Effects of a nursery CO_2 enriched atmosphere on the germination and seedling morphology of two Mediterranean oaks with contrasting leaf habit

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Key words: Nursery techniques, Forest restoration, Mediterranean-type ecosystems, Wildfire, *Q. ilex, Q. cerrioides*.

Abstract: The use of an enriched CO_2 atmosphere in tree nurseries has been envisaged as a promising technique to increase productivity and to obtain seedlings with a higher root/shoot ratio, an essential trait to respond to water stress in Mediterranean-type ecosystems. In that framework, we have analyzed the effects of three levels of atmospheric CO_2 concentration (350, 500 and 700 ppm) on the germination rate, growth and morphology of seedlings of two Mediterranean oaks used in reforestation programs: the evergreen *Quercus ilex* L. and the deciduous *Quercus cerrioides* Wilk. et Costa. CO_2 enrichment increased the germination rate of *Q. cerrioides* (from 70±7 to 81±3 %) while it decreased that of *Q. ilex* (from 71±10 to 41±12 %). Seedlings of both species increased approximately 60% their total biomass in response to CO_2 enrichment but at two different CO_2 concentrations: 500 ppm for *Q. cerrioides* and 700 ppm for *Q. ilex*. This increase in seedlings biomass was entirely due to an augmentation of root biomass. Considering germination and biomass partitioning, an enriched CO_2 atmosphere might not be appropriate for growing Mediterranean evergreen oaks, such as *Q. ilex*, since it reduces acorn germination and the only gains in root biomass occur at a high concentration (700 ppm). On the other hand, a moderate CO_2 enrichment (500 ppm) appears as a promising nursery technique to stimulate the germination, growth and root/shoot ratio of deciduous oaks, such as *Q. cerrioides*.

Resumen: El uso de una atmósfera enriquecida en CO_2 durante la fase de vivero puede contribuir a aumentar la producción viverística, a la vez que ayudar a conseguir plántulas con una mayor relación biomasa subterránea/biomasa aérea, más adecuadas para hacer frente al severo estrés hídrico que generalmente limita el éxito de las repoblaciones en el clima Mediterráneo. En este estudio hemos analizado el efecto de tres niveles de abonado carbónico atmosférico (350, 500 y 750 ppm) en la germinación y morfología de plántulas de encina (*Quercus ilex*) y roble cerrioide (*Quercus cerrioides*). Una atmósfera enriquecida en CO_2 incrementó la germinación de *Q. cerrioides* (de 70±7 a 81±3 %) mientras que disminuyó la de *Q. ilex* (de 71±10 a 41±12 %). Las plántulas de ambas especies incrementaron aproximadamente un 60% su biomasa en respuesta a una mayor concentración de CO_2, aunque esta respuesta se produjo a diferentes dosis: 500 ppm en *Q. cerrioides* y 700 ppm en *Q. ilex*. El aumento en la biomasa total de las plántulas se debió enteramente a un mayor desarrollo de su sistema radical, Considerando tanto la germinación como los efectos sobre la relación biomasa subterránea/biomasa aérea, una atmósfera enriquecida en CO_2 no parece ser un tratamiento adecuado para la producción en vivero de plántulas de *Q.ilex*, puesto que diminuye su germinación y solo aumenta su sistema radicular a dosis muy elevadas (700 ppm). Por el contrario, un aumento moderado en la concentración de CO_2 (500 ppm) aparece como una técnica interesante para estimular el crecimiento y obtener plántulas de *Q. cerrioides* con un sistema radical más desarrollado.

