, sound acorns and infested acorns were separated. Acorns were installed in plates filled with turf (twenty acorns per plate). For each species, ten plates with infested acorns and three control plates with sound acorns were installed. The experiment was set up in November 2000. In January 2001, we revised all acorns, and we counted the number of germinated acorns (those with an emerged root ≥ 2 mm). The effect of species and acorn state (sound, infested) on the percent of germination was analysed by a two-way ANOVA

model. Inspection of residuals was carried out to check for normality and homoscedasticity. Data of % of germination was normalised by an arcsin transformation.

Germination in field conditions

Germination ability of both species was tested in a field experiment. We examined the effects of forest type (open, intermediate and close forest) on seed germination in the same sites (three sites per forest type) where the post-dispersal seed removal experiments were carried out. Ten mesh cashes (five per species), that avoided acorn predation, were installed in each site separated 1 m from the neighbours. Four acorns slightly covered by litter were placed under each cash. The experiment started in November 2000, and all acorns were recovered in February 2001. At the laboratory, a careful review distinguished between germinated and non germinated acorns.

The effects of species (*Q. ilex, Q. cerrioides*), forest type (closed, intermediate, open) and site (nested within forest type) on seed germination in the field have been analysed by a two-way ANOVA model. Data of % of germination was normalised by an arcsin transformation. Fisher LSD post-hoc test was used to compare the different forest types.

*The recruitment model*

The reproductive steps described above were integrated in a measure of recruitment of *Q. ilex* and *Q. cerrioides* across the spatial variability found in the study area to estimate the probability of a potential acorn becoming a seedling. In each case, the final value was calculated as the mean number of potential acorns produced per tree and year multiplied by the three transition probabilities between consecutive stages in the recruitment process: 1) from potential crop to real crop, 2) from real crop to acorns escaping post-dispersal removal, and 3) from surviving to germinated acorns. This recruitment expectancy was calculated for each species and forest type.

**RESULTS**

**Acorn production and dispersal**

The effects of the different factors on the variables related to acorn production are summarised in Table 1. Potential crop values were extremely variable, since most factors and interactions were significant. There were differences between species, because potential crop of *Q. cerrioides* was larger than that of *Q. ilex* (223.1±21.9 and 130.6±17.8 potential acorns per tree, respectively). Real crop also varied markedly between species: *Q. cerrioides* produced more acorns per tree than *Q. ilex* (30.1±4.8 and 9.8±2.7 acorns per tree, respectively). There were

also differences in acorn production among years, but with a different pattern depending on species (Interaction SPECIES x YEAR in Table 1).

**Table 1.** F values from ANOVA tests of effects of SPECIES, FOREST TYPE (closed, intermediate) and YEAR (1998, 1999, 2000) on the Potential acorn production, the Real crop and the Percentage of infested acorns. Statistical coefficients (at α=0.05 when the sequential Bonferroni method is employed) are indicated in bold.

| Factor | Potential acorn production | Real Crop | Percentage of infested acorns |
|---|---|---|---|
| Species (Sp) | **79.6** | **42.4** | **7.3** |
| Forest Type (FT) | 0.4 | 2.5 | 3.7 |
| Site (Forest Type) | **3.3** | **3.2** | 1.4 |
| Year (Y) | **35.5** | **6.0** | 0.0 |
| Sp x FT | **17.7** | 0.0 | 1.7 |
| Sp x Y | **15.8** | 3.5 | 0.3 |
| FT x Y | **9.7** | 0.1 | 2.0 |
| Sp x FT x Y | 4.8 | 3.4 | 0.1 |

Potential acorn crop increased from 1998 to 2000, in a similar way for both species (Figure 2A). Concerning Real crop, *Q. cerrioides* had similar acorn production in 1998, 1999 and 2000, whereas *Q. ilex* had a small crop in 1998 followed by a production peak in 1999 and a decrease in 2000 (Figure 2B). The interaction between species and forest type was significant for Potential crop, but not for Real crop. Thus, potential crop was similar in both species (*Q. cerrioides*: 210.7±33.4 acorns per tree; *Q. ilex*: 181.8±30.7 acorns per tree) in the closed forest, while that of *Q. cerrioides* was higher than that of *Q. ilex* in the intermediate forest (233.3±29.1 and 84.1±19.1 potential acorns per tree, respectively).

According to table 1, the percent of infestation was higher in *Q. cerrioides* (52.3±3.4%) than in *Q. ilex* (19.2±5.2%), but did not vary between forest types, sites or years. The interactions between these factors were neither significant.

Differences in tree size between producing and non-producing individuals of both species were significant because acorn producing trees of both species were larger (F=5.7, p=0.017 for dbh; F=12.6, p=0.0004 for height) than non-producing trees.

The dispersal curves of the two species displayed large interannual variability (Figure 3). The curves of the two species were similar in 1999 ($G^2$=0.7, p>0.10) and 2001 ($G^2$=6.7, p>0.10), but differed significantly in 2000 ($G^2$=16.3, p=0.007), because the dispersal peak of *Q. cerrioides* was achieved one month earlier than that of *Q. ilex*.
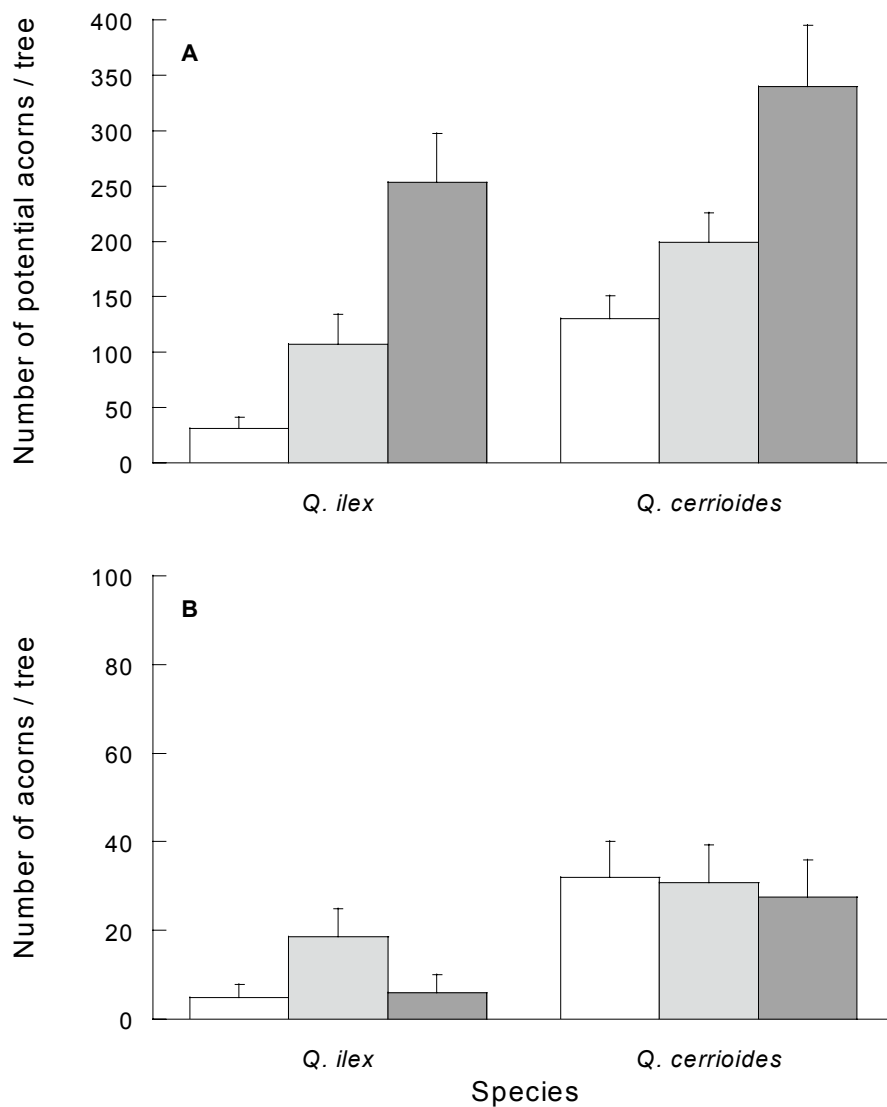


**Figure 2.** (A) Mean (+ SE) Potential acorn production (potential number acorns per tree) and (B) Real crop (number acorns per tree) of *Q. ilex* and *Q. cerrioides* individuals in 1998 (white), 1999 (light grey) and 2000 (dark grey).
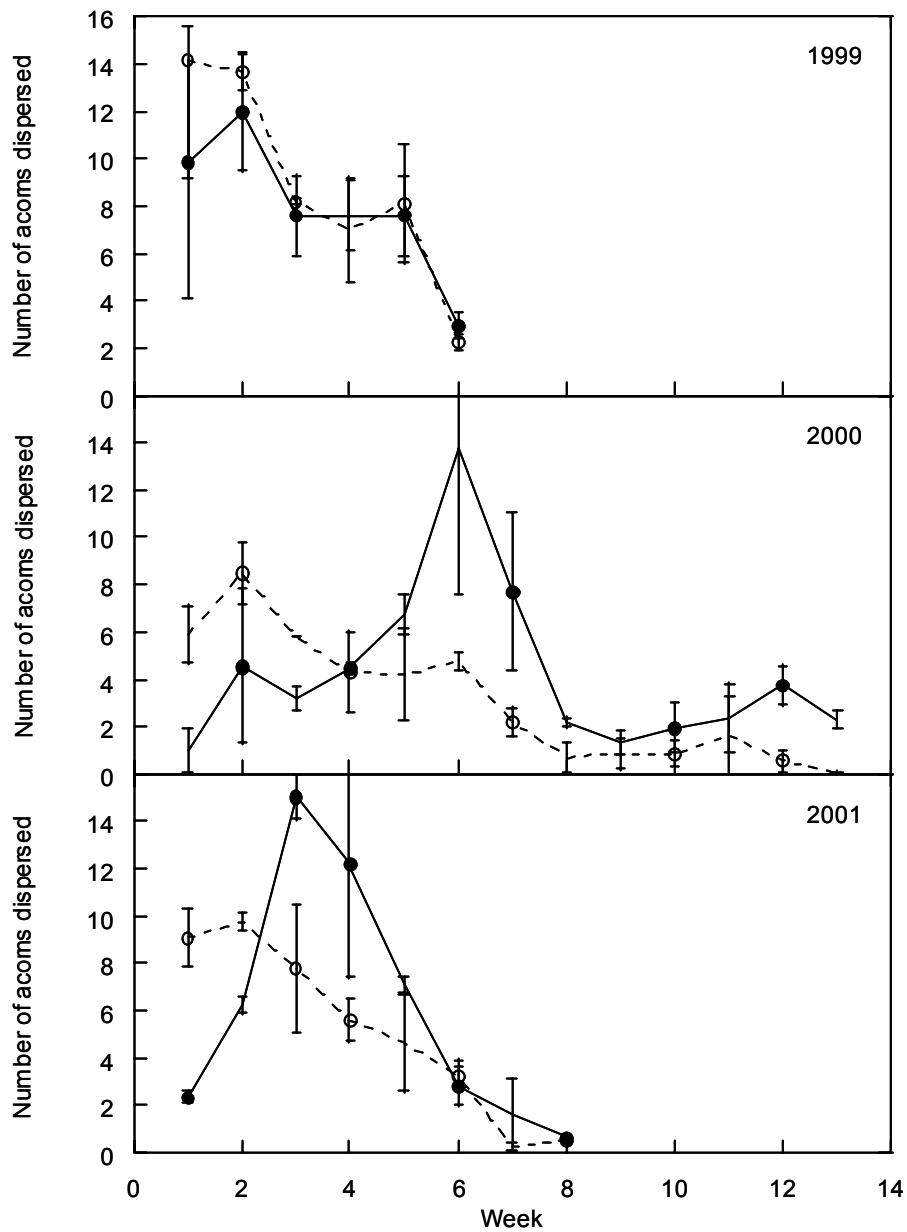
**Figure 3.** Mean (± SE) number of acorns fallen from *Q. ilex* (black dots) and *Q. cerrioides* (white dots) trees during the whole dispersal period in 1999, 2000 and 2001.


**Post dispersal acorn removal**

Post-dispersal seed removal did not depend on species (Table 2). Total removal was similar in both species (*Q. ilex*: 36.9±3.8%; *Q. cerrioides*: 35.1±3.7%), and also removal rate (103±19 days in the case of *Q. ilex* and 112±21 days in the case of *Q. cerrioides* were needed to

disappear the 50% of the acorns). However there were significant differences among forest types (and also among sites within forest types). Thus total removal was higher in intermediate forests (51.3±4.2%), and lower in closed (37.2±4.0%) and open forests (19.5±2.9%). D50 was larger in open forests (183±30 days), than in intermediate (49±6 days) or closed (94±22 days) forests.

**Table 2.** F values from ANOVA tests of effects of SPECIES, FOREST TYPE (closed, intermediate, open) and DISPERSAL PEAK (Q. ilex's peak, Q. cerrioides' peak) on Total removal and Removal rate. Statistical significance: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

| Factor | Total removal | Removal rate |
|---|---|---|
| Species (Sp) | 0.1 | 0.0 |
| Forest Type (FT) | 49.5*** | 26.0*** |
| Site (Forest Type) | 13.5*** | 8.6*** |
| Dispersal Peak (DP) | 0.3 | 0.0 |
| Sp x FT | 3.0 | 0.9 |
| Spx DP | 2.6 | 2.5 |
| FT x DP | 8.9*** | 4.9* |
| Sp x FT x DP | 0.1 | 0.4 |

**Acorn germination**

Acorn viability

The experiment of germination at laboratory pointed out that the loss of viability differed between species (F=84.1, p<0.0001), among months (F=44.3, p<0.0001), and that the interaction Species x Month was also significant (F=12.4, p<0.0001). As shown in Figure 4, viability of *Q. ilex* acorns was high during the first three months, and progressively decreased, whereas that of *Q. cerrioides* acorns decreased and reached very low values after the second month of storage.

Germination of infested acorns

The experiment of germination of sound and infested acorns pointed out that the state of the acorns affected total percent of germination (F=44.0, p<0.0001), because 90.7±2.8% of sound acorns germinated, but only 40.4±5.8% of infested acorns did so. The interaction Species x State was also significant (F=11.0, p=0.0032): the percentage of germination of sound acorns of

both species was similar, but the percentage of infested acorns of *Q. cerrioides* that germinated was higher than that of *Q. ilex* (Figure 5).
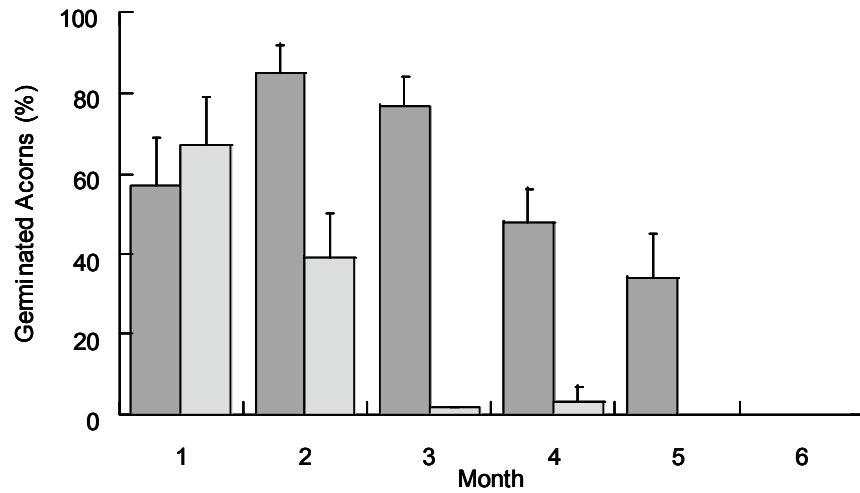


**Figure 4.** Percentage of germination (mean+SE) of *Q. ilex* (dark grey) and *Q. cerrioides* (light grey) acorns put to germinate from the first to the sixth month after ripening.
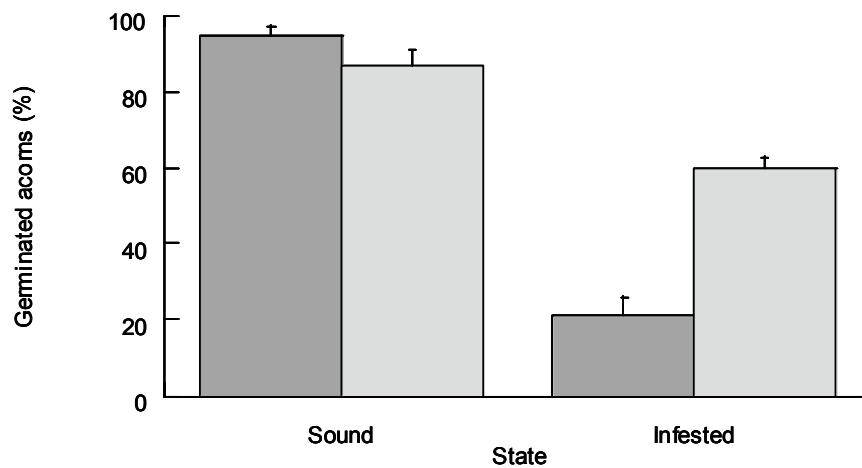


**Figure 5:** Percentage of germination (mean+SE) of sound and infested acorns of *Q. ilex* (dark grey) and *Q. cerrioides* (light grey).

Germination in field conditions

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Acorn germination in the field was similar for both species (F=0.6, p=0.42; mean germination values: *Q. ilex*:, 77.8±4.3%; *Q. cerrioides,* 80.5±5.2%). There were not significant differences among the three forest types (F=2.4, p=0.18). However, the interaction Species x Forest Type was slightly significant (F=3.6, p=0.03): germination of *Q. cerrioides* acorns in closed and intermediate forests was quite similar and increased in open forests, while germination of *Q. ilex* acorns showed a tendency to increase under closed canopies (see Figure 6).
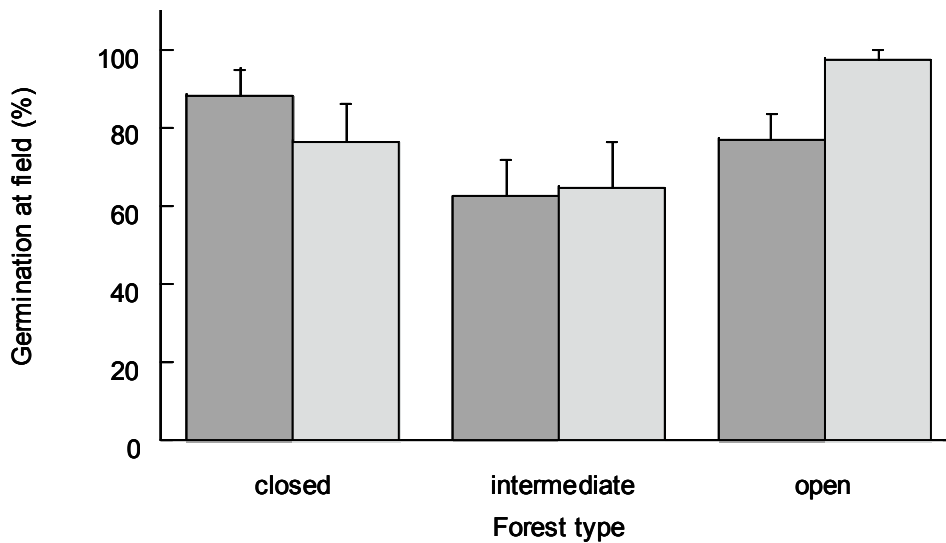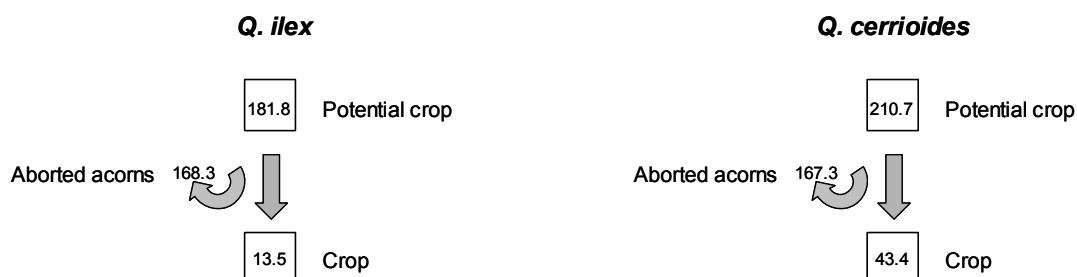


**Figure 6.** Mean (+ SE) germinated acorns (%) of *Q. ilex* (dark grey) and *Q. cerrioides* (light grey) in the three forest types (closed, intermediate, open).

**Recruitment probabilities**

The average number of potential seedlings of each species recruited from a single tree in closed and intermediate forests is represented in Figure 7. Absolute recruitment values of *Q. cerrioides* were always higher than those of *Q. ilex* in both forest types. In the closed forest, the initial values of Potential crop were quite similar, and the differences between species started in the Crop stage. The differences between species in the intermediate forest started in the size of the Potential crop, and remained, and even increased, through the successive reproductive stages. Both species had higher recruitment values in closed than in intermediate forests.

