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GROWTH AND DEVELOPMENT OF SESSILE OAK (*QUERCUS PETRAEA*) AND TURKEY OAK (*QUERCUS CERRIS*) SEEDLINGS IN RESPONSE TO VARYING LIGHT AND SOIL MOISTURE CONDITIONS

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Abstract: The results of a factorial experiment carried out on sessile oak and Turkey oak seedlings under three light intensities (50%, 30% and 5% of incoming solar radiation) and two soil moisture levels (humid and dry) are reported. Leaf area and total and component (leaves, stems and roots) biomass were measured on each seedling, and indices of net assimilation rate (NAR), specific leaf area (SLA) and root to stem ratios calculated. The imposed light and soil moisture treatments resulted in a higher death rate in sessile oak seedlings compared to Turkey oak, and greatly influenced seedling growth, leaf characteristics and biomass accumulation. Variation in light levels proved to be the most important factor. In both species, greatest biomass production occurred at intermediate light levels (i.e. 30% of full sunlight) and humid soil moisture conditions. Lowest biomass accumulation occurred at the lowest light levels. Although both species showed similar ecological responses to light and soil moisture, Turkey oak appears to be a more adaptable species whereas sessile oak is a more selective one. Hypotheses regarding the adaptive strategies of the two species, based on their observed responses to the experimental treatments, are discussed.

Introduction

Recently developed guidelines in natural resource management are aimed at restoring the complexity and structure of degraded ecological communities. To achieve this aim, solid knowledge of both species characteristics (i.e. their autecology and synecology) and the processes that have led to habitat degradation are required.

Scientific interest in sessile oak (*Quercus petraea* (Matt.) Liebl.) has recently increased, both from the ecological and cultivation points of view. However, the ecology of this species remains poorly understood, particularly at the southern limit of its natural distribution. Mixed stands of sessile oak, Turkey oak (*Q. cerris* L.), and other broadleaves are common in the montane regions of central Italy, particularly on siliceous substrates (e.g. Abbate & Paura 1993; Abbate et al. 1990; Arrigoni et al. 1990; Blasi 1984, 1994; Cutini & Mercurio 1995; Dowgiallo & Vannicelli 1993; Pignatti & Wikus Pignatti 1987; Scoppola & Filesi 1993). These stands have been strongly influenced by human activity (e.g. deforestation, grazing by domestic animals, and fire) so that they are quite impoverished in terms of their composition and structure. Today this area is mainly covered by coppices dominated by Turkey oak, together with sessile oak and other broadleaf species. In order to promote the restoration of these oak communities, especially those characterized by high biodiversity and complexity, the autecology of sessile oak and Turkey oak should be studied in detail to determine the environmental conditions favouring one or the other species during the early developmental stages.

This paper reports on results from a comparative experiment carried out on sessile oak and Turkey oak seedlings grown under three light intensities and two soil moisture levels. The objective of the experiment was to determine the ecological requirements of the two species during the crucial establishment phase. The existence of differences in the ecology and adaptive strategies between the two species is discussed, based on seedling characteristics and biomass partitioning (Grime 1979, Abrams & Kubiske 1990).

Materials and Methods

Seed from two different provenances were used in the experiment: Alto Tevere (43°43'N, 12°02'E) for Turkey oak, and Bosco di Sargiano (43°25'N, 11°51'E) for sessile oak. The seeds were sown in a nursery in a homogeneous mixture of 70% soil and 30% peat, in 900 cm^3 plastic pots. At the end of April, year-old seedlings of each species were selected from among the more well-developed ones. The seedlings were used in a two-factor experiment involving three light levels and two soil moisture treatments, to evaluate the effects of these factors on the growth, functionality, and distribution of resources among the various components (leaves, stems and roots). The three light levels used were: A = 50%, B = 30%, and C = 5% of incoming solar radiation. The seedlings were grown inside sheds covered with

Umbratex in order to obtain the required light levels. During the experiment, several daily cycles of PAR (photosynthetically active radiation, 400-700 nm) measurements were made using a Sunfleck Ceptometer (Delta T Devices, Burwell, U.K.). Two soil moisture levels were applied: H = humid, involving abundant and frequent watering (daily during the months of July and August) to maintain a constantly moist substrate, and D = dry by occasionally watering (1-2 times per week) to create water deficit conditions. Twelve seedlings (replicates) were used for each treatment combination. Thus, given the three light and two soil moisture levels, the experiment involved 3 x 2 x 12 = 72 sessile oak and 72 Turkey oak seedlings.