INTRODUCTION

Mediterranean-type ecosystems are particularly prone to degradation because of the occurrence of intense and recurrent disturbances such as wildfires, coupled with the presence of harsh climatic conditions: i.e. hot and dry summers and scarce rainfall with great intra and inter-annual variability (Naveh 1994). Moreover, in the Mediterranean Basin, the number of wildfires and, especially, the surface burned by forest fires, have increased considerably and large and more intense fires have repeatedly occurred (Piñol et al. 1998). In this scenario, reforestation is the most widespread large-scale restoration practice aimed at reducing fire effects (Vallejo et al. 2000; Espelta et al. 2003). Current restoration programs of degraded lands in the West Mediterranean Basin are shifting from the traditional plantation of relatively fast-growing low-resource-demanding species, such as pines (e.g. *Pinus halepensis*), towards the plantation of oaks (e.g. *Quercus* ilex, *Quercus cerrioides*, *Quercus coccifera*). This is due to the presumed better ability of oaks to withstand future disturbances through their resprouting ability (Vallejo and Alloza 1998). However, establishment of oak seedlings is difficult and high mortality rates are usually detected in plantations (Mesón and Montoya 1993). These poor results have been related to the fact that seedlings of these species are quite sensitive to water shortage and high light intensity during the seedling phase (see Retana et al. 1999). Furthermore, transplanted seedlings are particularly susceptible to water stress as they do not have root systems sufficiently developed to replace water lost through transpiration (Baeza et al. 1991), and they are acclimated to the previous environmental conditions of commercial nurseries (van den Driessche 1991a,b).

As water stress is the main factor limiting the success of plantations in Mediterranean-type ecosystems (Baeza et al. 1991), the best plants for revegetation in these areas are likely to be those which are best adapted to this constraint (Araújo-Alves et al. 2000). The response of plants to stressful environmental conditions can be changed during nursery production by using certain cultural practices (Sachs 1991). Concerning the morphological characteristics of seedlings, a high root/shoot ratio (McKay et al. 1999) can ensure a better water balance and thus improve seedling survival and growth after transplant (Biel 2002). In recent years, among the different nursery techniques used to manipulate seedling quality to cope with environmental stresses, the use of an enriched CO_2 atmosphere is gaining popularity in the production of Mediterranean slow-growing plants (Savé et al. 1998). This is because an elevated CO_2 atmosphere can enhance nursery productivity by reducing the time required to grow seedlings, but furthermore, because it has been postulated that seedlings growing under high CO_2 concentrations might show a preferential allocation to roots, thus increasing their root/shoot ratio (see reviews in Curtis and Wang 1998; Norby et al. 1999; Tingey et al. 2000).

However, there is still scarce information concerning the effects that CO_2 enrichment may have in the germination rate, growth and morphology of Mediterranean oaks. Moreover, CO_2 effects can vary widely according to the leaf-habit of the species, as differences in the leaf life span can lead to differences in the response to environmental cues. An evergreen habit usually involves a lower responsiveness to environmental changes, such as CO_2, because of the trade-off between plant traits that reduce nutrient losses and those leading to high rates of dry matter production (Aerts and van der Peijl 1993). In the other hand, the lower specific leaf weight in the deciduous species (Cornelissen et al. 1996) can result in a greater response to CO_2 enrichment (Poorter et al. 1996). The main aim of this study is to analyze the effects of the application of a CO_2 enriched atmosphere, as a nursery technique to increase the germination rate, growth and root/shoot ratio of seedlings of two Mediterranean oaks with contrasting leaf habit, the evergreen *Quercus ilex* and the deciduous *Quercus cerrioides,* both extensively used in reforestation programmes.