Closed forests

*Q. ilex*                                        *Q. cerrioides*

181.8  Potential crop                      210.7  Potential crop

Aborted acorns  168.3                    Aborted acorns  167.3                    50

13.5  Crop                                    43.4  Crop

# Intermediate forests

**Q. ilex**                                    **Q. cerrioides**

| 84.1 | Potential crop |
|------|----------------|

Aborted acorns 77.8

| 6.3 | Crop |
|-----|------|

Predated acorns 3.3

| 3.0 | Surviving acorns |
|-----|------------------|

Dessicated and
infected acorns 1.7

| 1.3 | Germinate acorns |
|-----|------------------|

| 233.3 | Potential crop |
|-------|----------------|

Aborted acorns 214.2

| 19.1 | Crop |
|------|------|

Predated acorns 9.8

| 9.3 | Surviving acorns |
|-----|------------------|

Dessicated and
infected acorns 2.8

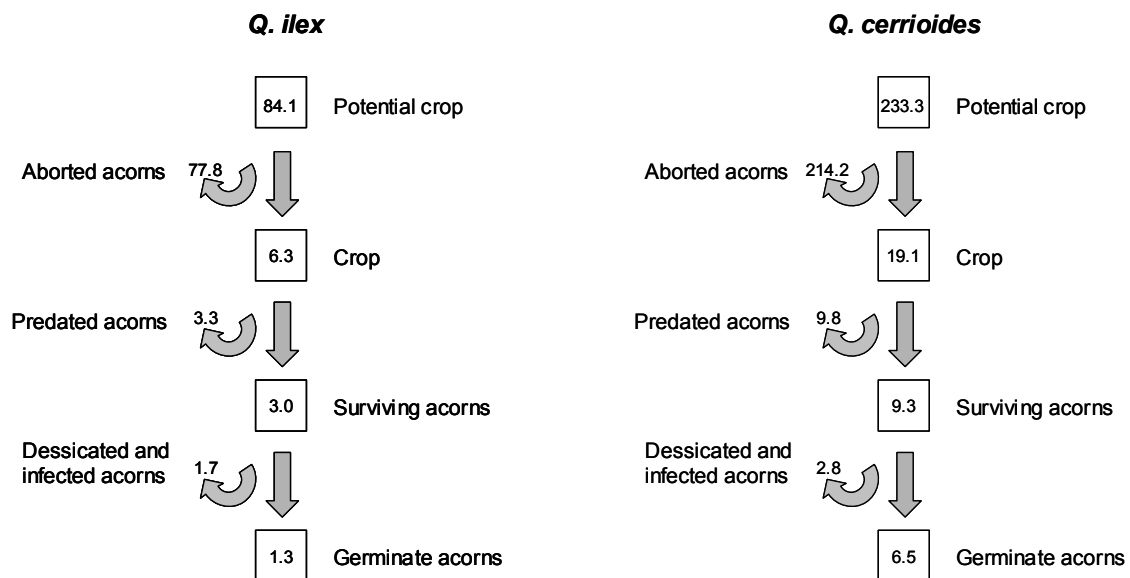| 6.5 | Germinate acorns |
|-----|------------------|

**Figure 7:** Recruitment of *Q. ilex* and *Q. cerrioides* in each forest type (closed, intermediate). The number of effectives in each stage was calculated multiplying the initial mean of potential acorns per tree and year (Potential Crop) by the transition probabilities (%) between each stage. These transition probabilities were: the probability of Potential Crop per tree and year becoming Real Crop; the probability of survival (obtained multiplying the percentage of Real Crop multiplied by the percentage of survivorship) and finally the probability of germination (calculated multiplying the percentage of surviving acorns multiplied by the percentage of germination). Final values represent the mean of the number of fertilised flowers of a single tree per year becoming a germinated acorn.

## DISCUSSION

*Quercus ilex* and *Q. cerrioides* showed significant differences in some of the processes determining seed performance. Thus, potential crop of *Q. cerrioides* almost doubled that of *Q. ilex*, while differences between species in real crop were even larger, with *Q. cerrioides*

producing almost three times the number of acorns of *Q. ilex* trees (Table 1). These results point out different flower production and sensibility of the two species to factors that could affect survival from flower to fruit (ovule development, fertilization and premature acorn abortion). As an example, potential crop of 2000 was the highest of the three years monitoring in the two species, and *Q. cerrioides* produced a high real crop, but *Q. ilex* aborted most of the potential crop (Figure 2). Sork et al. (1993) suggest that weather may have a significant impact on acorn production of oak species. In this case, precipitation variables did not differ among years and only the slightly higher mean maximum summer temperatures of 2000 compared to the previous years (mean ± SE in 2000: 31 ± 1.2 ºC; 1998: 27± 0.8 ºC; 1999: 27±1.2 ºC) could have higher effect on the survival of *Q. ilex* than to *Q. ilex* flowers, which develop later in the season (pers. obs.)

Despite the initial advantage of *Q. cerrioides* in the recruitment process due to its highest acorn production, this species showed more than 50 % of acorns infested by larvae of the weevil *Curculio* ssp*.* whereas only 19 % of those of *Q. ilex* were infested. High pre-dispersal reproductive losses by insect parasitism have been reported previously (see Traveset 1995 and for reviews, Crawley 1989 and 1992) and in some cases have been shown to limit plant recruitment (Louda 1982; Auld 1986; Kaye 1999). This different infection degree between the two species could be related to the phenology of seed development: *Q. cerrioides* produced and ripened their acorns some weeks before than *Q. ilex* (3-4 weeks before in 2000), and the main consequence of this delay would be that *Q. cerrioides* acorns were more advanced in their development than those of *Q. ilex* in June/July, when the weevil females inoculate their eggs (Fuentes-Sanchez 1994)*.*

These seed production patterns were modulated by the habitats were trees grown. Considering the drought period characterising the Mediterranean climate, the intermediate-canopy forests would result a stressful habitat during summer period due to the highest evaporative demand and desiccative environment that would suffer trees and acorns grown in these conditions. This would explain why there were no significant differences in Real crop in the two Forest types, despite some studies have demonstrated that seed production is usually higher in gaps than in close forests (Levey 1990; Ellison et al. 1993). These studies were carried out in tropical and temperate forests where plants are more limited by light availability than by water, and lower tree density reduces competition for light resources (Knapp et al. 2001).

Concerning acorn predation, there were no differences in the removal rate or in the final percent of removed acorns between the two species. The lack of differences between species was expected to a certain point, since they do not differ in acorn mass or caloric content (Pique 1997), which are some of the criteria used by predators to select the seeds that preferentially consume (Willson and Whelan 1990; Reader 1993; Kollmann et al. 1998). Differences in the timing of seed ripening and dispersal could affect the predation rates of the acorns of the two

species, because condition seed availability for post-dispersal consumers (Herrera 1984; Denslow 1987; Murray 1987; Gry and Dominguez 1996). However, the absence of significance of the interaction Species x Dispersal Peak indicates that the likelihood of predation was the same despite the identity (either *Q. ilex* or *Q. cerrioides* acorns) of the most abundant seeds in the soil. This may be due to the continuity of activity of predators in the area of study throughout the extend of the ripening and dispersion events of both species, because of the mild weather conditions. The only differences in predation rates were those among forest types: acorn removal was lower in open forests than in intermediate and closed forests (as also reported in the literature: Whelan et al. 1991; Bonfil and Soberón 1999; Díaz et al. 1999; Alcántara et al. 2000), suggesting that seed consumers prefer close areas where the risk of attack by predators decreases (Lima and Dill 1990; Lagos et al. 1995; Mason and Stiles 1998). Some authors have found that seed predation influences plant recruitment twofold, limiting the number and spatial distribution of recruited plants and determining the identity of the recruits (Louda, 1995; Hulme 1998; Alcántara et al. 2000). But in this study, the observed values of seed removal (lower than 40 %) imply that removal did not limit recruitment of *Q. cerrioides* and *Q. ilex* directly. Moreover, the lack of selection of acorn species consumed by predators did not determine the identity of the survival seeds and consequently the identity of the recruits.

Both species disperse their seeds during the autumn months and acorns start to germinate almost immediately favoured by humidity and temperature conditions found in this season. The experiment of loss of viability pointed out that *Q. cerrioides* acorns loose their viability before than *Q. ilex* ones, maybe due to the sooner development and ripening of the acorns of *Q. cerrioides*. However, germination of acorns did not limit population recruitment of both species because the percentages of acorn germination in the field were quite high (as reported by Kollmann and Schill, 1996, for other oak species). The values of the two species were similar which matches with the fact that the acorns of the two species do not differ in their weight, which is one of the main factors influencing germination (Tripathi and Khan 1990; Seiwa 2000). There were only differences in the percent of germination of infested acorns, that was almost the double in *Q. cerrioides* than in *Q. ilex*. There were also differences in germination among forest types which showed differences in environmental conditions (degree of canopy opening, degree of understory development, litter content, water availability, photon flux density and temperature) that could affect seed germination (Bazzaz and Wayne 1994; Chambers and McMahon 1994; Vázquez-Yanes and Orozco-Segovia 1994). The highest values of seed germination were those of *Q. cerrioides* in open forests, while germination in the other two forest types were lower and similar for the two species. Thus, open forests offer better environmental conditions for *Q. cerrioides* and, from the point of view of population dynamics, this fact joint with the lower seed predation in these habitats, would imply a higher relative advantage (in potential number of descendents) of *Q. cerrioides* respect to *Q. ilex*.

**Comparative reproductive output of the two species**

The results of the demographic model showed a different reproductive success in the two species and spatial differences in recruitment in the different forest types (Figure 7). *Q. cerrioides* had always higher values in each step of the recruitment process than *Q. ilex*, and both performed better in closed forests than in intermediate forests. In intermediate forests, the differences between species started in the size of the Potential crop, whereas in closed forests the initial differences in Potential crop were lower, but *Q. ilex* aborted a higher percentage of its potential crop than *Q. cerrioides*. In both forest types, there was a dominance of *Q. cerrioides* recruits. Studies about the regeneration dynamics in free-perturbations periods have highlighted two factors as a responsible of the intraspecific differences in recruitment: in one hand the availability of seeds (Lloret and Zedler 1991; Fenner 1992) and in the other hand the degree of shadow tolerance of each species (Keeley 1992; St-Jaques and Bellefleur 1993). In this sense. studies concerning seedling performance (Espelta et al. 1995; Espelta et al. in preparation) have reported that both species present the highest growth rates under intermediate-canopy closure (corresponding to 36 % PAR measured by Espelta et al. in preparation). Thus, the favourable light environment of intermediate forests joint the highest number of *Q. cerrioides* recruits should favour *Q. cerrioides* dominance over *Q. ilex* in those habitats. On the other hand, in closed forest, the shady environment generated by canopy closure could slow-down the incorporation of new individuals (Espelta et al. 1995), generating higher levels of uncertainty in the final outcome of the recruitment process, because there are more opportunities to biotic and abiotic factors affecting the performance of young individuals.

*Q. ilex* has been considered a key-stone species of the potential vegetation in the north-west of the Mediterranean Basin, partly because of its evergreen habit (Terradas 1999). The dominance of *Q. ilex* over *Q. cerrioides* was due to the human action that indirectly or directly favoured the former species (Barbero et al. 1992; Riera-Mora 1995). Thus the high recurrence of perturbations in Mediterranean Basin ecosystems, associated to the human presence, would explain the dominance of *Q. ilex*. However, when those perturbations (thinning, browsing, fire, etc) cease, as in the recent decades, sexual reproduction might take higher relevance in determining community species composition. This study about the sexual regeneration of both oaks demonstrates that *Q. cerrioides* has higher reproductive success than *Q. ilex* and this advantage starts in the seeds production phase. Other factors and processes that could modify this different success, as the post dispersal seed predation and the rate of germination, did not differ between species. This should be due to the similar characteristics (weight, caloric content) of the acorns of both oaks as well as to the fact that the timing of ripening, which differed between species, did not condition the removal process. In conclusion, perturbations (e.g. browsing, in Habrouk 2002) seem to favour *Q. ilex* , but in large periods between perturbations, when sexual regeneration takes place, *Q. cerrioides* has higher reproduction success than *Q. ilex* and this could invert the patterns of dominance.

**REFERENCES**

Alcántara, J.M.; Rey, P.J.; Sánchez-Lafuente, A.M. and Valera, F. 2000. Early effects of rodent post-dispersal seed predation on the outcome of the plant-seed disperser interaction. Oikos, 88: 362-370.

Auld, T.D. 1986. Population dynamics of the shrub *Acacia suaveolens* (Sm.) Willd.: Fire and the transition to seedlings. Australian Journal of Ecology, 11: 373-385.

Barbero, M; Loisel, R. and Quézel, P. 1992. Biogeography, ecology and history of Mediterranean Quercus ilex ecosystems. Vegetatio 99/100: 19-34.

Bazzaz, F.A. and Wayne, P.M. 1994. Coping with environmental heterogeneity: The physiological ecology of tree seedling regeneration across the gap-understory continuum. In: M.M. Caldwell and R.W. Pearcy (eds.) Exploitation of Environmental Heterogeneity by Plants. Ecophysiological Processes Above- and Belowground. Academic Press, San Diego, California.

Blate, G.M.; Peart, D.R. and Leighton, M. 1998. Post-dispersal predation on isolated seeds: a comparative study of 40 tree species in a Southeast Asian rainforest. Oikos, 82: 522-538.

Bonfil, C. and Soberon, J. 1999. *Quercus rugosa* seedlings dynamics in relation to its re-introduction in a disturbed Mexican landscape. Applied Vegetation Science, 2: 189-200.

Callaway, R and Davis, F.W. 1998. Recruitment of Quercus agrifolia in central California: the importance of shrub-dominated patches. Journal of Vegetation Science 9: 647-656.

Ceballos L, and Ruiz de la Torre J. 1971. Arboles y arbustos. IFIE-Escuela Técnica Superior de Ingenieros de Montes , Madrid.

Chambers, J.C. and MacMahon, J.A. 1994. A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. Annual Review of Ecology and Systematics, 25: 263-292.

Crawley, M.J. 1989. Insect herbivores and plant population dynamics. Annual Review of Entomology, 34: 531-564.

Crawley, M.J. 1992. Seed predators and plant population dynamics. In: M. Fenner (ed.) Seeds, the ecology of regeneration in plant communities. CAB International, Wallingford.

Crow, T.R. 1988. Reproductive mode and mechanisms for self-replacement of Northern red oak (*Quercus rubra*)- A review. Forest Science, 34: 19-40.

Crow, T.R. 1992. Population dynamics and growth patterns for a cohort of northern red oak (*Quercus rubra*) seedlings. Oecologia, 91: 192-200.

Denslow, JS. 1987. Fruit-removal from aggregated and isolated bushes of the red elderberry, *Sambucus pubens*. Canadian Journal of Botany, 65: 1229-1235.

Díaz, I.; Papic, C. and Armesto, J.J. 1999. An assessment of post-dispersal seed predation in temperate rain forest fragments in Chiloé Island, Chile. Oikos, 87: 228-238.

Ellison, A.M; Denslow, J.S; Loiselle, B.A. and Brenes, D.M. 1993. Seed and seedling ecology of neotropical Melastomataceae. Ecology, 74: 1733-1749.

Espelta, JM.; Riba, M. and Retana, J. 1995. Patterns of seedling recruitment in West-Mediterranean Quercus ilex forests influenced by canopy development. Journal of Vegetation Science, X: 465-472.

Fenner, M. 1992. Seeds. The ecology of regeneration in plant communities. C.A.B. International, Wallingford.

Fuentes-Sanchez, C., 1994. La encina en el centro y suroeste de España (su aprovechamiento y el de su entorno). Junta de Castilla y León, Consejería de Medio Ambiente y Ordenación del Territorio. Castilla y León..

Germaine, H.L. and McPherson, G.R. 1998. Effects of timing of precipitation and acorn harvest date on emergence of *Quercus emoryi*. Journal of Vegetation Science, 9: 157-160.

Gracia, C.; Burriel, J.A.; Ibáñez, J.J.; Mata, T. and Vayreda, J. (2000) Inventari ecològic i forestal de Catalunya. Regió forestal IV. Centre de Recerca Ecològica i Aplicacions Forestals, Barcelona.

Greenberg, CH. 2000. Individual variation in acorn production by five species of southern Appalachian oaks. Forest Ecology and Management, 132: 199-210.

Gryj, E.O. and Domínguez, C.A. 1996. Fruit removal and postdispersal survivorship in the tropical dry forest shrub *Erythroxylum havanense*: ecological and evolutionary implications. Oecologia, 108: 368-374.

Habrouk, A. 2002. Regeneración natural y restauración de la zona afectada por el gran incendio del Bages y Berguedà de 1994. Tesis doctoral. UAB, Bellaterra. Barcelona.

Healy, W.M.; Lewis, A.M. and Boose, E.F. 1999. Variation of red oak acorn production. Forest Ecology and Management, 116: 1-11.

Herrera, CM. 1984. Adaptation to frugivory of Mediterranean avian seed dispersers. Ecology, 65: 609-617.

Holt, R.D; Pacala, S.W.; Smith, T.W. and Liu, J. 1995. Linking contemporary vegetation models with spatially explicit animal population models. Ecological Applications, 5: 20-27.

Hulme, PE. 1994. Post-dispersal seed predation in grassland: its magnitude and sources of variation. Journal of Ecology, 82: 645-652.

Hulme, P.E. 1998. Post-dispersal seed predation: consequences for plant demography and evolution. Perspectives of Plant Ecology, Evolution and Systematics, 1: 32-46.

Johnson, WC.; Thomas, L and Adkisson, CS. 1993. Dietary circumvention of acorn tannins by blue jays. Implications for oak demography. Oecologia, 94: 159-164.

Kaye, T. N. 1999. From flowering to dispersal: Reproductive ecology of an endemic plant, Astragalus australis var. olympicus (Fabaceae). American Journal of Botany, 86: 1248-1256.

Ke, G. and Werger, M.J.A. (1999) Different responses to shade of evergreen and deciduous oak seedlings and the effect of acorn size. Acta Oecologica. Vol. 20, pp. 579-586.

Keely, J.E. 1992. Recruitment of seedlings and vegetative sprouts in unburned chaparral. Ecology, 73: 1194-1208.

Knapp, E.E.; Goedde, M.A. and Rice, K.J. 2001. Pollen-limited reproduction in blue oak: implications for wind pollination in fragmented populations. Oecologia, 128: 48-55.

Koenig, WD., Mumme, RL.; Carmen, WJ. And Stanback, MT. 1994. Acorn production by oaks in central coastal California: variation within and among years. Ecology, 75: 99-109.

Kollmann, J. and Schill, H.P. 1996. Spatial patterns of dispersal, seed predation and germination during colonization of abandoned grassland by *Quercus petraea* and *Corylus avellana*. Vegetatio, 125: 193-205.

Kollmann, J.; Coomnes, D.A. and White, M. 1998. Consistencies in post-dispersal seed predation of temperate fleshy-fruited species among seasons, years and sites. Functional Ecology, 12: 683-690.

Lagos, V.O.; Contreras, L.C.; Meserve, P.L.; Gutierrez, J.R. and Jaksic, F.M. 1995. Effects of predaton risk on space use by small mammals: a field experiment with a Neotropical rodent. Oikos, 74: 259-264.

Latham, R.E. 1992. Co-occurring tree species change rank in seedling performance with resources varied experimentally. Ecology 73.

Levey, D.J. 1990. Habitat-dependent fruiting behaviour of an understorey tree, *Miconia centrodesma* , and tropical treefall gaps as keystone habitats for frugivores in Costa Rica. Journal of Tropical Ecology, 6: 409-420.

Lima, S.L. and Dill, L.M. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology, 68: 619-640.

Lloret, F. and Zedler, P.H. 1991. Recruitment patterns of Rhus integrifolia populations in periods between fire in chaparral. Journal of Vegetation Science, 2: 217-230.

Louda, S.M. 1982. Limitation of the recruitment of the shrub *Haplopappus squarrosus* (Asteraceae) by flower – and seed-feeding insects. Journal of Ecology, 70: 43-53.

Louda, S.M. 1995. Effect of seed predation on plant regeneration: evidence from Pacific Basin Mediterranean scrub communities. In: Arroyo, M.T.K.; Zedler, P.H. and Fox, M.D. (eds.) Ecology and biogeography of Mediterranean ecosystems in Chile, California and Australia. Springer-Verlag, New York.

Mason, R.H. and Stiles, E.W. 1998. Links between microhabitat preferences and seed predation by small mammals in old fields. Oikos, 82: 37-50.

Montgomery, W.I. and Gurnell, J. 1985. The behaviour of *Apodemus.* Symp Zool Soc Lond 55: 89-115.

Murray, KG. 1987. Selection for optimal fruit-crop size in bird-dispersed plants. American Naturalist, 129: 18-31.

Ostfeld, R.S.; Mason, R.H. and Canham, C.D. 1997. Effects of rodents on tree invasion of old fields. Ecology, 78: 1531-1542.

Piqué, J. 1997. Ecoetologia i biologia de l'esquirol (*Sciurus vulgaris*, Linnaeus, 1758) en dos hàbitats de predictibilitat alimentària contínua que difereixen en l'abundància d'aliment. Tesi. Universitat de Barcelona. Barcelona.

Price, M.V. and Jenkins, S.H. 1986. Rodents as seeds consumers and dispersers. In: Murray, D.R. (ed.). Seed Dispersal. Academic Press, Orlando.

Reader, RJ. 1993. Control of seedling emergence by ground cover and seed predation in relation to seed size for some old-field species. Journal of Ecology, 81: 169-175.

Retana, J.; Espelta, J.M; Gracia, M. and Riba, M. 1999. Seedling recruitment. In Ecology of Mediterranean evergreen oak forests. Rodà, F; Retana, J; Gracia, C.A. and Bellot, J. (eds.) Springer-Verlag, Berlin.

Rice, W.R. 1989. Analyzing tables of statistical tests. Evolution, 43: 223-225.

Riera i Mora, S. 1995. Evolució del paisatge vegetal holocè al Pla de Barcelona a partir de les dades pol.líniques. Tesi doctoral U.B. Barcelona.

Schupp, E.W. 1988. Factors affecting post-dispersal seed survival in a tropical forest. Oecologia, 76: 525-530.

Schupp, E.W. 1990. Annual variation in seedfall, postdispersal predation and recruitment of a neotropical tree. Ecology, 71: 504-515.

Seiwa, K. 2000. Effects of seed size and emergence time on tree seedling establishment: importance of developmental constraints. Oecologia 123: 208-215.

Silvertown, J.W. 1980. The evolutionary ecology of mast seeding in trees. Biological Journal of the Linnean Society, 14: 235-250.

Sonesson, LK. 1994. Growth and survival after cotyledon removal in *Quercus robur* seedlings, grown in different natural soil types. Oikos, 69: 65-70.

Sork, VL.; Bramble, J. and Sexton, O. 1993. Ecology of mast-fruiting in three species of Missouri oaks, *Quercus alba, Quercus rubra*, and *Quercus velutina* (Fagaceae). Ecology, 74: 528-541.

St-Jaques, C. and Bellefleur, P. 1993. Light requeriments of some broadleaf tree seedlings in natural conditions. Forest Ecology and Management, 56: 329-341.

Swaine, M.D.; Lieberman, D. and Putz, F.E. 1987. The dynamics of tree populations in tropical forest: A review. Journal of Tropical Ecology, 3: 359-366.

Terradas, J. 1999. Holm oak and holm oak forests: an introduction. In Ecology of Mediterranean evergreen oak forests. Rodà, F; Retana, J; Gracia, C.A. and Bellot, J. (eds.) Springer-Verlag, Berlin.

Traveset, A. 1995. Spatio-temporal variation in pre-dispersal reproductive losses of a Mediterranean shrub, *Euphorbia dendroides* L. Oecologia, 103: 118-126.

Tripathi, R.S. and Khan, M.L. 1990. Effects of seed weight and microsite characteristics on germination and seedling fitness in two species of *Quercus* in a subtropical wet hill forest. Oikos, 57: 289-296.

Valverde, T. and Silvertown, J. 1995. Spatial variation in the seed ecology of a woodland herb (*Primula vulgaris)* in relation to light environment. Functional Ecology, 9: 942-950.

Vázquez-Yanes, C. and Orozco-Segovia, A. 1994. Patterns of seed longevity and germination in the tropical rainforest. Annual Review of Ecology and Systematics, 24: 69-88.

Whelan, C.J.; Willson, M.F.; Tuma, C.A. and Souza Pinto, I. 1991. Spatial and temporal patterns of post-dispersal seed predation. Canadian Journal of Botany, 69: 428-436.

Willson, M.F. and Whelan, C.J. 1990. Variation in post-dispersal survival of vertebrate-dispersed seeds: effects of density, habitat, location, season and species. Oikos, 57: 191-198.

# Differences in biomass partitioning and plasticity in response to resource co-variation do not involve differences in growth of seedlings of two Mediterranean oaks with contrasting leaf habit

**INTRODUCTION**

At the level of tree seedlings, the forest environment can be extremely heterogeneous due to temporal changes in light, water and nutrient availability caused by canopy dynamics, competition with the understory vegetation or heterogeneity in soil structure and fertility (Bazzaz, 1996). To cope with environmental variability, seedlings adjust their biomass allocation and physiology to increase acquisition of diminishing resources, both above and below-ground (Bell & Lechowicz, 1994). However, species differ in their plasticity (sensu Bradshaw, 1965), that is, in the degree to which they can modify physiological and morphological traits expressing different phenotypes in contrasted environments (see Bazzaz & Wayne, 1994). To some extent, differences in plasticity have been proven to be related to the plant growth form: i.e. deciduous species often show a higher plasticity in leaf size and net assimilation rate in response to light heterogeneity than evergreens (Cornelissen *et al.*, 1998, Ke & Werger, 1999). Those statements have been crucial to explain the regeneration patterns of temperate and tropical forests (see Strauss-Debenedetti & Bazzaz, 1991; Walters *et al.*, 1993; Valladares *et al.*, 2000a) but remain confined to habitats where light is the major cause of environmental heterogeneity, and have rarely been confirmed or contrasted in other scenarios. Particularly, much less research has been focused on the role of plasticity in habitats where a strong co-variation of several environmental resources occurs, or in harsh or highly unpredictable environments (however see Ögren & Sundin, 1996, Valladares *et al.*, 2000b).

Mediterranean-type ecosystems provide a good framework to investigate the role of plasticity under a highly heterogeneous environment. Mediterranean-type ecosystems are characterised by hot and dry summers, scarce rainfall with great intra and inter-annual variability, and high edaphic heterogeneity (Aschmann, 1973). In this scenario, seedlings of tree species have to face a highly variable and unpredictable environment, dominated by a chronic water stress. Some of the commonest tree species spread all over the Mediterranean Basin are oaks, with *Quercus ilex* L. and *Quercus cerrioides* Wk. et Costa extensively present as monospecific or mixed forests in the north-eastern part of the Iberian Peninsula (Terradas, 1999). Both species share similar life history-traits, such as resprouting ability after disturbances, slow growth, and establishment mainly occurring in stands under a closed canopy and deep litter layer (Gracia *et al.,* 2001). However, they differ markedly in their leaf habit: *Q. cerrioides* is a winter deciduous oak, while *Q. ilex* is an evergreen one. These differences in leaf life-span may result in differences in the use of resources. Evergreen habit has been considered to be an adaptation to poor environments, both in nutrient and water availability, because of its lower resource-losses ratios (Aerts & van der Peijl, 1993; Berendse, 1994). Alternatively, deciduousness involves a shorter photosynthetically active period that needs to be offset by a higher rate of light-saturated assimilation (Eamus, 1999), thus requiring higher levels of nutrients and water availability.

The goal of this study is to analyse the extent of the plastic response on growth morphology, biomass allocation, nutrient content of leaves and δ $^{13}$C of seedlings of *Q. cerrioides* and *Q. ilex* in response to the variability of light, water and nutrients. We have included also an evaluation of the survival response to the experimental factors, because it ultimately indicates plant performance although it is a trait rarely included in experimental studies dealing with plasticity. The first hypothesis we address is that characteristic co-variation of several environmental resources in Mediterranean-type ecosystems will limit the degree of plasticity. Moreover, considering that water availability is the most irregular resource, which in turn affects nutrient availability, we predict that a lower degree of plasticity will be exhibited toward those two factors than toward light intensity. The second hypothesis refers to the two closely-related species. We hypothesize that according to the aforementioned differences between deciduous and evergreen plants, the deciduous leaf habit of *Q. cerrioides* will enable this species to respond strongly to resource variation. These hypotheses have been tested through an experimental study where we have evaluated the response of *Q. cerrioides* and *Q. ilex* seedlings to a combination of different levels of light intensity, water availability and nutrients availability.

## MATERIAL AND METHODS

### Experimental design

*Q. ilex* and *Q. cerrioides* acorns were collected in a mixed forest at the Collserola Park, a protected mountain area near Barcelona (NE Spain; 41$^{o}$ 24' N, 2$^{o}$ 6' E). All seeds were carefully examined to discard aborted, infected or dried individuals and were set under optimal conditions to promote germination. Germinated acorns were transferred to individual plastic pots filled with 1.5 l of oligotrophic substratum (TKS1-Floragard). Pots were placed outdoors in the common garden of the Autonomous University of Barcelona under a transparent plastic roof 6 m high, to provide almost natural atmospheric conditions, but to exclude rainfall.

The experimental design included different levels of light, water and nutrient availability:

*Light:* Three levels of light intensity (% Photosynthetic Active Radiation, PAR) were created with neutral density shade mesh in order to mimic a similar range to that experienced by seedlings in forest environments. According to previous fieldwork results (Espelta *et al.* 1995), the three experimental levels tested reproduced those that young seedlings would encounter under a dense ($L_8$ = 8% of PAR), intermediate ($L_{36}$ = 36% of PAR) and open ($L_{80}$ = 80% of PAR) oak canopy, respectively.

_Water:_ Two levels of water availability were tested, a shallow ($W_{500}$ = 500 mm m-2 year-1) and a higher level ($W_{800}$ = 800 mm m-2 year-1). To provide a realistic approach, the annual amount of water was distributed monthly following the Mediterranean seasonal pattern characterised by a rainy spring and autumn, a moist winter and a dry summer. Monthly watering (% of annual total) was calculated by taking as a reference data the monthly precipitation over the last 25 years in Collserola (see Table 1). Watering was carried out twice a month (every two weeks).

**Table 1.** Monthly watering doses (l m-2) applied in the two water availability levels ($W_{500}$ and $W_{800}$).

|  | _Jan._ | _Feb._ | _March_ | _April_ | _May_ | _June_ | _July_ | _Aug._ | _Sept_ | _Oct._ | _Nov._ | _Dec._ | _Total_ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| $W_{500}$ | 35 | 30 | 35 | 45 | 55 | 35 | 20 | 40 | 55 | 60 | 50 | 40 | 500 |
| $W_{800}$ | 56 | 48 | 56 | 72 | 88 | 56 | 32 | 64 | 88 | 96 | 90 | 64 | 800 |
| % total annual | 7 | 6 | 7 | 9 | 11 | 7 | 4 | 8 | 11 | 12 | 10 | 8 | 100 |

_Nutrients_: Two levels of nutrient availability were tested: (N-) where seedlings only had the nutrients from the organic (Fervo 35 45N 45P 10K) substrate (1.6 kg m-3 of N, 1.6 kg m-3 of P and 0.8 kg m-3 of K); and a higher level (N+) that received an extra dose of fertiliser (0.1 kg m-3 of N, 0.1 kg m-3 of P and 0.1 kg m-3 of K) at the beginning of the experiment.

The four experimental factors (light, water, nutrient and species) were randomly arranged following a split-split-plot design, with light x water as the whole-plot, nutrients as the split-plot and species as the split-split-plot. Each combination of light, water and nutrients included 21 seedlings per species and was repeated in three replications. Seedlings were grown in those conditions for one year, and their survival was monitored monthly. At the end of the experiment, 12 _Q. ilex_ and 12 _Q. cerrioides_ seedlings of each treatment were randomly chosen (four per replication) and total biomass was separated into leaves, stems and roots. Roots were carefully washed out and their area and length measured with a Dias Root Length (Delta-T Devices, United Kingdom). Leaf area was measured with a LI-COR Model 3100 area meter (LI-COR, USA) and leaf thickness was determined with a Micrometer 0.01 mm precision Model 3000 (Baxlo, USA). Dry weight of roots, shoots and leaves was calculated after drying them out at 70º (72h).

Leaves of all seedlings harvested per treatment and replication were grouped and finely ground with a grinder. A sub-sample was sent to the SXAI institute (Santiago de Compostela, Spain) to

determine the carbon ($^{13}$C) isotopic composition, and nitrogen content of leaves. Carbon isotope ratio and the percentage of nitrogen were determined in an elemental analyser (Carlo Erba Instruments EA 1108 CHNS/O), connected with an isotope ratio mass spectrometer (DELTA$^{plus}$, Finnigan MAT). The sample precision of the analysis was ± 0.2 ‰. The $^{13}$C values are expressed in delta notation as $\delta^{13}$C (‰) relative to the Pee Dee Belemnite (PDB) standard. Leaf N content is expressed on both dry mass basis (% dry mass) and leaf area basis (g m -2).

Morphological and structural variables used to characterise seedling response to the experimental factors included: total biomass, root biomass, stem biomass, leaf biomass, leaf number, and several morphological and biomass allocation indices derived from those primary data: root biomass/aerial biomass (root-shoot), root weight ratio (RWR), stem weight ratio (SWR), leaf weight ratio (LWR), leaf area ratio (LAR), specific leaf weight (SLW) and mean unit leaf area (ULA).

At the end of the experiment, acorn size was determined by measuring its major and minor diameter after carefully removing it from each seedling. As there were no significant differences in acorn size between both species (ANOVA; d.f.= 50, F= 1.5, p= 0.1, *Q. ilex* = 9.0 ± 1.0 mm 3 and *Q. cerrioides* = 8.3 ± 1.4 mm 3) or treatments (data not shown), total plant biomass at the end of the experiment was considered as an estimate of the net growth of seedlings, and acorn size was not included as a covariate.

**Data analysis**

A four-way ANOVA for split-split-plot designs was used to test for effects of species, light, water, and nutrient availability on seedlings survival. Due to the high mortality rates observed in some of the experimental treatments (see the Results section) we had to carry out two separate analyses for the effects of light, water, and nutrient availability on the growth, morphology, biomass allocation, $\delta^{13}$C and nitrogen content of leaves. In the first one, the response to light ($L_8$, $L_{36}$, $L_{80}$) and nutrient availability (N-, N+) were tested for a single water treatment ($W_{800}$), through a three-way ANOVA (species, light, nutrient). In the second, the effects of light ($L_8$, $L_{36}$) and water availability ($W_{500}$, $W_{800}$) were analysed for a single nutrient level (N-) through a three-way ANOVA (species, light, water). In all analyses, inspection of residuals was carried out to check for normality and homoscedasticity. Survival data were angular transformed prior to analysis. The sequential Bonferroni method was used to control the group-wide type I error rate (Rice, 1989).

Differences in plasticity between the two species in the different variables analysed were considered significant according to the *P*-value for the species factor, as a principal factor, and the treatment x species interaction in the corresponding ANOVAs (see Schlichting, 1986; Valladares *et al.*, 2000a).

**RESULTS**

Light, water and to a lesser extent nutrient availability had a major influence on the survival of *Q. cerrioides* and *Q. ilex* seedlings (Table 2). Survival of both species increased with water availability and decreased with light intensity. Moreover, the light x water interaction revealed that survivorship was extremely low, less than 20%, in all water levels under the highest light intensity ($L_{80}$), and in the lower water level ($W_{500}$) under the intermediate light environment ($L_{36}$). Despite this general trend, a different sensitivity to light was observed in both species (species x light interaction in Table 2). As shown in Figure 1, *Q. cerrioides* exhibited a higher survival rate than *Q. ilex* in the shadiest environment (Mean comparison, F=6.9, p=0.013), while the reverse trend occurred at the intermediate light level (Mean comparison, F=6.5, p=0.016) and no specific differences appeared under the highest light level (Mean comparison, F=0.5, p=0.463). Concerning nutrient availability, fertilisation also affected seedling survival (Table 2), and the two species exhibited a significantly higher survival rate at the low-nutrient level ($39.2 \pm 5.5\%$) in comparison with the high-nutrient one ($30.6 \pm 5.2$ %).

**Table 2**. Analysis of variance for the effects of species, light, water, and nutrient availability on the percentage of seedling survivorship. Angular transformed data were used for this analysis. Statistical significance: ns= not significant, *, $p<0.05$; **, $p<0.01$; ***, $p<0.001$.

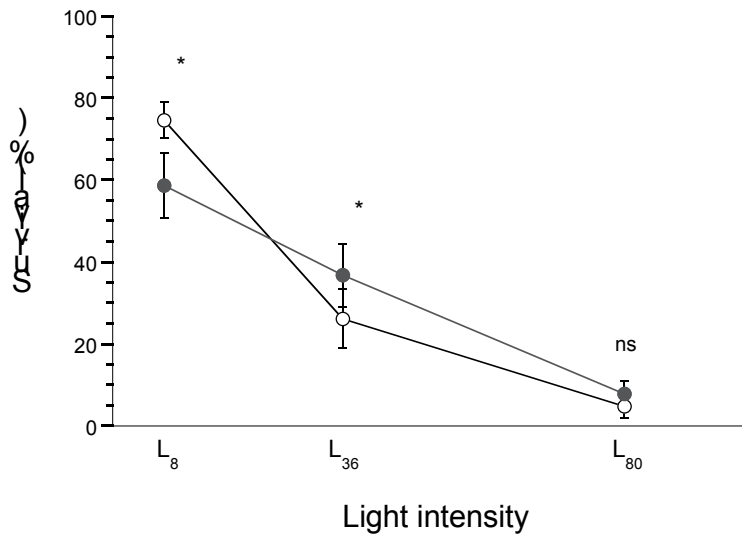| Source of Variation | df | F |
|---|---|---|
| Species (S) | 1 | 0.3 ns |
| Light (L) | 2 | 212.0 *** |
| Water (W) | 1 | 152.0 *** |
| Nutrient (N) | 1 | 8.8 ** |
| S × L | 2 | 7.1 ** |
| S × W | 1 | 2.3 ns |
| S × N | 1 | 1.3 ns |
| L × W | 2 | 9.1 ** |
| L × N | 2 | 2.4 ns |
| W × N | 1 | 0.1 ns |
| S × L × W | 2 | 1.0 ns |
| S × L × N | 2 | 0.3 ns |
| S × W × N | 1 | 0.3 ns |
| L × W × N | 2 | 0.1 ns |
| S × L × W × N | 2 | 0.3 ns |
| Residual | 36 | |

**Figure 1**. Mean (± 1 SE) survival of *Q. cerrioides* seedlings (hollow dots) and *Q. ilex* seedlings (filled dots) in the three light levels. Statistical significance between species in each light level according to the mean comparison test is indicated. ns = not significant, *, *p*<0.05.

The analysis including the effects of species, light and nutrients on total biomass, biomass allocation, N content of leaves, and isotopic discrimination ($\delta^{13}$C) of seedlings is summarised in Table 3. Total biomass of seedlings did not show significant differences between species (*Q. cerrioides* = 0.73 ± 0.09 g and *Q. ilex* = 0.70 ± 0.06 g), although they differed markedly in their main morphological traits and biomass allocation patterns (Figure 2). *Q. cerrioides* exhibited a higher RWR and lower LWR than *Q. ilex* (Figure 2a, b). Differences in biomass partitioning were related to the fact that, for a similar root and stem biomass, *Q. cerrioides* had lower leaf biomass than *Q. ilex* (Figure 2c), due to the fewer and thinner leaves of the former species (Figure 2d, e, f). *Q. cerrioides* leaves had a higher content of N in a mass basis than *Q. ilex* (*Q. cerrioides* = 1.5 ± 0.1 %; *Q. ilex* = 1.2 ± 0.1 %), but no differences between species were found in N content expressed in an area-basis (*Q. cerrioides* = 1.1 ± 0.1 mg cm-2; *Q. ilex* = 1.2± 0.1 mg cm-2). Significant differences in the carbon isotope ratio indicated that *Q. cerrioides* presented higher δ $^{13}$C values than *Q. ilex* (*Q. cerrioides* = -27.75 ± 0.18 $^0/_{00}$; *Q. ilex* = –28.95 ± 0.16 $^0/_{00}$)

**Table 3.** Effects of species, light (L$_8$,L$_{36}$,L$_{80}$) and nutrient (N-,N+) availability on morphological and biomass allocation traits of seedlings: total biomass, root biomass, stem biomass, leaf biomass, root length, root area, root/shoot (R/S), root weight ratio (RWR), stem weight ratio (SWR), leaf weight ratio (LWR), leaf area ratio (LAR), specific leaf area (SLA), unit leaf area (ULA), leaf number, leaf thickness, Nitrogen content in a mass basis (%), Nitrogen content in an area basis (mg cm-2) and δ $^{13}$C. F values of ANOVAs are given. Significant coefficients (at =0.05 after applying the sequential Bonferroni method) are indicated in bold.