MATERIAL AND METHODS

Experimental design

Q. ilex and *Q. cerrioides* acorns were collected in a mixed native oak stand at the Collserola Park, a protected area near Barcelona (NE Spain; 41º 24' N, 2º 6' E). All seeds were carefully examined to discard aborted, infected or dried individuals. Acorns were sown in 'Forest-pot' of 300 cm^3 filled with oligotrophic substratum (composted fragments of pine bark). The nursery trial was carried out in a multitunnel greenhouse (a span tunnel type divided into three modules of 77 m^2 each) located at IRTA (Cabrils, Barcelona). Each module had a different CO_2 concentration: high (700±45 ppm), intermediate (500±30 ppm) and control (350±20 ppm). In the 700 and 500 ppm modules, the air was enriched with a constant flow of pure industrial CO_2 (Carburos Metálicos, S.A.) through polythene vessels. CO_2 concentration was continuously measured by an infrared gas analyser (IRGA) LIRA Model 3600 (MSA, Spain) and controlled by an automata PLC OMRON C20K connected to a personal computer. This automatic system provided a CO_2 flux that was enough to reach the concentration desired. To avoid high humidity and high temperatures effects, roof windows of all modules were opened once a day (from 10:30 am to 15:00 pm). During this period, CO_2 concentration was kept constant through increasing flux rates. The film cover of the three modules had the same transmittance (64±5%), and received the same mean radiation (1772±113 W m^{-2} d^{-1}).

To analyze acorn germination, three trays (=replicates) of 50 forest pots (50 acorns) per species were placed in each module. Trays were watered twice daily to allow optimum germination and growth conditions. Watering levels varied during the experiment according to the season (2 $l \cdot m^{-2}$ per day from November until February and 4 $l \cdot m^{-2}$ per day in March). These watering levels correspond to complete substrate saturation plus 30% of drainage (the common watering strategy in commercial nurseries in the area). The location of trays in each module was rearranged weekly to avoid possible effects of location.

Seedlings harvesting was carried out five months after the onset of the experiment. To analyze growth and morphological characteristics of seedlings, 15 *Q. ilex* and 15 *Q. cerrioides* seedlings of each CO_2 level (5 seedlings per tray) were randomly chosen and their total biomass was separated into three compartments: leaves, stems and roots. Dry weight of each compartment was calculated after drying at 70º (72h). Leaf area was measured with a LI-COR area meter (LI-COR Model 3100, USA)..

Variables used to characterise the response of seedlings to the CO_2 treatment included: days needed to germinate 50% of the acorns (D50), total percentage of germinated acorns, seedling height, shoot diameter, leaf biomass, stem biomass, root biomass, total biomass, leaf area and several morphological and biomass allocation indices derived from those primary data: root-shoot (root mass/aerial mass), specific leaf weight (SLW: leaf weight/leaf area), leaf area ratio (LAR: leaf area/total plant weight), leaf weight ratio (LWR: leaf weight/total plant weight), stem weight ratio (SWR: stem weight/total plant weight) and root weight ratio (RWR: root weight/total plant weight).

Data analysis.

The effect of SPECIES (*Q. ilex, Q. cerrioides*) and CO_2 treatment (350, 500, 700 ppm) on D50, the percent of germination, morphology and biomass allocation of seedlings was analysed by two-way ANOVA models. Inspection of residuals was carried out to check for normality and homoscedasticity. Data of percent of germination was normalised with an arcsin transformation, those of D50, LAR and LWR with a log transformation and those of RWR with an inverse log transformation.

RESULTS

Q. cerrioides and *Q. ilex* showed differences both in the final percentage of acorn germination and in the time taken to germinate (Table 1). Acorns of *Q. cerrioides* germinated in a higher percentage (73.0 ± 3.0 %) than those of *Q. ilex* (54.0 ± 7.0 %). However, the interaction SPECIES x CO_2 revealed specific differences among the three CO_2 levels assayed (Figure 1). A similar germination rate in both species was obtained under the control CO_2 level (350 ppm), but acorn germination of *Q. cerrioides* increased from 500 to 700 ppm, whereas that of *Q. ilex* decreased when raising the CO_2 concentration. On the other hand, *Q. cerrioides* acorns germinated before (D50= 54.8 ± 3.0 days) those of *Q. ilex* (D50= 99.3 ± 16.9 days), but this variable did not depend on CO_2 enrichment (Table 1).

Several morphological and biomass allocation traits of seedlings varied according to the CO2 levels applied (Table 1). The interaction SPECIES x CO2 indicated that CO2 enrichment affected the height and biomass of seedlings in a different way in *Q. ilex* and *Q. cerrioides*. Height of *Q. cerrioides* seedlings slightly decreased in the CO_2 gradient, while that of *Q. ilex* increased in the 700 ppm treatment (Figure 2A). The biomass of seedlings increased in the two species with CO_2 enrichment. However, as shown in Figure 2B, while biomass for *Q. cerrioides* was maximum under the 500 ppm CO_2 level and then decreased in 700 ppm, the highest biomass of *Q. ilex* was reached under 700 ppm. As no changes occurred in leaf or stem biomass in the two species (see ANOVA in Table 1), this total biomass increase was entirely due to an increase in root biomass under the aforementioned CO_2 treatments (Figure 2C), As a result of this increase in the root compartment, seedlings exhibited a lower leafiness (e.g. LAR) under the 500 ppm CO_2 level for *Q. cerrioides* and under 700 ppm for *Q. ilex* (Figure 2D). In relation to the leaf characteristics, CO_2 enrichment did not modify the specific leaf weight of seedlings: SLW was higher in *Q. ilex* in comparison with *Q. cerrioides* (0.114±0.004 and 0.091±0.004 mg.mm^{-2}, respectively).

DISCUSSION

Cultural treatments increasing the germination rates and growth of seedlings while reducing the time required may be very important to enhance the production of Mediterranean slow-growing tree species for restoration practices (Savé et al. 2002). Concerning our first goal of increasing the germination rates of the two species through CO_2 enrichment, our results show a nil effect of CO_2 in the time taken for acorn germination, while contrasting effects were found on the germination rates of the two species: *Q. cerrioides* increased while that of *Q. ilex* decreased with CO_2. Although the response to CO_2 in germination has been presumed to be in general positive because of an enhancement in ethylene production by CO_2 (Esashi et al. 1986), different studies have provided contradictory results (Ward and Strain 1999). Reported effects of CO_2 enrichment on germination may range from positive (Wulff and Alexander 1985), neutral (Garbutt et al. 1990) or negative (Andalo et al. 1996), with a strong dependence on the species studied (Hussain et al. 2001). Thus, the higher stimulation of *Q. cerrioides* germination in comparison with *Q. ilex* could be linked to a lower ABA concentration in the acorns of the former species (for the inhibitory effects of ABA in germination, see Black 1991), that would allow a higher effect of CO_2 in the synthesis of ethylene and consequently promote a higher germination rate (see Salisbury and Marinos 1985).

Growth, morphology and biomass partitioning of *Q.cerrioides* and *Q.ilex* seedlings varied with CO_2 levels. Total biomass increased with CO_2 enrichment; probably due to up regulation of the photosynthesis rates as has been previously reported in studies dealing with the effects of an elevated CO_2 atmosphere (see, among others, the review by Ward and Strain 1999). However, it is important to stress that the increase in the biomass of seedlings occurred at different CO_2 levels in the two species (500 ppm in *Q. cerrioides* vs. 700 ppm in *Q.ilex*). A stronger response of deciduous in comparison with evergreen species to environmental factors has been previously found in other studies dealing with light, water or nutrient availability (see Ke and Werger 1999; Valladares et al. 2000). In the case of CO_2 enrichment, deciduous species tend to respond strongly because they have a lower specific leaf weight and lower investments in structural carbohydrates and other leaf components that protect and lengthen the lifespan of leaves in evergreen species (Cornelissen et al. 1999). Notwithstanding this, it is important to stress the fact that seedlings of *Q. cerrioides* grown under 500 ppm got better results than those under 700 ppm. A higher stimulation of growth at intermediate CO_2 levels (500 ppm) compared to higher CO_2 levels (700 ppm) has been reported in other studies, and attributed either to physiological limitations, such as foliar N dilution leading to decrease photosynthetic capacity (Luo et al. 1997) or an exceedingly high concentrations of some micronutrients (Walker et al., 2000). On the other hand, the scleropyllous nature of *Q. ilex* leaves, as well as their tendency to accumulate secondary compounds such as tannins and phenols (see Llussià 1998), is likely to favour this lower reaction to CO_2 enrichment until a high concentration (700 ppm) is reached (see Körner and Miglietta 1994 for the effects of CO_2 on non structural carbohydrates). In both species, the increase in growth in the enriched CO_2 treatments was entirely due to an increase in the biomass of roots (see Figure 2C). This pattern can be attributed to the preferential allocation of biomass to structures involved in the uptake of the most limiting resources (e.g. water or nutrients) in contrast with the elevated CO_2 presence (Rogers et al. 1994; Ward and Strain 1999; Tingey et al. 2000). Thus, through increasing the atmospheric $C0_2$ concentration in the nursery, we reached our second target of obtaining seedlings with a higher root/shoot ratio, presumably better adapted to face a water stress environment after transplant (Royo et al. 2001).