| Source of variation | df | Total biom. | Root biom. | Stem biom. | Leaf biom. | Root length | Root area | R/S | RWR | SWR | LWR | LAR | SLW | ULA | Leaf n° | Leaf thick. | Nitrog. (mass) | Nitrog. (area) | δ $^{13}$C |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species (S) | 1 | 8.7 | 7.8 | 2.7 | **34.3** | **85.5** | **179.3** | **161.9** | **100.3** | 8.9 | **76.0** | 9.1 | **103.5** | 2.2 | **22.6** | **49.5** | **56.3** | 1.1 | **78.4** |
| Light (L) | 2 | **34.5** | **31.4** | 0.5 | 5.1 | 2.9 | 4.8 | **109.2** | **285.2** | **61.0** | **328.3** | **295.3** | **341.6** | 7.6 | **33.8** | **27.6** | **50.1** | 6.1 | 29.0 |
| Nutrients (N) | 1 | 1.2 | 0.5 | 3.4 | 2.8 | 0.7 | 2.9 | 1.7 | 0.3 | 0.5 | 0.1 | 0.1 | 0.2 | 1.7 | 0.5 | 1.2 | **25.2** | **17.0** | 3.9 |
| S x L | 2 | 1.3 | 1.9 | 0.9 | 2.3 | **14.7** | **23.5** | **28.5** | 4.3 | 1.5 | 3.8 | 1.4 | 6.4 | 0.7 | 0.9 | 1.5 | **13.1** | 8.4 | 0.1 |
| S x N | 1 | 2.2 | 1.8 | 0.3 | 3.4 | **18.0** | **29.5** | 0.5 | 0.7 | 0.6 | 2.9 | 0.9 | 1.3 | 1.3 | 2.5 | 0.9 | 1.2 | 1.7 | 0.5 |
| L x N | 2 | 0.3 | 0.5 | 0.1 | 0.6 | 2.6 | 6.2 | 2.1 | 2.0 | 0.3 | 2.1 | 0.8 | 1.2 | 3.0 | 0.6 | 1.9 | 1.7 | 2.7 | 1.8 |
| S x L x N | 2 | 1.9 | 1.8 | 1.2 | 0.8 | **11.4** | **23.4** | 1.3 | 1.1 | 0.1 | 1.7 | 0.9 | 0.6 | 0.5 | 0.2 | 3.8 | **14.2** | 2.3 | 0.7 |
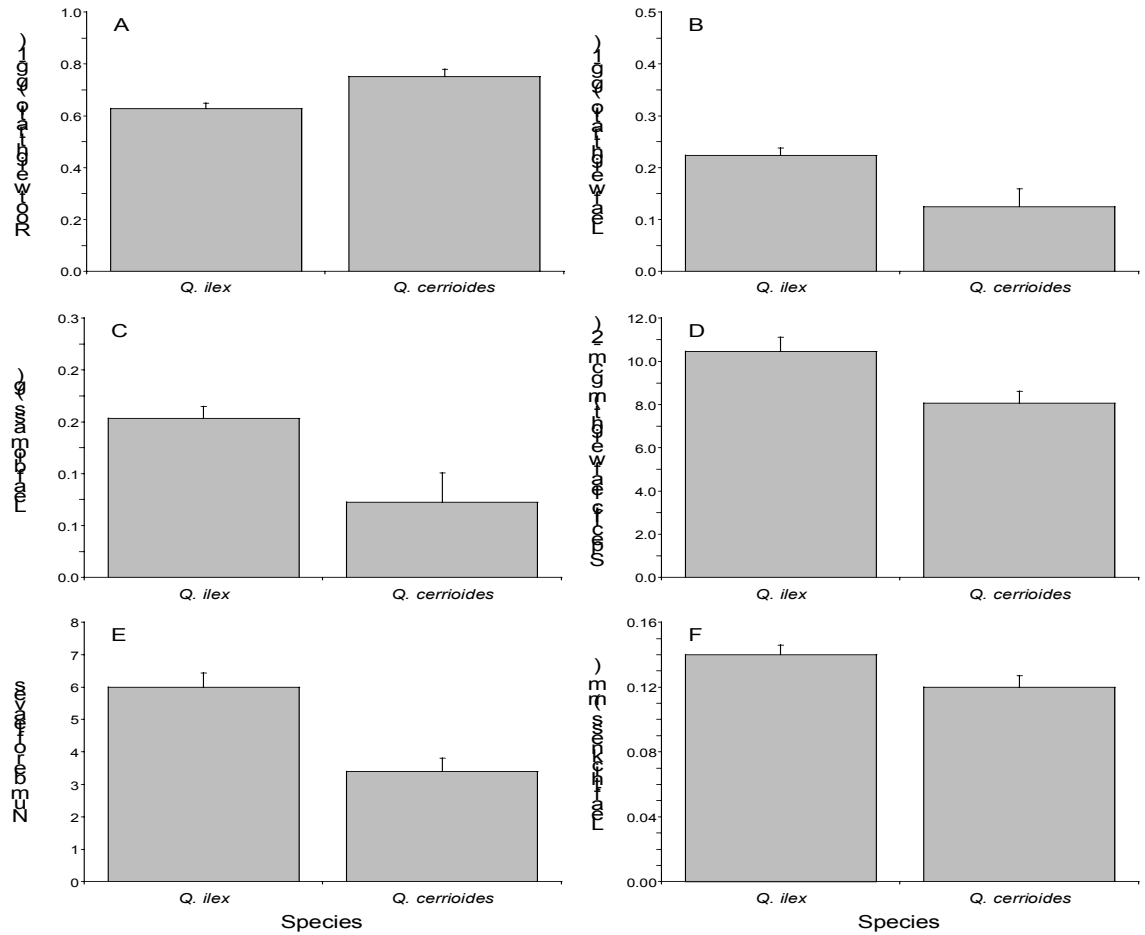
**Figure 2**. Mean (+ SE) root weight ratio (A), leaf weight ratio (B), leaf biomass (C), specific leaf weight (D), number of leaves (E) and leaf thickness (F) of *Q. cerrioides* and *Q. ilex* seedlings

In the two species, total biomass was enhanced by light availability but, as shown in Figure 3a, the maximum total biomass of seedlings was achieved under the intermediate light level, $L_{36}$, with a tendency to decrease under the highest light intensity. This higher total biomass exhibited by plants grown under the intermediate light regime was due to their higher root biomass (Figure 3b). The importance of $L_{36}$ as a breaking point in seedlings response to light was also detected in other traits. SWR and LWR decreased with light (Figure 3c, d) but LAR, leaf number and thickness, did not vary from $L_{36}$ towards $L_{80}$ (Figure 3e, f, g). Moreover, the same threshold was found in the reduction of the N content of leaves (expressed in a mass-basis, Figure 3h). On the other hand, $\delta^{13}C$ increased with light, but remained similar under $L_{36}$ and $L_{80}$ ($L_8$= -29.04± 0.22, $L_{36}$= -27.95± 0.21, $L_{80}$= -27.94± 0.27 $^0/_{00}$). According to the significance of the species and species x light interaction (Table 2) both species differed in their plasticity in response to light intensity: *Q. cerrioides* exhibited greater plasticity than *Q. ilex* in root length, root area and root/shoot (Figure 4a, b, c), while *Q. ilex* exhibited a higher plasticity than *Q. cerrioides* in N content of leaves in a mass-basis (Figure 4d).

As a main factor, nutrient availability modified neither growth of seedlings nor their morphology and biomass allocation pattern (Table 3). However, nutrient availability interacted with species and light on the length and area of roots and the N content of leaves (see Table 3). Specific differences in root length and area (higher values in *Q. cerrioides*) increased in the poor-nutrient (N-) treatment under both intermediate ($L_{36}$) and maximum ($L_{80}$) light intensity levels (Figure 5a, b). On the other hand, greater differences between species in the nitrogen content (% dry mass) were found under the $L_{36}$ poor-nutrient (N-) treatment and $L_{80}$ rich-nutrient (N+) treatment, *Q. cerrioides* having higher nitrogen content than *Q. ilex* (Figure 5c).
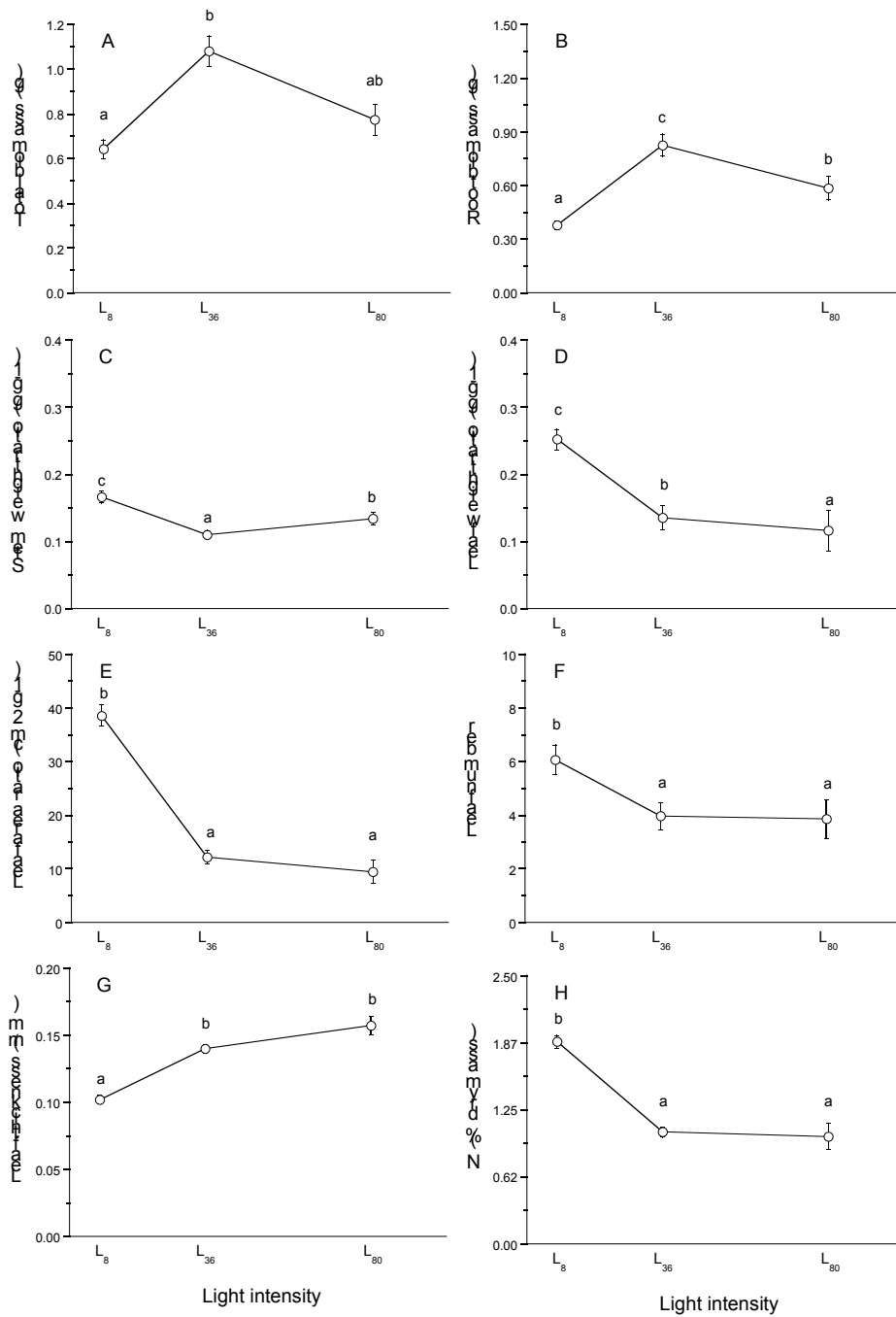
**Figure 3.** Mean (± SE) total biomass (A), root biomass (B), stem weight ratio (C) , leaf weight ratio (D) , leaf area ratio (E), leaf number (F), leaf thickness (G) and percentage of N (H) of the seedlings of *Q. cerrioides* and *Q. ilex* in the three light levels tested. Letters indicate significant differences among light levels according to the Fisher PSLD post-hoc test.
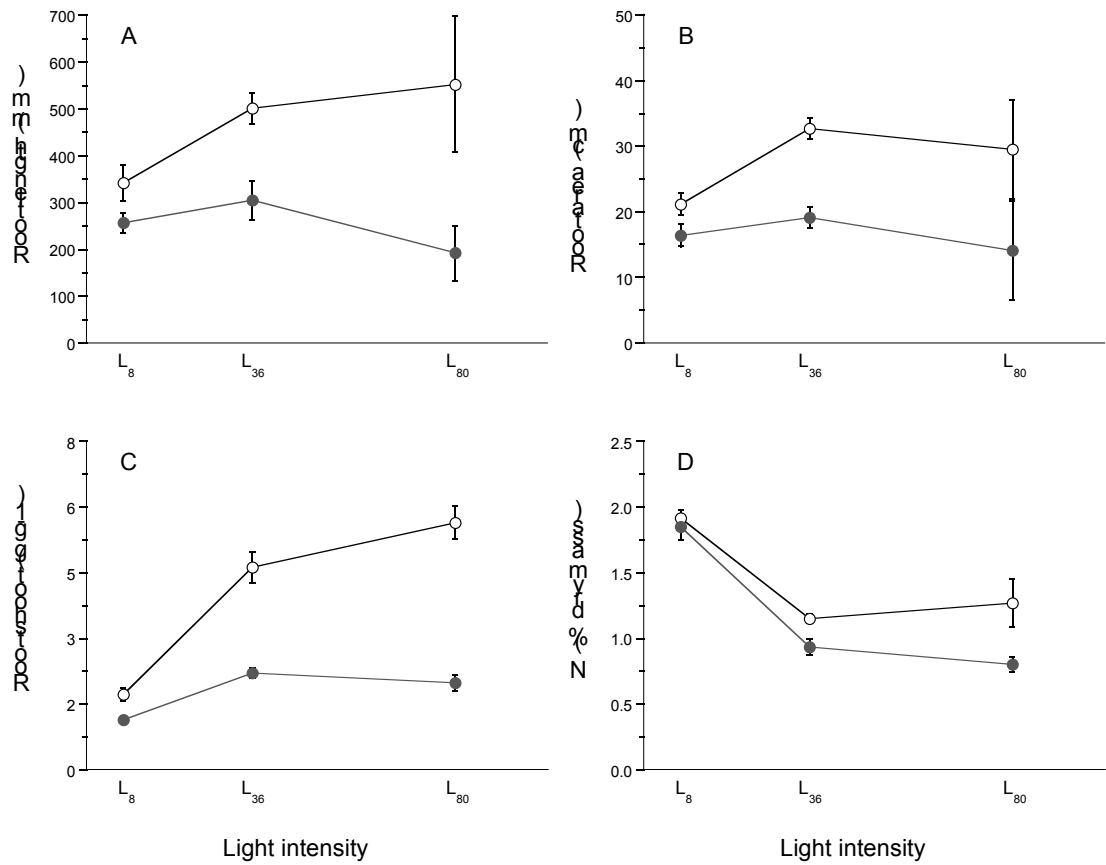
**Figure 4**. Mean (± SE) root length (A), root area (B) , Root/Shoot (C), and N content of leaves (D), of *Q. cerrioides* (hollow dots) and *Q. ilex* seedlings (filled dots) in the three light levels tested.
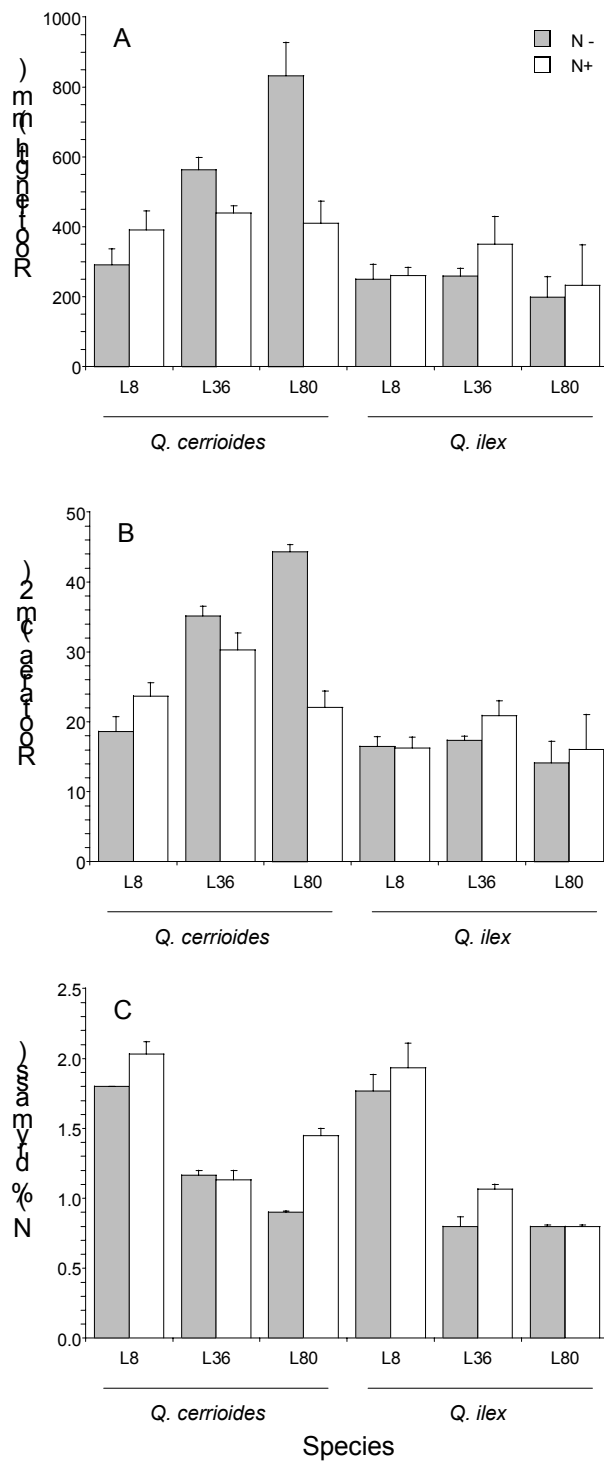
**Figure 5**. Mean (+ SE) root length (A), root area (B) and N content of leaves (C) of *Q. cerrioides* and *Q. ilex* seedlings in the three light levels ($L_8$, $L_{36}$, $L_{36}$) and the two nutrient availability levels tested (N - = grey bar, N+ = white bar)

The second analysis including the effects of species, light and water on morphology, N content of leaves, and $\delta^{13}$C of seedlings is shown in Table 4. Differences between species and the influence of light on growth and biomass allocation patterns followed a similar trend to that previously shown in the former analysis. However, it is important to remark that water availability influenced neither the growth of seedlings nor most of their morphology, N content of leaves, and isotopic discrimination (Table 4). Thus, the lack of significant species x water interactions for most of the variables studied (except LWR and LAR) indicated a similar plasticity of both species in response to the two levels of water tested. However, the species x light x water interaction (Table 4) pointed to an effect of the watering level on the leafiness of seedlings (LWR and LAR). As shown in Figure 6, seedlings of *Q. ilex* reduced their LAR and LWR in response to increasing light intensity, but in the two water levels they presented similar values, while *Q. cerrioides* presented a similar pattern of reduction in response to light, but in the two light environments seedlings that received the higher water amount presented larger LAR and LWR.

**Table 4.** Effects of species, light ($L_8$,$L_{36}$) and water ($W_{500}$,$W_{800}$) availability on morphological and biomass allocation traits of seedlings: total biomass, root biomass, stem biomass, leaf biomass, root length, root area, root/shoot (R/S), root weight ratio (RWR), stem weight ratio (SWR), leaf weight ratio (LWR), leaf area ratio (LAR), specific leaf area (SLA), unit leaf area (ULA), leaf number, leaf thickness, Nitrogen content in a mass basis (%), Nitrogen content in an area basis (mg cm-2) and $\delta^{13}$C. F values of ANOVAs are given. Significant coefficients (at  =0.05 after applying the sequential Bonferroni method) are indicated in bold.

| Source of variation | d.f. | Total biom. | Root biom. | Stem biom. | Leaf biom. | Root length | Root area | R/S | RWR | SWR | LWR | LAR | SLW | ULA | Leaf nº | Leaf thick. | Nitrog. (mass) | Nitrog. (area) | $\delta^{13}$C |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species (S) | 1 | 0.4 | 5.3 | 4.9 | **64.6** | **29.9** | **73.6** | **123.7** | **74.3** | 5.5 | **331.4** | **34.8** | **123.3** | 7.5 | **23.3** | 13.5 | **27.3** | 0.1 | **60.1** |
| Light (L) | 1 | **56.5** | **76.0** | 8.6 | 2.3 | 11.0 | **39.7** | **62.0** | **44.2** | 21.9 | **43.4** | **128.9** | **151.8** | 7.5 | 5.7 | **132.5** | **26.5** | 6.7 | **26.4** |
| Water (W) | 1 | 9.5 | 5.6 | 7.0 | 15.2 | 4.1 | 10.4 | 0.1 | 0.5 | 0.1 | 1.8 | 0.8 | 7.6 | 1.2 | 0.7 | 11.4 | 2.7 | 11.0 | 5.3 |
| S x L | 1 | 2.5 | 3.6 | 1.5 | 2.5 | 7.5 | 18.7 | **44.0** | 1.2 | 0.1 | 12.2 | 4.8 | 15.5 | 0.1 | 0.8 | 0.6 | 5.7 | 8.7 | 0.1 |
| S x W | 1 | 0.4 | 0.1 | 0.4 | 5.5 | 0.7 | 0.3 | 0.1 | 0.2 | 0.1 | 0.8 | 5.5 | 2.4 | 2.1 | 0.1 | 2.8 | 1.0 | 1.6 | 0.1 |
| L x W | 1 | 0.2 | 1.6 | 3.1 | 4.1 | 0.8 | 2.4 | 4.0 | 4.9 | 2.6 | 5.3 | 5.3 | 1.5 | 0.1 | 2.4 | 3.6 | 4.9 | 1.7 | 1.4 |
| S x L x W | 1 | 0.8 | 0.9 | 4.0 | 1.9 | 0.7 | 4.1 | 4.1 | 3.7 | 0.5 | **51.4** | **23.7** | 1.0 | 8.5 | 2.4 | 0.1 | 1.3 | 0.4 | 0.1 |
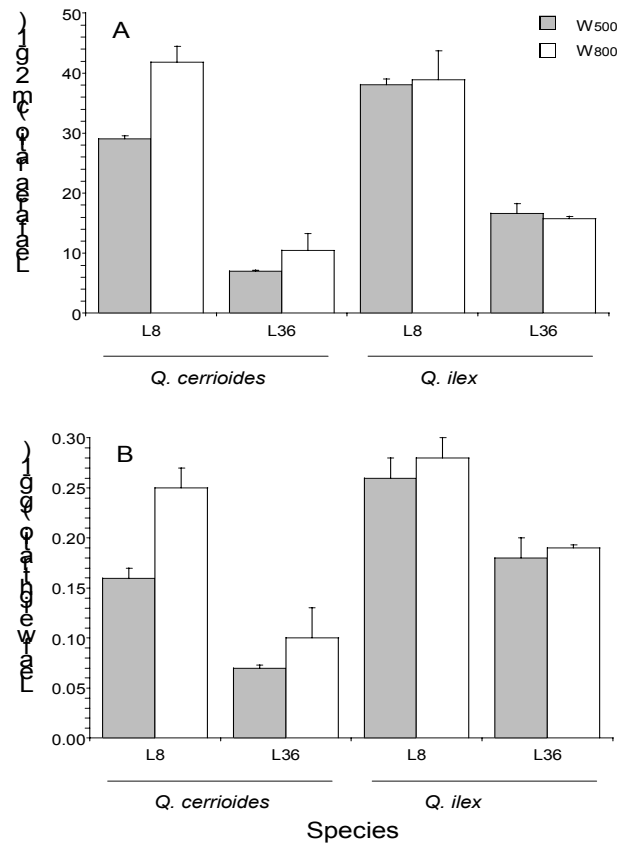
**Figure 6.** Mean (+ SE) leaf area ratio (A) and leaf weight ratio (B) of *Q. cerrioides* and *Q. ilex* seedlings in the two light levels ($L_8$, $L_{36}$) and the two water availability levels tested ($W_{500}$ = grey bar, $W_{800}$ = white bar).

**DISCUSSION**

Water availability enhanced seedling survival, as could be expected under a Mediterranean-type climate, but the benefits of a higher total water disposal vanished with increasing light (i.e. survival of well-watered seedlings accounted for less than 20% under full light). The importance of partial shading for seedling recruitment in this climate has been previously suggested by field studies (DeSimone & Zedler, 1999), as partial cover of seedlings may reduce temperature and water demand (Rousset & Lepart 2000), and thus prevents the risk of cavitation during summer drought (Tognetti *et al.* 1998). While it is easy to recognise the major effect of water and light availability in survival, it is less straightforward to interpret the negative effect that a higher nutrient availability had on the survival of seedlings. This effect could be considered in the light of a possible trade-off between the changes promoted by a high nutrient availability in the seedlings and their ability to cope with water stress (see Bazzaz, 1996), as the architecture induced by a high nutrient disposal could further compromise survival during the drought period (Broncano *et al.* 1998). This hypothesis seems to be feasible at least for *Q. cerrioides*, which showed a lower root length and area when growing in the higher nutrient level, under L36 and L80 (Figure 5), possibly hindering their subsequent water status during summer. However this does not hold for *Q. ilex*, whose root traits remained fairly similar in the entire light/nutrient gradient.

Notwithstanding the key effects of light, water and nutrients on survival, results concerning growth patterns and biomass partitioning of *Q. ilex* and *Q. cerrioides* seedlings confirmed our initial hypothesis presuming a low plasticity, particularly in front of water and nutrient availability. In fact, neither water nor nutrient availability affected total biomass in the two species (Tables 2 and 3), and had only a minor impact on their patterns of biomass partitioning. Of the different traits analysed, including both morphological and biomass allocation ratios, water availability only influenced LWR and LAR, while nutrient availability modified root length and root area (Tables 2 and 3). The lack of a major morphological and biomass allocation response to those resources could be explained because: i) the two species display a strong conservative strategy as presumed in plants living in adverse conditions ("stress resistance syndrome" sensu Chapin *et al.*, 1993) or ii) fluctuations in water, due to the different seasonal watering, precluded seedlings from being able to adopt an optimal partitioning model in response to this resource and also nutrients availability (see for a similar response linked to temporally varying nutrient regimes Gedroc *et al.*, 1996). As hypothesised, in comparison to the few changes induced by water or nutrients, a larger array of modifications was promoted by light intensity. In both species, response to higher light intensities included the typical adjustments in favour of an increase in leaf thickness, SLW and root/shoot and a decrease in leafiness (leaf number, LAR and LWR), in a similar way to the response reported in temperate and tropical species (see, among others, Reich *et al.*, 1992; Tanouchi, 1996). However, there was a rather early limit to

plasticity both in growth and leaf traits, occurring at the intermediate light level (36% PAR), with no further changes beyond that point in total biomass, leaf number, leaf thickness, LWR or LAR. Despite this limited response, results confirmed our second hypothesis: a slightly higher phenotypic plasticity to light in the deciduous *Q. cerrioides* (Table 2). Interestingly, those differences were not associated with leaf characteristics (e.g. SLW), as might be expected from their contrasted leaf-habit, but were related to R/S, root length and root area. The higher variation of R/S in *Q. cerrioides* in response to light was mainly due to a greater leaf biomass reduction when light intensity increased, coupled with a similar pattern in the two species in the increase of root weight and the maintenance of stem weight. This reduction of leafiness in *Q. cerrioides* seedling was due in part to partial shedding (unpubl. data) and might be viewed as an ultimate mechanism to maintain water balance (Damesin & Rambal, 1995). This higher sensitivity to water stress of *Q. cerrioides* in comparison to *Q. ilex* seedlings also appears to be proven by the fact that the former species exhibited: i) higher values of $\delta$ $^{13}$C, showing that it closes its stomata before *Q. ilex* seedlings do (see Damesin *et al.*, 1997) and, ii) a larger increase in root area and length when light intensity increased (see Reader *et al.*, 1993, and for Mediterranean oaks, Canadell *et al.*, 1999).

Regardless of the large differences in biomass partitioning and to a lesser extent, in plasticity reported in the two species, they attained the same growth in biomass along the entire light gradient. These results reveal that although major differences between deciduous and evergreen Mediterranean oak seedlings may occur in their morphology in response to environmental heterogeneity, they lead to a similar performance, at least in terms of growth. Several traits associated with higher SLW and sclerophylly of leaves of the evergreen *Q ilex*, such as greater diffusional restrictions and greater irradiance limitations - due to reflectance and/or internal shading (Lloyd *et al.*, 1992) - can cause, as in other evergreen species (Reich *et al.*, 1995), a reduction of the maximum rate of photosynthesis (Castell *et al.*, 1994). However, this lower rate of photosynthesis might be offset by the maintenance of an extensive period of photosynthetic activity (Eamus, 1999) and, as shown in our study, higher values of leafiness (LAR), even under intense light radiation (see also Damesin *et al.*, 1998). On the other hand, the growth rate of *Q. cerrioides* could be constrained and therefore similar to that of *Q. ilex*, not only due to a shorter photosynthetic period, but ultimately, as shown in this study, due to a greater reduction in leafiness when light intensity increases, coupled with the costs of maintaining a larger R/S. These results contrast with previous comparison between deciduous and evergreen species from temperate ecosystems, which have found the former to be more productive (Aerts, 1990; Reich *et al.*, 1992; Cornelissen *et al.*, 1996), because the greater morphological plasticity of deciduous seedlings allows them to take better advantage of favourable growing conditions (see Ke and Werger, 1999; Valladares *et al.* 2002).

A higher phenotypic plasticity has long been considered a major means whereby plants enhance their performance in variable environments (Ryser & Eck, 2000), but may be worthless in unproductive or highly unpredictable habitats where resource capture may depend on long-lived tissues, storage pools and strong reliance on resource pulse interception (Grime, 1994). In that context, our results with *Q. cerrioides* and *Q. ilex* seedlings allow us to draw two major conclusions: i) in Mediterranean-type ecosystems, environmental heterogeneity may constrain the expression of plasticity, at least in morphological and biomass allocation traits, ii) despite differences in the partitioning model and plasticity between the deciduous *Q. cerrioides* and the evergreen *Q. ilex* seedlings, they appear as two different but rather successful strategies in coping with environmental variation, only  leading to a slight advantage in survival of the former in the shadiest understory and of the latter in fragmented light environments. Thus, the ecological inference of our results indicates that coexistence or substitution among *Q. cerrioides* and *Q. ilex* is likely to rely on differences between the species in other traits, such as the reproductive outcome (Cortes*,* unpublished) or the response to disturbances (Espelta et al., *in press*), rather than on differences in plasticity in response to environmental heterogeneity.

**REFERENCES**

Aerts, R. 1990. Nutrient use efficiency in evergreen and deciduous species from heathlands. Oecologia, 84: 391-397.

Aerts, R. and van der Peijl M.J. 1993. A simple model to explain the dominance of low-productive perennials in nutrient-poor habitats. Oikos, 66: 144-147.

Aschmann, H. 1973. Distribution and Peculiarity of Mediterranean Ecosystems. In: di Castri, F. and Mooney, H.A (eds.) Mediterranean-type ecosystems. Origin and structure. Berlin, Germany: Springer-Verlag.

Bazzaz, F.A. 1996. Plants in changing environments: linking physiological, population, and community ecology. Cambridge, UK. Cambridge University Press.

Bazzaz, F.A. and Wayne, P.M. 1994. Coping with environmental heterogeneity: the physiological ecology of tree seedling regeneration across the gap-understory continuum. In: Cadwell, M.M. and Pearcy, R.W. (eds.) Exploitation of environmental heterogeneity by plants. Ecophysiological processes above and belowground. London, UK. Academic Press.

Bell, G. and Lechowicz, M.J. 1994. Spatial Heterogeneity at Small Scales and How Plants Respond to It. In: Cadwell, M.M. and Pearcy, R.W. (eds.) Exploitation of environmental heterogeneity by plants. Ecophysiological processes above and belowground. London, UK. Academic Press.

Berendse, F. 1994. Competition between plant populations at low and high nutrient supplies. Oikos, 71: 253-260.

Bradshaw, A.D. 1965. Evolutionary significance of phenotypic plasticity in plants. Advances in Genetics, 13: 115-155.

Broncano, M.J; Riba, M. and Retana, J. 1998. Seed germination and seedling performance of two Mediterranean tree species, holm oak (*Quercus ilex* L.) and Aleppo pine (*Pinus halepensis* Mill.): a multifactor experimental approach. Plant Ecology, 138: 17-26.

Canadell, J; Djema, A; López, B; Lloret, F; Sabaté, S; Siscart, D. and Gracia, C.A. 1999. Structure and dynamics of the root system. In: Rodà, F; Retana, J; Gracia, C.A. and Bellot, J. (eds.) Ecology of Mediterranean evergreen oak forests. Berlin, Germany. Springer Verlag.

Castell, C; Terradas, J. and Tenhunen, J.D. 1994. Water relations, gas exchange, and growth of resprouts and mature plant shoots of Arbutus unedo L. and Quercus ilex L. Oecologia, 98: 201-211.

Chapin, F.S; Autumn, K. and Puignaire, F. 1993. Evolution of suites of traits in response to environmental stress. American Naturalist, 142: 578-592.

Cornelissen, J.H.C; Castro, Diez P. and Hunt, R. 1996. Seedling growth, allocation and leaf attributes in a wide range of woody plant species and types. Journal of Ecology, 84: 755-765.

Cornelissen, J.H.C; Castro Diez, P. and Carnelli, P.A.L. 1998. Variation in relative growth rate among woody species. In: Lambers, H; Poorter, H. and van Vuuren M.M.I. (eds.) Inherent variation in plant growth, physiological mechanisms and ecological consequences. Leiden, The Netherlands. Backhuys Publishers.

Damesin, C. and Rambal, S. 1995. Field study of leaf photosynthetic performance by a Mediterranean deciduous oak tree (Quercus pubescens) during a severe summer drought. New Phytologist, 131: 159-167.

Damesin, C; Rambal, S. and Joffre, R. 1997. Between-tree variations in leaf $\delta^{13}$C of Quercus pubescens and Quercus ilex among Mediterranean habitats with different water availability. Oecologia, 111: 26-35.

Damesin, C; Rambal, S. and Joffre, R. 1998. Co-occurrence of trees with different leaf habit: a functional approach on Mediterranean oaks. Acta Oecologica, 19: 195-204.

DeSimone, S.A. and Zedler, P.H. 1999. Shrub seedling recruitment in unburned Californian coastal sage scrub and adjacent grassland. Ecology, 80: 2018-2032.

Eamus, D. 1999. Ecophysiological traits of deciduous and evergreen woody species in the seasonally dry tropics. Trends in Ecology and Evolution, 14: 11-16.

Espelta, J.M; Riba, M. and Retana, J. 1995. Patterns of seedling recruitment in West-Mediterranean Quercus ilex forests influenced by canopy development. Journal of Vegetation Science, 6: 465-472.

Espelta, J.M; Retana, J. and Habrouk. A. Resprouting patterns after fire and response to stool cleaning of two coexisting Mediterranean oaks with constrasting leaf habits on two different sites. Forest Ecology and Management, in press.

Gedroc JJ, McConnaughay KDM, Coleman JS. 1996. Plasticity in root/shoot partitioning: optimal, ontogenetic, or both? Functional Ecology 10:44-50.

Gracia, M; Retana, J. and Picó, X. 2001. Seedling bank dynamics in managed holm oak (Quercus ilex) forests. Annals of Forest Science, 58: 843-852.

Grime, J.P. 1994. The role of plasticity in exploiting environmental heterogeneity. In: Caldwell, M.M. and Pearcy, R.W. (eds.) Exploitation of environmental heterogeneity by plants. Ecophysiological processes above and belowground. London, UK: Academic Press, 1-19.

Ke G, Werger MJA. 1999. Different responses to shade of evergreen and deciduous oak seedlings and the effect of acorn size. Acta Oecologica 20:579-586.

Kitajima K, Mulkey SS, Wright SJ. 1997. Seasonal leaf phenotypes in the canopy of a tropical dry forest: photosynthetic characteristics and associated traits. Oecologia 109: 490-498.

Lloyd J, Syvertsen JP, Kriedemann PE, Farquhar GD. 1992. Low conductances for $CO_2$ diffusion from stomata to the sites of carboxylation in leaves of woody species. Plant Cell and Environment 15:873-899.

Ögren E, Sundin U. 1996. Photosynthetic responses to variable light: a comparison of species from contrasting habitats. Oecologia 106:18-27.

Reader RJ, Jalili A, Grime JP, Spencer RE, Mathews N. 1993. A comparative study of plasticity in seedling rooting depth in drying soil. Journal of Ecology 81:123-128.

Reich PB, Walters MB, Ellsworth DS. 1992. Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. Ecological Monographs 62:365-392.

Reich PB, Kloeppel BD, Ellsworth DS, Walters MB. 1995. Different photosynthesis-nitrogen relations in deciduous hardwood and evergreen coniferous tree species. Oecologia 104:24-30.

Rice WR. 1989. Analyzing tables of statistical tests. Evolution 43:223-225.

Rousset O, Lepart J. 2000. Positive and negative interactions at different life stages of a colonising species (Quercus humilis). Journal of Ecology 88:401-412.

Ryser P, Eck L. 2000. Consequences of phenotypic plasticity vs. interspecific differences in leaf and root traits for acquisition of aboveground and belowground resources. American Journal of Botany 87:402-411.

Schlichting CD 1986. The evolution of phenotypic plasticity in plants. Annual Review of Ecology and Systematics 17:667-693.

Strauss-Debenedetti S, Bazzaz FA. 1991. Plasticity and acclimation to light in tropical Moraceae of different successional positions. Oecologia 87:377-387.

Tanouchi H. 1996. Survival and growth of two coexisting evergreen oak species after germination under different light conditions. International Journal of Plant Science 157:516-522.

Terradas J. 1999. Holm oak and holm oak forests: an introduction. In: Rodà F, Retana J, Gracia CA, Bellot J, eds. Ecology of Mediterranean evergreen oak forests. Berlin, Germany: Springer Verlag, 3-14.

Tognetti T, Longobucco A, Raschi A. 1998. Vulnerability of xylem to embolism in relation to plant hydraulic resistance in Quercus pubescens and Quercus ilex co-occurring in a Mediterranean coppice stand in central Italy. New Phytologist 139:437-447.

Valladares F, Wright J, Lasso E, Kitajima K, Pearcy RW. 2000a. Plastic phenotypic response to light of 16 congeneric shrubs from a Panamanian rainforest. Ecology 81:1925-1936.

Valladares F, Martinez-Ferri E, Balaguer L, Perez-Corona E, Manrique E. 2000b. Low leaf-level response to light and nutrients in Mediterranean evergreen oaks: a conservative resource-use strategy? New Phytologist 148:79-91.

Valladares F, Chico JM, Aranda I, Balaguer L, Dizengremel P, Manrique E, Dreyer E. 2002. The greater seedling high-light tolerance of Quercus robur over Fagus sylvatica is linked to a greater physiological plasticity. Trees 16:395-403.

Walters MB, Kruger EL, Reich PB. 1993. Growth, biomass distribution and $CO_2$ exchange of northern hardwood seedlings in high and low light: relationships with successional status and shade tolerance. Oecologia 94:7-16.

# RESPONSE TO REPEATED DISTURBANCES OF AN EVERGREEN AND A DECIDUOUS OAK COEXISTING IN THE NORTHEAST OF THE IBERIAN PENINSULA

**INTRODUCTION**

The role of disturbance as a force that shapes the structure and dynamics of ecological communities has long been recognized (Levin and Paine 1974; Sousa 1984; Pickett and White 1985). Many life-history attributes of plant species have evolved as a consequence of disturbances (Grime 1979; Clark 1991; Iwasa and Kubo 1997; Bellingham 2000), which have also been used to explain the actual and past distributions of many dominant tree species. Disturbances have been pervasive in the Mediterranean basin, whose long history of land use has had a profound impact on its biota and landscape (Barberó et al. 1992; Blondel and Aronson 1995; Ojeda 2001), and both vegetation structure and individual species show a wide array of adaptations to anthropogenic disturbances, including forest fires, clear cutting, or browsing (Naveh and Liberman 1984; Fox and Fox 1986; Blondel and Aronson 1999). The variation on the scale, intensity and frequency of these disturbances has merged with a heterogeneous physical environment, creating a patchy landscape in which plants must face a harsh climate characterized by hot, dry summers and humid, cool winters.

There are several studies aimed at assessing the effects of disturbances in plant communities and particular species in Mediterranean ecosystems (Keeley 1986; Canadell et al. 1991; Lloret and López Soria 1993; Canadell and López Soria 1998; Lloret 1998; Riba 1998; Verdú 2000). However, the responses of oaks to disturbances have been studied in only a few species (Malanson and Trabaud 1988; Pausas 1997; Espelta et al. 1999; Espelta et al. 2002), although the genus *Quercus* has a wide distribution in the Mediterranean, and oaks play important roles in many ecosystems of the region (Blondel and Aronson 1999). As acorns do not survive fire and oak regeneration by seeds is almost nil after disturbances (Retana et al. 1999), most studies on the ecology of regeneration of oak species after disturbances have focused in resprouting, which is the most common response of oaks when faced to disturbances: the production of sprouts in case of shoot damage or death is carried out both by seedlings (Strenght et al. 1989; Crow 1992; Thadani and Ashton 1995; Bonfil 1998; Retana et al. 1999) and adult trees (Ross et al. 1986; Crow 1988; Retana et al. 1992; Bonfil 1998; Espelta et al. 1999). The presence of established oaks in the overstorey of a stand has been related to past stand disturbances (Johnson et al. 2002), but there is still lack of knowledge on the regeneration response of different species to varying kinds and intensities of disturbances, and therefore on the role disturbances play in the coexistence and segregation of oak species.

In the case of Mediterranean oaks, it has been frequently considered that the occurrence of disturbance has favoured the evergreen sclerophyllous oaks versus the deciduous broadleaved ones. Palinological records have shown that similar proportions of deciduous and evergreen oaks appeared in NE Spain after 5000 B.P. (Riera-Mora 1995), while evergreens expanded in more recent times, probably as a consequence of human action (Pons and Vernet 1971; Pons and Quezel 1985; García-Latorre and García-Latorre 1996). The latter included both

management practices directly favouring evergreen oaks (because of its use for fuel and feeding cattle), and an increased regime of disturbances –such as fires, grazing or coppicing– associated to the human presence. It has also been postulated that the abandonment of coppicing practices in some regions will cause the gradual invasion of deciduous oaks in forests previously dominated by evergreens (Bacilieri et al. 1993; Bonin and Romane 1996), which implies that coexistence of these species may be disturbance-mediated (Mazzoleni and Spada 1992).

This study analyses the response of two oak species with different leaf habit to repeated disturbances. *Q. ilex* L., which has been considered a Mediterranean paradigm because its evergreen leaf habit (Terradas 1999), dominates in a wide variety of woodlands and scrublands in the western and central parts of the Mediterranean basin (Barberó et al. 1992; Blondel and Aronson 1999; Terradas 1999). The deciduous *Q. cerrioides* Willk. et Costa is distributed more restrictedly in the plains of NE Spain (Ceballos and Ruiz de la Torre 1971). Both species form extensive monospecific or mixed forests in the northeast of the Iberian Peninsula (Gracia et al. 2000). They have expanded in recent years as a result of fire, as large areas previously dominated by *Pinus nigra* Arnold (Espelta et al. 2001) show nil regeneration after fire, while a very high percentage of the burned oaks present in the understorey survive and resprout from the stool (Retana et al. 2002). The resprouting responses of these two oak species to experimentally applied disturbances are evaluated in order to gain insight in the role that disturbances have played in their coexistence, and to provide relevant information to model their dynamics in face of the ongoing changes in disturbance regimes in their area of distribution. As forest fire is one of the most important disturbances that have shaped Mediterranean plant communities (Keeley 1986; Barberó et al. 1987; Trabaud 1987; Lloret 1996; Lloret and Vilá 1997), this was the main factor analysed. Therefore, the main objective of the present study is to evaluate survival and growth of *Q. ilex* and *Q. cerrioides* in response to different fire histories (defined by different periods of fire recurrence) and types of experimental disturbances applied. The latter included fire, cutting or pruning, either before or after summer, a critical season for the stress it imposes on plants living in areas having a Mediterranean climate.