The demand for seedlings for reforestation programs tends to vary significantly from year to year, and nurseries usually have to provide large numbers of seedlings in a very short time (Clewell and Rieger 1997). Moreover, reforestation practitioners are increasingly demanding seedlings better adapted to the environmental conditions where reforestation is going to be carried out (Bayley and Kietzlka 1996). Our results reveal that increasing the atmospheric concentration of CO_2 in the nursery could not be entirely appropriate for evergreen oaks, such as *Q. ilex*, since an elevated CO_2 atmosphere decreases acorn germination and the only gains in root biomass occur at a rather high concentration (700 ppm). In contrast, the use of a moderate CO_2 enriched atmosphere (500 ppm) may be a potential nursery technique to stimulate the germination and the growth of deciduous oaks, such as *Q. cerrioides*. Moreover, the increase in root biomass and root-shoot ratio at that CO_2 level may help to produce seedlings that are better adapted to face water stress after transplant. In spite of these promising results, to have better insight concerning this potential use of CO_2 as a nursery technique to grow Mediterranean species, further research should evaluate the economic cost of using air carbon fertilization as well as the possibilities of combining this treatment with other hardening techniques, such as restricted watering (Biel 2002).

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Table 1. F values from ANOVA tests for the effects of species (*Q. ilex, Q. cerrioides*) and CO_2 levels (350, 500, 700 ppm) on the percentage of acorns germination (% germ.), time to germinate (D50) and different morphological and biomass allocation traits of seedlings: height, stem diameter, leaves biomass, stem biomass, root biomass, root-shoot, leaves area, specific leaf weight (SLW), leaf area ratio (LAR), leaf weight ratio (LWR), stem weight ratio (SWR) and root weight ratio (RWR). n = 3 trays per treatment for germination variables; n = 15 seedlings per treatment for seedlings traits. Statistical significance: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Factor	% germ.	D50	Height	Diameter	Leaves biomass	Stem biomass	Root biomass	Total biomass	Root / Shoot	Leaves area	SLW	LAR	LWR	SWR	RWR
Species (Sp)	9.0 *	16.0 **	4.0	0.4	1.9	0.1	3.7	1.8	5.7*	0.4	14.6***	0.1	6.0*	1.5	4.9*
CO_2	1.6	0.8	1.2	1.1	3.1	0.3	1.8	1.8	1.8	2.3	1.8	1.8	1.5	3.2	0.7
Sp x CO_2	3.9 *	3.1	5.3*	2.8	1.7	1.7	5.9**	5.0*	6.4**	2.0	1.8	6.0**	6.4**	2.2	5.3*

FIGURE CAPTIONS

Figure 1. Mean (± 1SE) percentage germination of *Quercus cerrioides* (filled dots) and *Quercus ilex* (hollow dots) according to the different levels of atmospheric CO_2 enrichment.

Figure 2. Mean (± 1SE) height (A), total biomass (B), root biomass (C), and leaf area ratio (D) of *Quercus cerrioides* (filled dots) and *Quercus ilex* (hollow dots) seedlings according to the different levels of atmospheric CO_2 enrichment.