**METHODS**

**Study site**

This study was carried out in Central Catalonia (northeastern Spain), a region affected by two of the largest historically recorded wildfires in NE Spain: the Bages-Berguedà fire, which burned ca. 24300 forested ha in July 1994, and the Solsonès fire, which burned ca. 14300 ha in 1998 (Figure 1). Before these fire events, theses areas had not burned from at least 70 years ago.

The climate of the region is dry-subhumid Mediterranean (according to the Thornwaite index), with mean annual temperature of 10-13 °C and mean annual precipitation of 600-700 mm. According to the data provided by the Ecological Forest Inventory of Catalonia (IEFC) (Gracia et al. 2000), and the Spanish Second National Forest Inventory (IFN2) (ICONA, 1993), both carried out in 1993, black pine (*P. nigra*) forests were dominant before the fires (78% of the burned surface), with *Q. ilex* and *Q. cerrioides* extensively present in their understory. After the fires, and due to the failure of *P. nigra* regeneration (Espelta et al. 2001; Retana et al. 2002), resprouting of most *Quercus* individuals transformed most forested areas into mixed *Quercus* forests, with the typical structure of a coppice with numerous multi-stemmed stools (Espelta et al. in press).
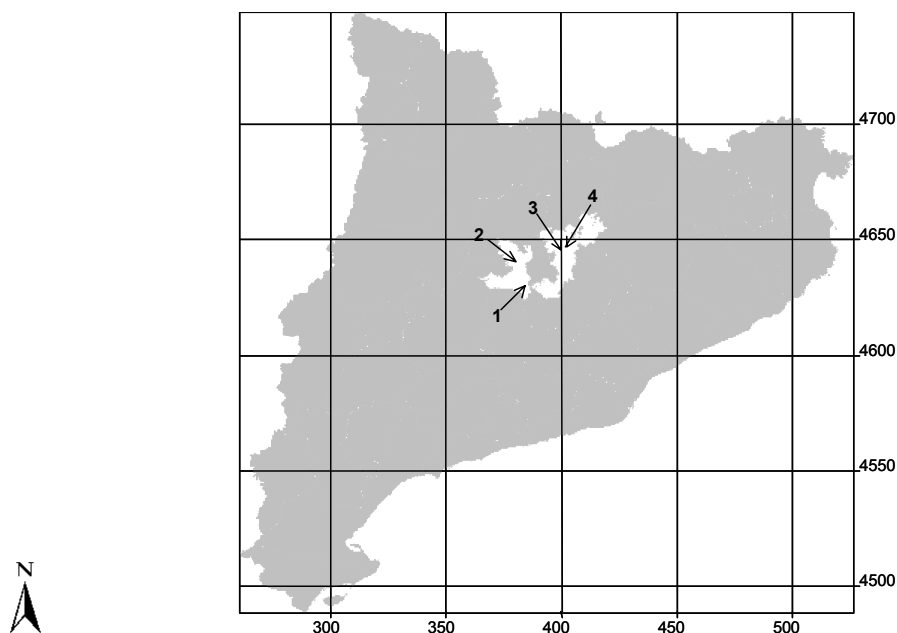


**Figure 1.** Geographical location of the sites sampled in this study along the area affected by the 1994 and 1998 large wildfires (white). Study sites: 1, Castelltallat; 2, Freixenet; 3, Soler d'en Jaumas; 4, Viladasses.

*Experimental design*

To analyse the response of *Q. ilex* and *Q. cerrioides* to repeated disturbances the experimental design included three variables: i) fire history, ii) site, and iii) experimental disturbance:

*Fire history:* All the areas selected for this study had experienced at least one forest fire and, consequently, the aboveground part of all *Q. ilex* and *Q. cerrioides* individuals had originated from resprouting. Three different fire trajectories were selected, according to the time since the last fire or the recurrence of fire: areas that had experienced a forest fire in 1994 ("older burned area", thereafter F94), areas that had suffered a forest fire in 1998 ("recently burned area",

thereafter F98), and areas that had experienced a natural forest fire in 1994 and a controlled fire in 1998 ("recurrently burned area", thereafter F94+98). As we applied the experimental treatments in 1999, plants in F94 had grown five years and those in F98 and F94+98 had grown one year.

_Site_: In each fire history area (F94, F98 and F94+98), two experimental sites (distanced between 4.5 and 14.0 km) were chosen to test for the effects of the spatial heterogeneity in the response of the two species to the experimental disturbances applied: Soler d'en Jaumas and Viladasses in F94 and F94+98, and Castelltallat and Freixenet in F98. The sites were dominated by mixed and homogeneous _Q. ilex_ and _Q. cerrioides_ coppices but differed in some of their environmental characteristics (Table 1). In each site, 16 plants per species were randomly assigned to the seven experimental treatments (112 plants per species and site and a total of 1344 plants studied).

_Experimental disturbance_: In each area, seven disturbance treatments were applied to _Q. ilex_ and _Q. cerrioides_ individuals. Treatments consisted in applying three different types of disturbance: burning, cutting or clipping (half of the aerial biomass of each plant) on two different dates (before summer and after summer), and a control treatment (not disturbed). Therefore, the seven treatments were: i) burning before summer (B1), ii) burning after summer (B2), iii) cutting before summer (C1), iv) cutting after summer (C2), v) clipping before summer (P1) vi) clipping after summer (P2) and vii) control (CT). Cutting and burning were selected as two different disturbance treatments although both involve the complete destruction of the aboveground part of the plant, because burning may be more negative for the plant, as it may destroy part of the bud bank located at the stool base, while cutting does not cause such effect (Espelta et al. 1999). Clipping was considered as an estimate of partial losses caused by grazing, which is a frequent disturbance experienced by plants in the post-fire scenario (Habrouk 2002). The two dates chosen to apply the experimental treatments (before summer and after summer) were selected because summer is a critical season for plants living in a Mediterranean-type climate as they are subjected to harsh conditions (high water demand and temperature). This constrains photosynthetic assimilation and promotes a large consumption of plant reserves that in turn may largely restrict the response to disturbances (Canadell and Lopez-Soria 1998). Treatments before summer were applied at the end of June 1999, while those after summer were applied in early September 1999.

Before applying the experimental treatments, each plant was tagged and mapped, and its height, crown diameter, number of living resprouts and diameter of the burnt stump (an indicator of the size of the individual before the occurrence of the last forest fire) registered. Before the onset of the experiment, individuals differed in number of sprouts, height and standing biomass, depending on the fire history of the plots and the species (Table 2). Individuals burned five years earlier (F94) had higher height, biomass and number of sprouts than individuals burned a

**Table 1.** Main topographical, climatic and structural characteristics of the different sampling sites, according to data provided by the 5 nearest inventoried plots in the Ecological Forest Inventory of Catalonia (IEFC) (Gracia et al. 2000) surrounding each site.

| | Altitude (m) | Slope (°) | Aspect | Precipitation ($l\ m^{-2}\ yr^{-1}$) | Temperature (ºC) | Density ($trees\ ha^{-1}$) | Basal Area ($m^2\ ha^{-1}$) |
|---|---|---|---|---|---|---|---|
| Castelltallat | 800 ± 18 | 20 ± 2 | S-SW | 721 ± 19 | 11.4± 0.7 | 945 ± 128 | 19 ± 2 |
| Freixenet | 755 ± 22 | 9 ± 4 | N-NE | 699 ± 21 | 11.8 ± 0.8 | 1763 ± 128 | 27 ± 5 |
| Soler d'en Jaumas | 513 ± 18 | 14 ± 2 | S-SW | 709 ± 18 | 12.7 ± 1.0 | 960 ± 152 | 18 ± 2 |
| Viladasses | 596 ± 26 | 13 ± 3 | N-NW | 750 ± 17 | 12.2 ± 1.3 | 1433 ± 240 | 18 ± 3 |

**Table 2**. F-values from ANOVA tests of effects of fire history, species, and site (nested in fire history) on biomass, height and number of resprouts of the individuals included in this study before the experiment onset. Significant coefficients (at p=0.05 when the sequential Bonferroni method is employed) are indicated in bold.

| Source | Df | Biomass | Height | N of resprouts |
|---|---|---|---|---|
| Fire history (F) | 2 | **210.0** | **1387.2** | **21.9** |
| Species (Sp) | 1 | **21.3** | **318.2** | **36.9** |
| Site (F) | 1 | **11.8** | **18.3** | 3.9 |
| F x Sp | 2 | **23.2** | **79.1** | 3.7 |
| Residual | 1088 | | | |

year before (either in F98 or F94+98): *Q. cerrioides* attained higher biomass and height in F94 and F94+98, while differences between species were less clear in F98 (Figure 2). On the other hand, number of resprouts was higher in *Q. ilex* than in *Q. cerrioides* in all fire history sites (respectively, 20±1 and 13±1). In the cutting and burning experimental treatments, all living shoots of each plant were cut down at the base and their fresh biomass assessed with a field scale. The burning treatment followed a similar methodology to that used in previous studies of experimental burning (Canadell et al. 1991; Lloret and Lopez-Soria 1993), which consisted in applying the flame of a propane torch directed to the base of the plant during three minutes at a mean temperature of 300 $^{o}$C. This temperature was controlled by measurements with thermocouple sensors placed on the base of the plant made every 15 s. When the stool was very large (i.e., there were many sprouts emerging from a relatively large stool) it was subdivided into sections, according to size, and each section received three min of fire. The clipping treatment consisted in the removal of half of the living shoots per plant. In order to separate approximately half of the standing biomass of each plant, all shoots were previously classified by size (diameter), so that half of those of each size could be removed. The fresh biomass of these shoots was weighted and those shoots remaining were tagged and their basal diameter registered. In the control plants (no treatment), every shoot was tagged and its basal diameter registered. To estimate the standing biomass of each individual before the experimental treatments, the following procedure was followed. In the cut or burnt individuals, where all living shoots were removed and weighted in the field, a sub-sample of each individual was brought to the laboratory, dried at 80 $^{o}$C during 48 h and its dry biomass assessed. The proportion dry/fresh biomass was used to calculate the whole dry biomass of these individuals.
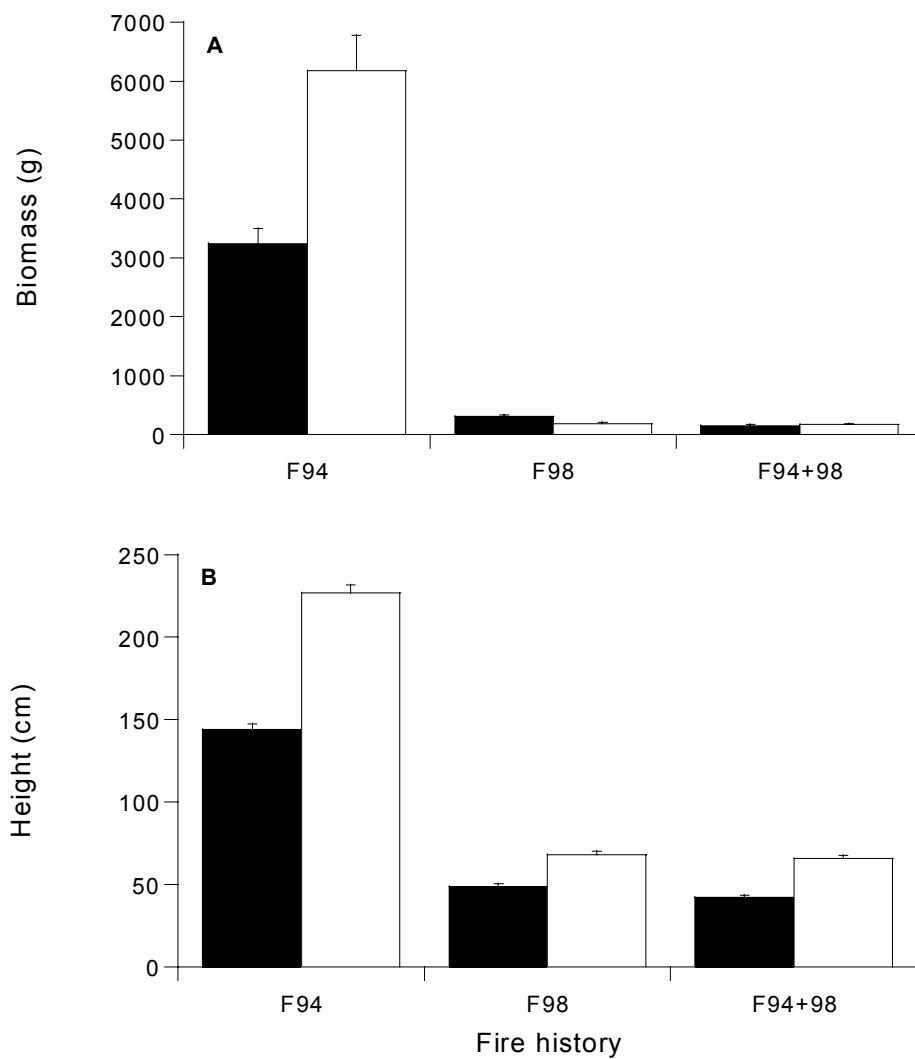
**Figure 2.** Mean (+ SE) values of (A) biomass and (B) height of individuals present in the areas with the three fire history types.

In the clipped individuals, the same method was used to estimate the biomass of the resprouts removed (half of the total).To calculate the biomass of control individuals (not disturbed) and that of the remaining resprouts in clipped individuals, we used specific allometric equations. In each study site, resprouts of plants of each species not included in the experiment were cut and their basal diameter and fresh weight registered. They were brought to the laboratory, dried at

80 $^{\circ}$C during 48 h and their dry biomass was determined. For those resprouts with diameter larger than 10 mm, specific regressions were built between basal diameter and dry mass. The regressions were: Biomass = -285.6 + 286.5 diameter ($R^2$=0.90, F=139.0, p<.00001) for *Q. ilex* and Biomass = -252.4 + 236.0 diameter ($R^2$=0.87, F=124.3, p<.00001) for *Q. cerrioides*. For resprouts smaller than 10 mm, two categories were considered, one including those with diameters <5 mm and the second including diameters between 5 and 10 mm. The mean dry biomass of a resprout of each category was obtained (out of a sample of 45 resprouts) for each species and this value was used to calculate the total biomass per category.

The response variables to the treatments applied were recorded on July 2000, one year after the experiment onset. They included plant survival, height, number of resprouts (in the abovementioned size categories) and plant biomass. Aboveground plant biomass was estimated using a similar procedure to that applied at the experiment onset, i. e., the diameter of each resprout was measured and the total biomass of each plant estimated by adding up the biomass obtained by the above-mentioned allometric regressions for resprouts >10 mm and, for the smaller size categories, the mean biomass of each shoot. In the clipped and control individuals, resprouts included those preserved when the experimental treatments were applied ("old" or tagged resprouts) as well as those produced afterwards, while in the cutting and burning treatments all resprouts were produced after the experimental treatments. Changes in biomass are expressed as: i) net increment in biomass (standing biomass of each individual at the end of the experiment minus biomass left after the application of the experimental treatments) and ii) relative biomass growth [ln (final biomass/initial biomass)]. In this case initial biomass was that of each individual *before* the application of the experimental treatments.

Additionally, in order to analyse the main architectural features of the new resprouts appeared after the experimental disturbances, the largest (longest) resprout of a sub-sample of cut, burned and clipped individuals was collected at the end of the study period, and its height, diameter and fresh weight registered. They were brought to the laboratory to obtain their leaf area (using a LI-COR Model 3100, USA) and dry biomass (after drying at 80º).

*Statistical analyses*

To analyse variations in survival according to the different factors tested, log-linear models were applied to the multiway contingency table obtained by indicating separately the number of living and dead individuals in each combination of the factors considered. The best model was considered to be the most parsimonious acceptable (goodness-of-fit p>0.05) one. The analyses were carried out with the program STATISTICA (StatSoft 2001).

The effects of Species, Fire History, Site (nested within Fire history) and Experimental disturbance in net increment and relative growth in biomass and number of resprouts produced were analyzed by ANOVA tests. To remove the effect of the size of individuals before the occurrence of the forest fires in these analyses, the residuals of the regressions of these variables against surface of the burnt stumps were employed instead of their original values (i.e., in the case of biomass a positive residual would indicate a larger than expected biomass according to the size of the stump, while a negative value a smaller than expected biomass). Data of net increment in biomass were log-transformed. Inspection of residuals was carried out to check for normality and homoscedasticity. The sequential Bonferroni method was employed to control the group-wide type I error rate (Rice 1989). Values in this paper are given as means ±1SE.  The same analyses were carried out in order to analyze the biomass, length and leaf area of the largest resprout of burned, cut and clipped individuals.

**RESULTS**

Survival of *Q. ilex* and *Q. cerrioides* was not significantly affected by the different experimental factors tested (log-linear model, goodness-of-fit $p<0.05$). Survival of the two species was over 99%, with only 14 individuals (seven of each species) not resprouting from the 1344 considered in the study. All dead individuals were included in those treatments involving a complete loss of aerial biomass i.e., burned (71%) or cut (29%). Most deaths occurred in the recently burned area (F98).

In both species, total and relative biomass growth and the number of resprouts produced after experimental treatments increased significantly with stool size (linear regression; $R^2=0.37$, $p<0.001$ for net increment in biomass; $R^2=0.11$, $p<0.001$ for relative biomass growth and $R^2=0.21$, $p<0.001$ for the number of resprouts). The effects of the factors tested (species, fire history, site -nested in fire history-, and experimental treatment applied) on these variables, once the effect of stool size had been removed, are summarized in Table 3.The net increment in biomass and the number of resprouts produced were highest in the older burned plots (F94) and lowest in recurrently burned plots (F94-98, Figure 3A, C), while the relative growth showed the opposite pattern (Figure 3B). The effect of site was also significant for the three variables analysed (Table 3), indicating spatial heterogeneity for these variables.

Concerning the interaction species x fire history, net increment in biomass and relative growth were higher in *Q. cerrioides* than in *Q. ilex* stools, and differences between species were higher in F94 and F94+98 than in F98 (Figure 4). However, *Q. ilex* produced more resprouts than *Q. cerrioides* (respectively, 25.6±1.2 and 18.7±0.9). The experimental treatments applied were

also important in all studied variables (Table 3). Thus, both net biomass increment and relative growth were higher in control individuals, slighter in clipped individuals and the lowest values were attained by those that were either burned or cut (Figure 5A, B). In all cases, individuals disturbed prior to the summer onset showed higher increment in biomass and relative growth than those disturbed at the end of summer. On the contrary, number of resprouts was higher in cut and burned stools, with maximum values reached in those disturbed after summer (Figure 5C).

**Table 3**. F-values from ANOVA tests of effects of fire history, species, experimental disturbance and site (nested in fire history), applied on net increment and relative growth in biomass and number of resprouts produced. To remove the effect of stool size, the residuals of the regressions of three variables against stool size have been used instead of the original values. Data of relative growth were log-transformed. Significant coefficients (at p=0.05 when the sequential Bonferroni method is employed) are indicated in bold.

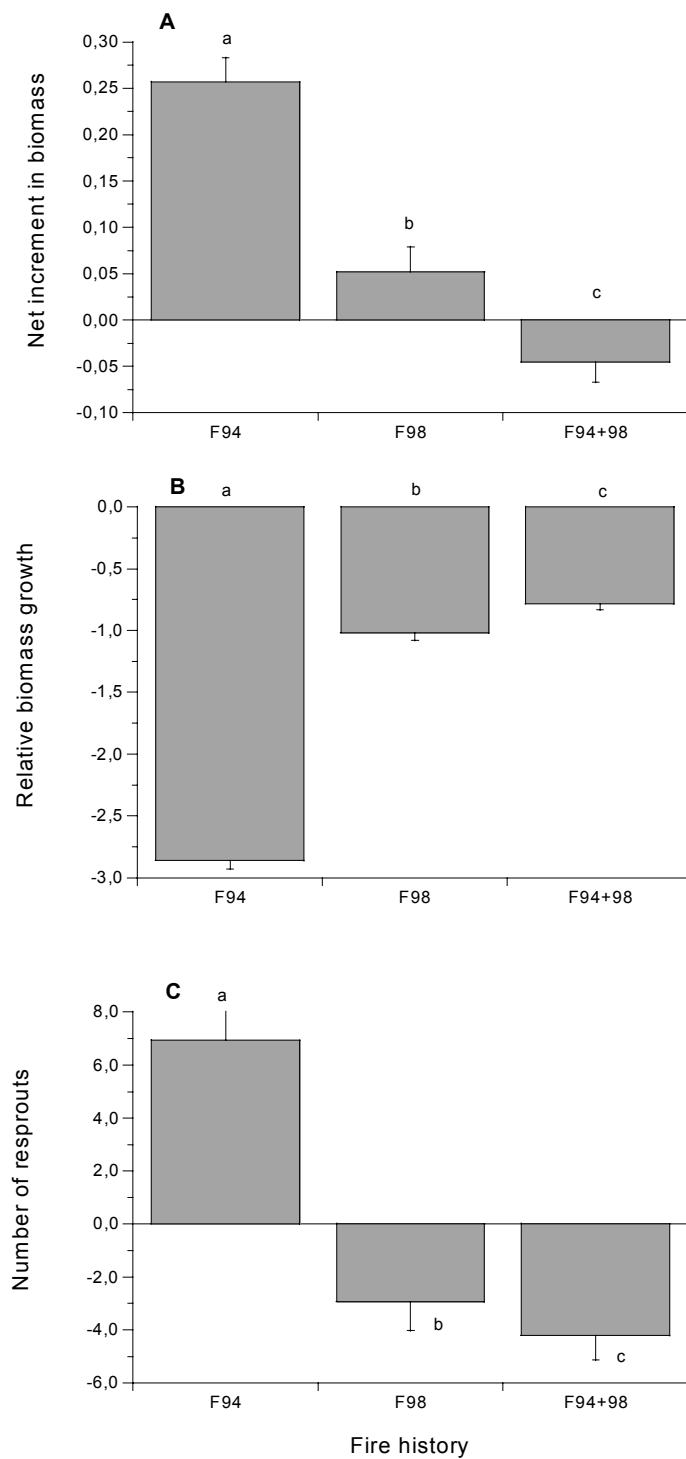| Source | Df | Net increment in biomass | Relative biomass growth | Number of resprouts |
|---|---|---|---|---|
| Fire history (F) | 2 | **44.2** | **521.6** | **17.9** |
| Species (Sp) | 1 | **57.5** | **9.8** | **9.9** |
| Experimental disturbance (D) | 6 | **10.3** | **60.1** | **22.3** |
| Site (F) | 3 | **14.8** | **28.6** | **5.9** |
| F x Sp | 2 | **5.1** | 1.9 | 4.2 |
| F x D | 12 | **5.8** | **9.7** | **3.6** |
| Sp x D | 6 | **3.8** | 2.6 | 0.3 |
| F x Sp x D | 12 | 0.6 | 0.7 | 0.6 |
| Residual | 1098 | | | |

**Figure 3.** Mean (+ SE) values of the residuals between stool size and (A) net increment in biomass, (B) relative biomass growth, and (C) number of resprouts produced of individuals present in the areas with the three fire history types
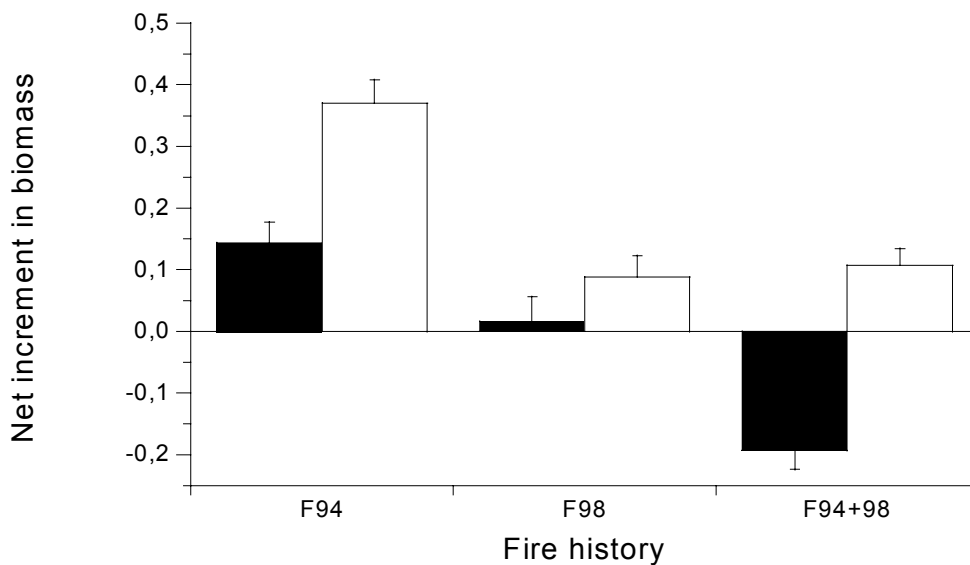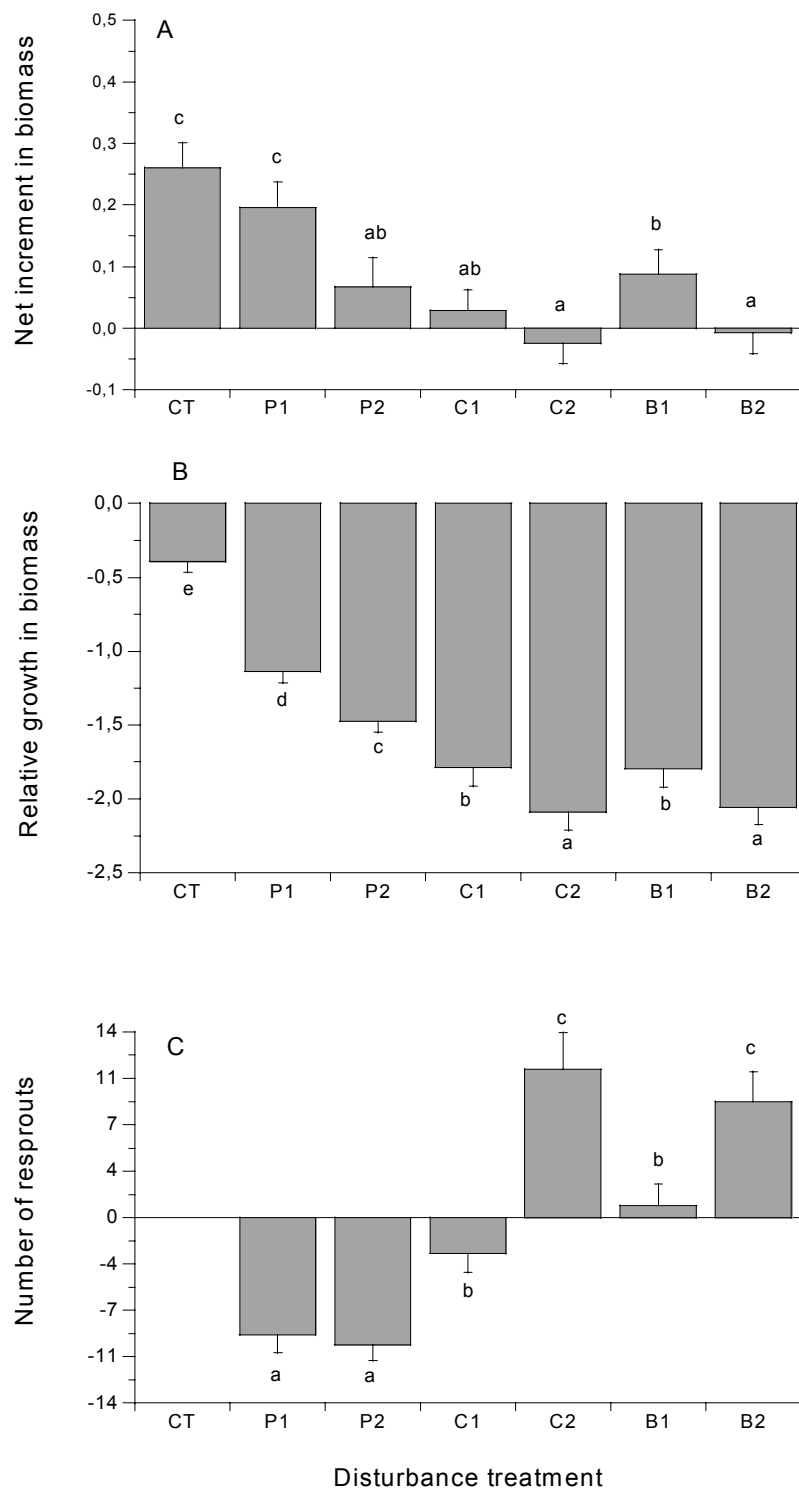
**Figure 4.** Mean (+ SE) values of the residuals between stool size and net increment in biomass, of *Q. ilex* (black bars) and *Q. cerrioides* (white bars) individuals present in the areas with the three fire history types.

The interaction fire history x experimental disturbance was also significant for the three variables (Table 3). Control individuals showed higher growth in recently disturbed plots (F98) than in the other two fire history categories, in comparison with individuals of the different disturbance treatments (Figure 6A, B). In the experimental treatments, net increment in biomass was higher in the older burned plots (F94) than in the other two fire categories, although relative growth showed the opposite trend, being especially low for burned and cut individuals in the F94 plots. Individuals burned or cut after summer showed higher production of new resprouts in the older burned area (F94) in comparison with the other fire histories (Figure 6C). The interaction species x experimental disturbance was also significant for net increment in biomass (Table 3). In this case, the increment in biomass of control and pre-summer clipped individuals was similar in both species, but attained higher values in *Q. cerrioides* than in *Q. ilex* in the other experimental treatments applied (Figure 7), especially when burned after summer.

**Figure 5**.

Mean (+ SE) values of the residuals between stool size and (A) net increment, (B) relative growth in biomass, and (C) number of sprouts of individuals disturbed by the different experimental treatments
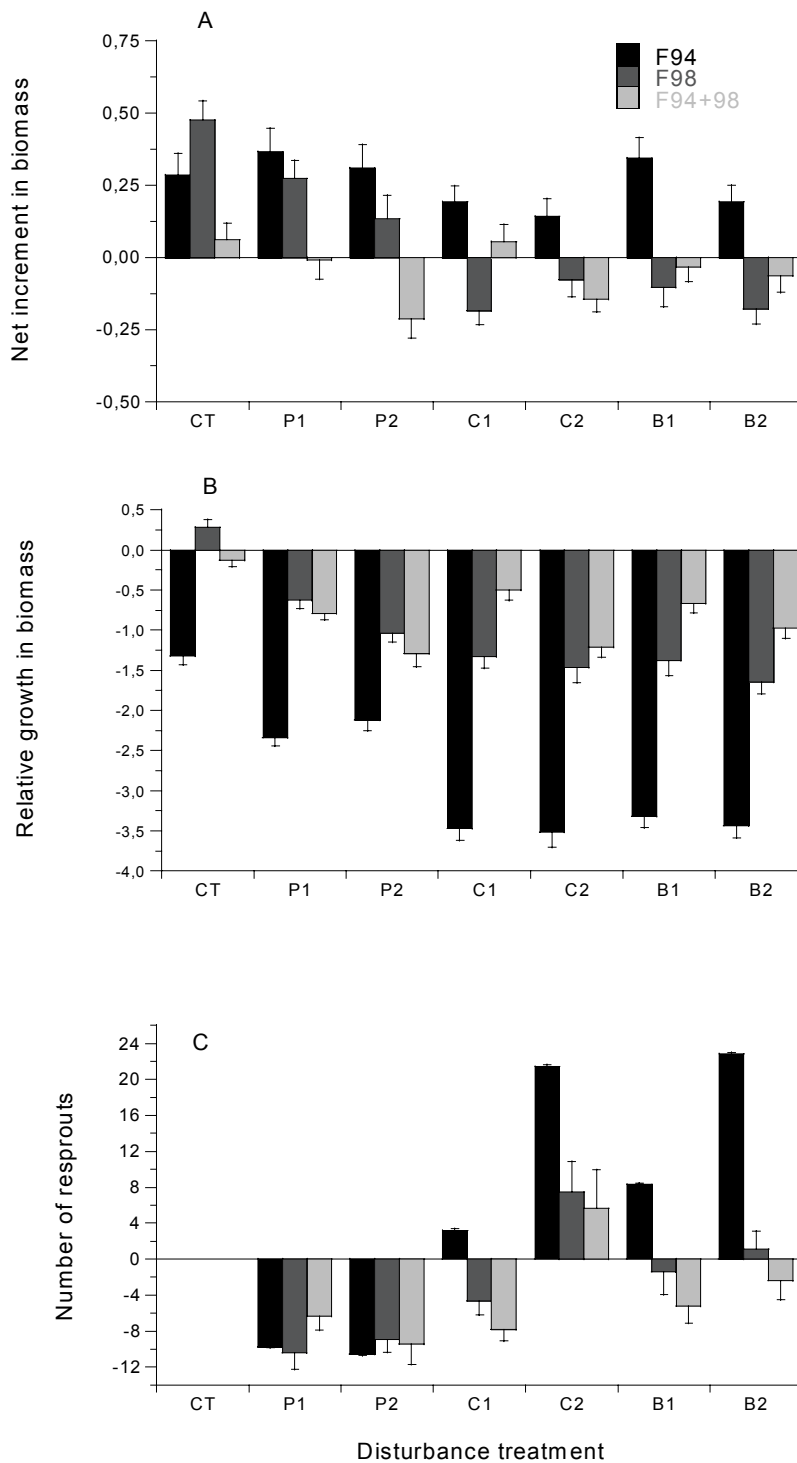
**Figure 6**. Mean (+ SE) values of the residuals between stool size and (A) net increment, (B) relative growth in biomass, and (C) number of sprouts of individuals present in the areas with the three fire history types and disturbed by the different experimental treatments.
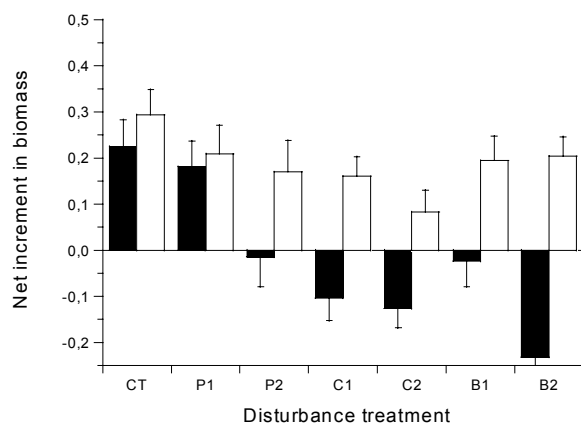
**Figure 7.** Mean (+ SE) values of the residuals between stool size and net increment in biomass of *Q. ilex* (black bar) and *Q. cerrioides* (white bar) individuals disturbed by the different experimental treatments.

Biomass and length of the largest resprout appearing after the experimental treatments increased significantly with stool size (linear regression; $R^2$=0.15, p<0.001 for resprout biomass; $R^2$=0.16, p<0.001 for resprout length), while leaf area did not (linear regression; p>0.10). The effects of the factors tested on these variables, once the effect of stool size had been removed, are summarized in Table 4.

**Table 4.** F-values from ANOVA tests of effects of fire history, species, experimental disturbance and site (nested in fire history), applied on total biomass, length and leaf area of the largest resprout of individuals experimentally disturbed. To remove the effect of stool size, the residuals of the regressions of the two variables against stool size have been used instead of the original values. Data of total biomass and length were log-transformed. Significant coefficients (at p=0.0.5 when the sequential Bonferroni method is employed) are indicated in bold.

| Source | df | Total biomass | Length | Leaf area |
|---|---|---|---|---|
| Fire history (F) | 2 | **5.9** | **9.9** | 0.7 |
| Species (Sp) | 1 | **39.3** | **138.9** | **20.9** |
| Experimental disturbance (D) | 5 | **54.4** | **33.0** | **6.9** |
| Site (F) | 3 | **14.6** | **21.5** | 1.0 |
| F x Sp | 2 | 0.9 | 0.1 | 1.3 |
| F x D | 10 | 1.4 | 1.4 | 0.2 |
| Sp x D | 5 | **5.2** | **4.7** | 1.9 |
| F x Sp x D | 10 | 1.1 | 1.4 | 0.4 |
| Residual | 378 | | | |

Biomass and length of this resprout followed the same pattern with fire history: they showed the highest values in older burned areas and the lowest in the recurrently burned areas. Concerning the treatments tested, the length, biomass and leaf area of this resprout were higher in burned and cut individuals than in clipped ones. The three variables analyzed showed significant differences between species (Table 4), with *Q. cerrioides* showing higher values than *Q. ilex* (length: 78 ± 3 and 48 ± 2 cm; biomass: 47 ± 5 and 22 ± 2 g; and leaf area: 856 ± 108 and 343 ± 29 cm$^2$, respectively). In the two species, this resprout registered low growth in the clipping treatments (Figure 8), while in the other treatments differences between species were larger, with *Q. cerrioides* attaining higher biomass and length than *Q. ilex*.
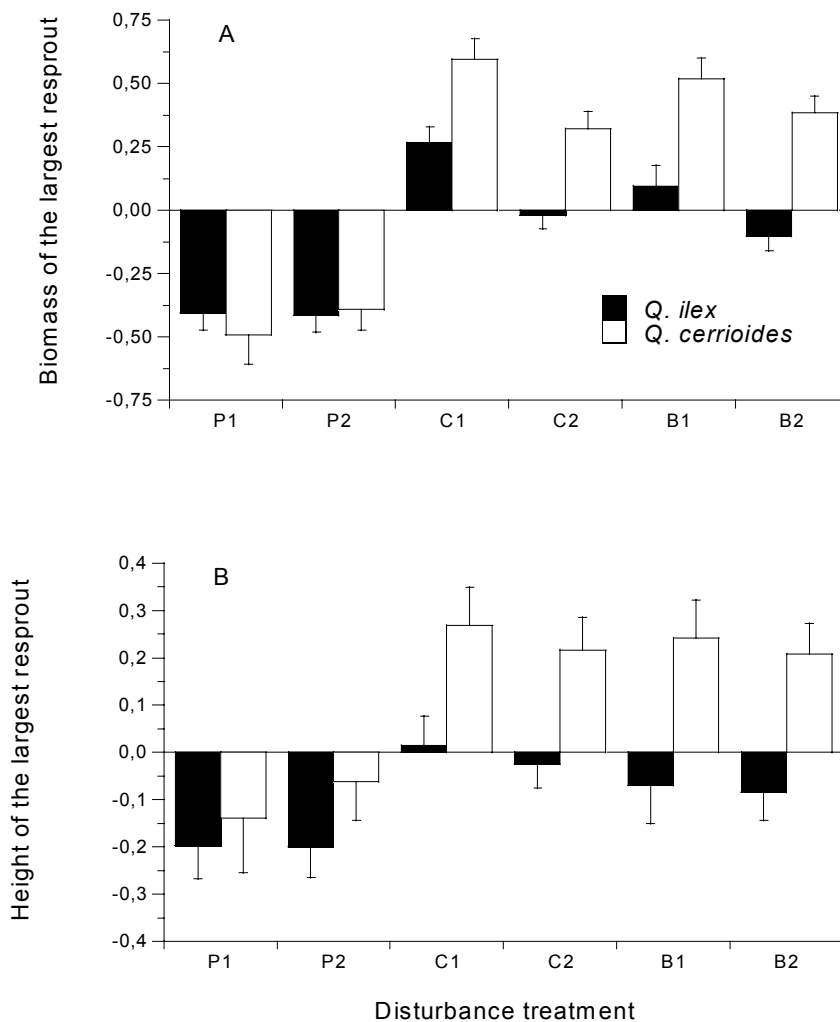


**Figure 8.** Mean (+ SE) values of the residuals between stool size and (A) total biomass and (B) length of the largest resprout of *Q. ilex* (black bar) and *Q. cerrioides* (white bar) individuals disturbed by the different experimental treatments.

**DISCUSSION**

The high survival rates registered show that both species are very resistant to disturbances, as only in the more severe experimental disturbances, particularly exposure to fire, there was some individual mortality. This agrees with the reported resistance of Mediterranean oaks to fire (Barbero et al. 1987; Espelta et al. 2002). Although survival was very high in all fire histories, mortality was slightly higher in those plots that had experienced a forest fire a year before the experiment (F98), and not in those suffering a reiteration of fire (F94+98). This could be related to the intensity of fire, as in the first case it was a natural fire that burned with a high intensity and affected a large area, while the second was a prescribed fire.

Differences in growth between species were clear: the larger growth rates of *Q. cerrioides* were consistent through all fire histories and experimental treatments, and Q. *ilex* growth proved more vulnerable to increased fire recurrence (Fig. 4) and intensity of the experimental disturbance (Fig. 7). It was also relatively more affected by the (after summer) season of disturbance than *Q. cerrioides*. The higher capacity to recover after disturbances of this deciduous oak latter could be related to a rapid recovery of foliage and the consequent synthesis of carbohydrates. If the largest new resprout is considered an unbiased sample of the individual, the largest leaf area found in *Q. cerrioides* resprouts could explain its higher capacity to produce biomass. The production of foliage in *Q. ilex* may be constrained by a larger investment in longer lasting, sclerophyllous leaves (Aerts 1995).

Growth after experimental disturbance was positively related to the size of the stool (i. e., to the size of the plant present before the forest fire occurred), as has been reported in other studies (Ducrey and Turrel 1992; Lloret and Lopez-Soria 1993). Larger individuals are likely to have both larger stored reserves and a larger bud bank, which can be mobilized to produce new shoots. Holm oaks allocate as much as half of their total biomass to the lignotuber (Canadell and Rodá 1991), and a high proportion of stored reserves in underground structures is to be expected in *Q. cerrioides*, as in other deciduous oak species (Reich et al. 1980; Rundel 1980). This positive correlation holds for the size range of the stools included in this study, as in larger root systems the sprouting capacity may decrease (Koslowsky 1991; Johnson et al. 2002), due to mechanical resistance of thicker bark.

The time period required to replenish root reserves after a forest fire has destroyed the aboveground biomass of these species is unknown, but the small differences in the initial size of individuals in the F98 and F94+98 plots (Figure 2), shows that the four year period between the two forest fires in the later allowed plants to recover and resprout vigorously, similarly as those not burned for many years before the forest fire of 1998. However, after the experimental treatments were applied, the effect of fire histories became more evident, as differences in the

biomass and number of resprouts produced became significant between the F98 and F94+98 plots (Figure 3), although in all cases smaller than those between these and plants in the older burned plots (F94). Therefore, the large differences in resprouting behavior of plants that had grown for five years and those that were burnt a year before the experimental treatments were applied show that the reiteration of disturbances in short term intervals decreases the capacity to grow and accumulate aerial biomass in both species. In addition to fire history, variations in edaphic and/or climatic conditions (site effect in Table 3) also affected the ability of individuals to resprout in response to disturbances, as shown in previous studies (López- Soria and Castell 1992; Gracia and Retana 1996; Riba 1998; Espelta et al. 2002).

Besides fire recurrence, the type of experimental disturbance plants experienced caused large differences in their growth response. The decrease in biomass increment and relative growth as biomass removal increased from partial to total aboveground loss (Figures 5A, B) is similar to the decrease in vigor associated to biomass loss in other Mediterranean plant species (Malanson and Trabaud 1988; Canadell and Lopez-Soria 1998; Riba 1998). The similar growth response of plants that received the cutting and burning experimental treatments shows that the experimental fire did not cause a major reduction in the bud bank, probably due to the fact that the root collar is frequently located an inch or more below the soil surface, where fire temperatures diminish (Johnson et al. 2002). On the contrary, the season of disturbance had great consequences in all experimental treatments (Figure 5). This is probably the result of the hydric stress that Mediterranean plants experience when disturbed after summer. Thus, resprout growth is affected by water availability at the beginning of the resprouting response in the Mediterranean shrub *Erica australis* (Cruz et al. 2002), and summer cutting has been shown to produce low number and height of resprouts in *Q. ilex* coppices (Ducrey and Turrel 1992). In our study, although the number of resprouts increased (Figure 5C), overall biomass growth decreased, and therefore the impact of disturbances was amplified when performed at the moment of the year when soil humidity was at its lowest.

The present study shed a new light on the response of the deciduous *Q. cerrioides* and the evergreen *Q. ilex* to repeated disturbances. The results obtained provide evidence of the relatively high susceptibility of *Q. ilex*, a view that disagrees with the traditional larger resilience this species compared with deciduous oaks (Barbero et al. 1987; Tatoni and Roche 1994). Based on the present results, the observed recent spread of deciduous oaks as a result of diminishing human disturbances (Bacilieri et al. 1993; Bonin and Romane 1996) could be explained as a result of the larger growth rates of deciduous oaks (Trabaud 1996; Espelta et al. 2002), which may outgrow and shade holm oak. On the long run, this could lead to its withdrawal of the areas where they coexist. In this context, there is evidence that survival of holm oak seedlings is more affected by shade than those of *Q. cerrioides*, and that the latter show greater plasticity to changes in light availability (Cortés 2001), although the key

information of the growth response of adults of both kinds of oaks to shaded conditions is still lacking. Overall, the responses of these species to disturbances along climatic gradients, especially in conditions of increased temperatures and hydric stress, remains to be explored, as the dominance between deciduous broadleaved and evergreen sclerophyllous species in Mediterranean environments may shift as a result of the interactions between disturbance, growth allocation patterns and water stress (Mazzoleni and Spada 1992).

**REFERENCES**

Aerts, R. 1995. The advantages of being evergreen. Trees 10: 402-407.

Bacilieri, R; Bouchet, M. A; Bran, D; Grandjanny, M; Maistre, M; Perret, P. and Romane, F. 1993. Germination and regeneration mechanisms in Mediterranean degenerate forests. Journal of Vegetation. Science, 4: 241-246.

Barbero, M; Bonnin, G; Loisel, R; Miglioreti, F. and Quezel, P. 1987. Impact of forest fires on structure and architecture of Mediterranean ecosystems. Ecología Mediterránea, XIII: 39-50.

Barbero, M ; Loisel, R. and Quèzel, P. 1992. Biogeography, ecology and history of Mediterranean *Quercus ilex* ecosystems. Vegetatio, 99-100: 19-34.

Bellingham, P. J. 2000. Resprouting as a life history strategy in woody plant communities. Oikos, 89: 409-416.

Blondel, J. and Aronson, J. 1995. Biodiversity and ecosystem function in the Mediterranean basin: human and non-human determinants.. In:. Davis, G. W. and Richardson, D. M. (eds). Mediterranean-type ecosystems: the function of biodiversity. Springer-Verlag, Berlin.

Blondel, J. and Aronson, J. 1999. Biology and Wildlife of the Mediterranean Region. Oxford Univ. Press.

Bonfil C. 1998. Dinámica poblacional y regeneración de *Quercus rugosa*: Implicaciones para la restauración de bosques templados. Ph D Thesis. Universidad Nacional Autónoma de México.

Bonin, G. and Romane, F. 1996. Chêne vert et chêne pubescent : Historire, principaux groupements, situation actuelle. Forêt Méditerranée XVII : 119-128.

Canadell, J; Lloret, F. and López-Soria, L. 1991. Resprouting vigour of two Mediterranean shrub species after experimental fire treatments. Vegetatio, 95: 119-126.

Canadell, J. and Rodà, F. 1991. Root biomass of *Quercus ilex* in a montane Mediterranean forest. Canadian Journal of Forest Research, 21: 1771-1778.

Canadell, J. and López Soria, L. 1998. Lignotuber reserves support regrowth following clipping of two Mediterranean shrubs. Functional Ecology, 12: 31-38.

Ceballos, L. and Ruiz de la Torre, J. 1971.Arboles y Arbustos. IFIE-Escuela Técnica Superior de Ingenieros de Montes, Madrid.

Clark, J. S. 1991. Disturbance and tree life history on the shifting mosaic landscape. Ecology, 72: 1102-1118.

Cortés, P. 2001. Response to light, water and nutrient availability of two Mediterranean oaks with contrasting leaf habit. Does phenotypic plasticity matter? Master dissertation. Universitat Autònoma de Barcelona, Barcelona.

Crow, T. R. 1988. Reproductive mode and mechanisms for self-replacement of northern red oak (*Quercus rubra*) - a review. Forest Science*,* 34: 19-40.

Crow, T. R. 1992. Population dynamics and growth patterns for a cohort of northern red oak (*Quercus rubra*) seedlings. Oecologia, 91: 192-200.

Ducrey, M. and Turrel, M. 1992. Influence of cutting methods and dates on stump sprouting in holm oak (*Quercus ilex* L.) coppice. Anales Sciences Forestieres, 49: 449-464.

Espelta, J. M.; Sabaté, S. and Retana, J. 1999. Resprouting dynamics. In: Rodà, F; Retana, J; Gracia, C. A. and Bellot, J. (eds.). Ecology of Mediterranean Evergreen Oak Forests. Ecological Studies 137.Springer-Verlag Berlin.

Espelta, J. M; Rodrigo, A; Habrouk, A; Meghelli, N; Ordóñez, J. L. and Retana, J. 2001. Land use changes, natural regeneration patterns, and restoration practices after large wildfire in NE Spain: challenges for fire ecology and landscape restoration. In: Trabaud, L. and Prodon, R. (eds.) Fire and Biological Processes. Backhuys Pub., Leiden, The Netherlands.

Espelta, J. M., Retana, J. and Habrouk, A. 2002. Resprouting patterns after fire and response to stool cleaning of two coexisting Mediterranean oaks with contrasting leaf habits on two different sites. Forest Ecology and Management*,* 6148: 1-14.

Espelta, J.M; Retana, J. and Habrouk, A. Resprouting patterns after fire and response to stool cleaning of two coexisting Mediterranean oaks with contrasting leaf habits on two different sites. Forest Ecology and Management, in press.

Fox, B. J. and Fox, M. D. 1986. Resilience of animal and plant communities to human disturbance. In: Dell, B; Hopkins, A. J. M. and Lammont, B. B. (eds.) Resilience in Mediterranean type ecosystems. Junk Publishers, Dordrecht.

García-Latorre, J. and García-Latorre, J. 1996. Sur la répartition actuelle et historique du chêne fagine (*Quercus faginea* Lam.) dans le sud-est de l'Espagne. Ecología Mediterránea, XXII: 59-66.

Gracia, C; Burriel, J. A; Ibáñez, J. J; Mata, T. and Vayreda, J. 2000. Inventari ecològic i forestal de Catalunya. Regió forestal IV. Publ. Centre de Recerca Ecològica i Aplicacions Forestals, Barcelona.

Gracia, M and Retana, J. 1996. Effect of site index and thining management on the structure of the holm oak forests of the Montseny and Les Guilleries massifs (NE Spain). Annales Sciences Forestières, 53: 571-584.

Grime J. P. 1979. Plant Strategies and Vegetation Process. John Wiley, U.K.

ICONA, 1993. Segundo inventario forestall nacional. Cataluña. Barcelona. 1986-1995. Publ. Ministerio Agricultura, Pesca y Alimentación.

Iwasa, Y. and Kubo, T. 1997. Optimal size of storage for recovery after unpredictable disturbances. Evolutionary Ecology, 11: 41-65.

Johnson, P. S; Shifley, S. and Rogers, R. 2002. The ecology and silviculture of oaks. CABI Publishing, New York.

Keeley J. E. 1986. Resilience of Mediterranean shrub communities to fires. In: Dell B; Hopkins A.J.M. and Lamont B.B. (eds.) Resilience in Mediterranean-type Ecosystems. Dr. W. Junk Pub, Dordrecht, The Netherlands.

Kozlowshi, T.T. 1991. Effects of Environmental Stresses on Deciduous Trees. In: Mooney, H.A.; Winner, W.E. and Pell, E.J. (eds.). Response of Plants to Multiple Stresses. Academic Press, San Diego, California.

Levin, S. A. and Paine, R. T. 1974. Disturbance, patch formation and community structure. Procedings of the Natural Academy of Sciences, USA, 71: 2744-2747.

Lloret, F. 1996. El foc en un context mediterrani. In: Terradas, J. (ed). Ecologia del Foc. Edicions Proa, S. A., Barcelona.

Lloret F. 1998. Fire, canopy cover and seedling dynamics in Mediterranean shrubland of Northeastern Spain. Journal of Vegetation Science, 9: 417-430.

Lloret F. and López Soria L. 1993. Resprouting of *Erica multiflora* after experimental fire treatments. Journal of Vegation Science, 4: 367-374.

Lloret, F. and Vilà, M. 1997. Clearing of vegetation in Mediterranean garrigue: response after a wildfire. Forest Ecology and Management, 93: 227-234.

López-Soria, L. and Castell, C. 1992. Comparative genet survival after fire in woody Mediterranean species. Oecologia, 91: 493-499.

Malanson, G. P. and Trabaud, L. 1988. Vigour of post-fire resprouting by *Quercus coccifera* L. Journal of Ecology 76: 351-365

Mazzoleni, S. and Spada, F. 1992. Deciduous broadleaved versus evergreen sclerophyllous forest. Disturbance and local shifting dominance in Mediterranean environments. In: Teller, A; Mathy, P. and Jeffers, J.N.R. Responses of forests ecosystems to environmental changes. Elsevier Science Publishers

Naveh, Z. and Liberman, A. S. 1984. Landscape Ecology. Theory and Application . Springer, Berlin.

Ojeda-Copete F. 2001. El fuego como factor clave en la evolución de las plantas mediterráneas. In: Zamora R. and Pugnaire F. I. (eds). Ecosistemas Mediterráneos. Análisis Funcional.Consejo Superior de Investigaciones Científicas. Asociación Española de Ecología Terrestre, España

Pausas, J. G. 1997. Resprouting of *Quercus suber* in NE Spain after fire. Journal of Vegetation Science, 8: 703-706.

Pallardy, S. G. and Rhoads, J. L. 1993. Morphological adaptations to drought in seedlings of deciduous angiosperms. Canandian Journal of Forest Restoration, 23: 1766-1774.

Picket, S. T. A. and White, P. S. 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, San Diego, California.

Pons, A. and Vernet, J. L. 1971. Une synthèse nouvelle de l'histoire du chêne vert (*Quercus ilex* L.). *Bull. Soc. Bot. Fr.* 118: 841-850.

Pons, A. and Quézel, P. 1985. The history of flora and vegetation and past and present disturbance in the Mediterranean area. In: Gómez Campo, C. (ed). Plant Conservation in the Mediterranean area.Dr. W. Junk Pub., Dordrecht.

Reich, R. B; Teskey, R. O; Johnson, P. S. and Hinckley, T. M. 1980. Periodic root and shoot growth in oaks. Forest Science, 26: 590-598.

Retana, J; Riba, M; Castell, C. and Espelta, J.M. 1992. Regeneration by sprouting of holm oak (*Quercus ilex*) stands exploited by selection thinning. Vegetatio, 99/100: 355-364.

Retana, J; Espelta, J. M; Gracia, M. and Riba, M. 1999. Seedling recruitment. In: Rodà, F; Retana, J; Gracia, C. A. and Bellot, J. (eds.) Ecology of Mediterranean Evergreen Forests. Springer-Verlag, Berlin.

Retana, J; Espelta, J. M; Habrouk, A; Ordoñez, J. L. and Solà-Morales, F. 2002. Regeneration patterns of three Mediterranean pines and forest changes after a large wildfire in North-eastern Spain. Ecoscience, 9: 89-97.

Riba, M. 1998. Effects of intensity and frequency of crown damage on resprouting of *Erica arborea* L. (Ericaceae). Acta Oecologica, 19: 9-16.

Rice, W.R. 1989. Analyzing tables of statistical tests. Evolution, 43: 223-225.

Riera i Mora, S. 1995. Evolució del paisatge vegetal holocè al Pla de Barcelona a partir de les dades pol.líniques. Tesi doctoral U.B. Barcelona.

Ross, M. S; Sharik, T. L., and Smith, D. W. 1986. Oak regeneration after clear felling in southwest Virginia. Forest Science, 32: 157-169.

Rundel P. W. 1980. Adaptations of Mediterranean-climate oaks to environmental stress. In: Ecology, management and utilization of Californian oaks. USDA For. Ser. Gen. Rep. PSW-44

StatSoft, Inc. (2001). STATISTICA (data analysis software system), version 6. www.statsoft.com.

Streng, D. R; Glitzenstein, J. S. and Harcombe, P. A. 1989. Woody seedling dynamics in an east Texas floodplain Forest. Ecological Monographs, 59: 177-204.

Sousa, W. P. 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics, 15: 353-391.

Tatoni, T. and Roche, B. 1994. Comparison of old-field and forest revegetation dynamics in Provence. Journal of Vegetation Science, 5: 295-302.

Thadani, R. and Ashton, P. M. S. 1995. Regeneration of banj oak (*Quercus leucotricophora* A. Camus) in the central Himalaya. Forest Ecology and Management, 78: 217-224.

Terradas, J. 1999. Holm oak and holm oak forests: an introduction. In: Rodà, F; Retana, J; Gracia, C. A. and Bellot, J. (eds.) Ecology of Mediterranean evergreen oak forests. Springer-Verlag, Berlin.

Trabaud, L. 1987. Dynamics after fire of sclerophyllous plant communities in the Mediterranean basin. Ecología Mediterránea, XIII: 26-37

Verdú, M. 2000. Ecological and evolutionary differences between Mediterranean seeders and resprouters. Journal of Vegetation Science, 11: 265-268.

Welker, J. M. and Menke J. W. 1990. The influence of simulated browsing on tissue water relations, growth and survival of *Quercus douglasii* (Hook and Arn.) seedlings under slow and rapid rates of soil drought. Functional Ecology, 4: 807-817.

**CONCLUSIONS**


**Chapter 1**


The present distribution patterns of *Q. ilex* and *Q. humilis* in Catalonia are mainly determined by temperature. Aspect and annual rainfall fine-tune these patterns over the landscape. Concerning the mixed forests of the two species, these formations show a wide distribution and are present in a broad range of environmental conditions.

In the mixed forests where both species co-occur, the major difference between species is that *Q. humilis* trees have higher growth rates than *Q. ilex* ones under all environmental conditions. Both species perform in a similar way in the mortality rate and the factors that affect the recruitment of saplings in the tree layer.


**Chapter 2**


The main difference in the seed ecology of *Q. ilex* and *Q. cerrioides* is that the later produces more acorns than the former. The following steps in the recruitment process are very similar in the two species: they do not differ in post dispersal seed predation or acorn germination.

The demographic model applied shows a different reproductive success in the two species and spatial differences in recruitment in the different forest types. *Q. cerrioides* has always higher fitness than *Q. ilex* as a consequence of this higher acorn production. The forest type also has a significant effect, because the two species perform better in closed forests than in intermediate forests, producing higher number of recruits under these forests conditions.


**Chapter 3**


The response of the seedlings of *Q. ilex* and *Q. cerrioides* to environmental heterogeneity, in terms of seedlings survivorship, shows that the more favourable conditions are those of high water availability, low light intensity and low nutrient availability. Moreover, the benefits of a higher total water disposal disappear as light intensity increases.

*Q. ilex* and *Q. cerrioides* seedlings show low plasticity values in the traits related to biomass partitioning and growth when they face with different levels of water and nutrient availability. However, *Q. cerrioides* shows a slightly higher phenotypic plasticity to light, and this difference is associated to root variables (R/S, root length and root area).

In spite of these differences in morphology and to a minor extent, in plasticity in response to environmental heterogeneity, *Q. ilex* and *Q. cerrioides* performed similarly in terms of seedling growth.

**Chapter 4**

The response of *Q. ilex* and *Q. cerrioides* to the disturbances is quite similar in terms of survival, because only in the most severe experimental disturbances, particularly in those plots that had experienced a forest fire one year before, there was certain individual mortality.

The main difference between species is that *Q. cerrioides* shows higher growth rates than *Q. ilex* in all fire histories and experimental treatments. Q. *ilex* growth is more affected by increased fire recurrence and intensity of the experimental disturbance, and by the season of disturbance.

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Hola amigo/a,

Te escribo para contarte que ya he terminado la tesis... y al verla encima de la mesa me ha venido un montón de recuerdos e imágenes a la cabeza, todos contenidos en todos estos años (cinco en realidad) en los que he estado embarcada en este proyecto.

...el inicio, imborrable, cuando me dijiste que sí, que adelante, que hiciera realidad mi sueño y empezara la tesis. Aquellos tiempos de principio, ¡me resultan tan entrañables! Recuerdo cuando empezamos a montar el experimento de las plántulas en los campos experimentales. Allí estuvimos, codo con codo, transplantado las bellotas, colocando los contenedores. Tú me contabas historias de tu familia, tan grande, y de tus orígenes y eso me hacía sentir muy acompañada. Luego llegó la otra parte del trabajo: que si las regamos cada quince días, que si les medimos las hojas, que si les limpiamos las raíces.... y encima con toda tu infinita paciencia para explicarme una y otra vez como funcionaba el medidor de áreas foliares cuando estábamos en el IRTA. Y cuando llegaba septiembre.....¿te acuerdas? empezaba nuestra aventura en busca de bellotas: trepar a los árboles, contarlas, a veces casi desesperando cuando eran años de poca producción o aguantando condiciones climatológicas varias, ¡que incluso un 24 de diciembre estuvimos todo el día muestreando bajo la lluvia! Pero resultaba tan divertido..... El trabajo de campo lo recuerdo como una época mítica, todos en el Nissan, camino al Berguedà, a quemar los pinches rebrotes, y a la hora de la comida hablando de mil temas, que allí me enseñaste muchas cosas sobre el Islam, México.....La verdad es que los primeros años fueron los más movidos, que incluso asistimos a dos congresos, en Granada y en Santiago de Compostela. Después la vida se hizo más sedentaria, y pasamos a compartir el día a día en el CREAF. Entonces llegaron otros momentos que también recuerdo con mucho cariño, como las "acampadas" en el césped a la hora de comer, las escapadas a la máquina de café, el té que preparabas en la cocina (por "culpa" tuya me he acostumbrado a ellos), las fantásticas fiestas de cumpleaños, que siempre incluían actuación musical, los (poquitos) partidos de fútbol, las comidas de Navidad.... Sí, la vida en el CREAF ha sido maravillosa.....aunque a veces yo no te la haya hecho fácil, con mis histerias, prisas y ataques de mal humor. ¿Cuántas veces habré acudido a tu despacho para pedirte consejo? ¿o preguntándote sobre facturas, llaves o sobres?, ¡por no olvidar cuándo te pedía que me corrigieras algún texto en diez minutos! Y sin embargo, a pesar de los ficheros equivocados, de las urgencias de siempre, tú has estado ahí,a mi lado. ¡Y quedan tantos, todavía quedan tantos recuerdos!....los datos del inventario, las tardes que me esperabas para llevarme a casa, tu mirada de ánimo

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