At the end of the growing season, the leaf area (LA), total dry biomass, and the dry biomass of each component (leaves, stems, and roots) were measured on each seedling. The leaf area was measured using an electronic area meter (Delta T Devices, Burwell, U.K.), while biomass values were obtained by massing the material after having placed it in a ventilated oven at ca. 80°C to achieve a constant dry mass. The following indices, describing growth, functionality and distribution of biomass among the various components, were calculated with the available data: (1) the net assimilation rate (Chiarello et al. 1989),

$$NAR = [2W] / [(LA)(t_2 - t_1)] \quad (1)$$

where W = root and stem dry biomass, $t_2 - t_1$ = time period of the experiment, and LA = leaf area; (2) the specific leaf area (SLA), which is the ratio of leaf area to total biomass; and (3) the root/stem index, which is the ratio of root to stem biomass.

The effects of light and soil moisture levels on biomass and its components, and on the growth indices, were evaluated using a two-factor analysis of variance (ANOVA) in order to determine the effects of each factor, and their interaction. Means were compared using the Tukey highly significant difference multiple comparison test.

Results

Seedling mortality in the experiment was low; sessile oak mortality was 10%, and Turkey oak mortality was 5%. The analysis of variance results indicate that light and soil moisture levels affect total biomass, root biomass, leaf area, SLA and NAR of seedlings in the two species (Table 1). Light and soil water content significantly influence leaf and stem biomass in the Turkey oak, but not in the sessile oak. In both species, variation in light levels has a greater effect than variation in soil moisture. Interactions were generally statistically significant, except for the SLA and the NAR in sessile oak seedlings, and root biomass in Turkey oak. In both species, the highest total biomass was obtained at intermediate light levels (B = 30% of incoming solar radiation) and higher soil moisture (H = humid). Highest biomass levels were seen in the B x H treatment combination (Fig. 1). In sessile oak, relatively high biomass values were obtained in the B x D treatment combination, while biomass accumulation was least at the lowest light levels (C = 5% of incoming solar radiation). In Turkey oak, seedling biomass was also high at the highest light level, particularly at high soil moisture levels (A x H treatment combination). For both species, growth was reduced at the lowest light level tested, although this effect was less pronounced in Turkey oak.

In both species, increased light levels resulted in decreased SLA values. However, soil moisture had little effect on SLA (Fig. 2). A similar trend is apparent for percent above-ground biomass. In contrast, percent root biomass increased with increased solar radiation, with highest values recorded in the B x H treatment combination for Turkey oak and the A x D treatment combination in sessile oak (Fig. 2). NAR values were lowest at the lowest light level (C = 5%), and increased with increasing light levels (Fig. 3).

Table 1. Factorial ANOVA of Turkey oak and sessile oak seedling biomass, characteristics and growth indexes (significant values in bold).

		Roots		Leaves		Stem		Total		Leaf area		SLA		NAR	
	D.F.	F	P	F	P	F	P	F	P	F	P	F	P	F	P
Q. cerris															
soil moist.	1	18.59	**<0.001**	1.53	0.221	0.50	0.489	9.79	**0.003**	3.44	**0.068**	2.37	0.129	4.19	**0.045**
radiation	2	14.90	**<0.001**	0.37	0.693	1.92	0.154	4.05	**0.022**	9.70	**<0.001**	7.62	**0.001**	19.96	**<0.001**
interaction	2	5.16	**0.008**	0.92	0.405	0.51	0.604	2.26	0.112	1.79	0.176	1.95	0.150	1.91	0.156
residual	66														
Q. petraea															
soil moist.	1	4.96	**0.030**	7.00	**0.010**	8.61	**0.005**	7.50	**0.008**	6.69	**0.012**	0.25	0.625	2.03	0.160
radiation	2	25.32	**<0.001**	25.87	**<0.001**	30.90	**<0.001**	32.40	**<0.001**	20.18	**<0.001**	6.84	**0.002**	3.31	**0.043**
interaction	2	7.25	**0.002**	6.24	**0.003**	5.53	**0.006**	8.76	**0.001**	6.92	**0.002**	0.16	0.852	0.28	0.757
residual	61														

Discussion

In this experiment, the death rate was higher in sessile oak seedlings than in Turkey oak, especially in those seedlings exposed to a water deficit stress (see also Cutini and Mercurio 1996). The water deficit caused a partial or total drying up and falling off of some leaves on the sessile oak, while this did not occur in the Turkey oak.

Both light and soil moisture levels strongly affect the growth, leaf characteristics (Jakucs & Virágh 1975) and productivity of oak seedlings. Our experimental results suggest that light is the more important factor. By comparing the various treatment combinations, it is evident that a 30% solar radiation level results in the highest growth (biomass accumulation) in both sessile oak and Turkey oak. At this light level, there is also an increase in root development. The com-

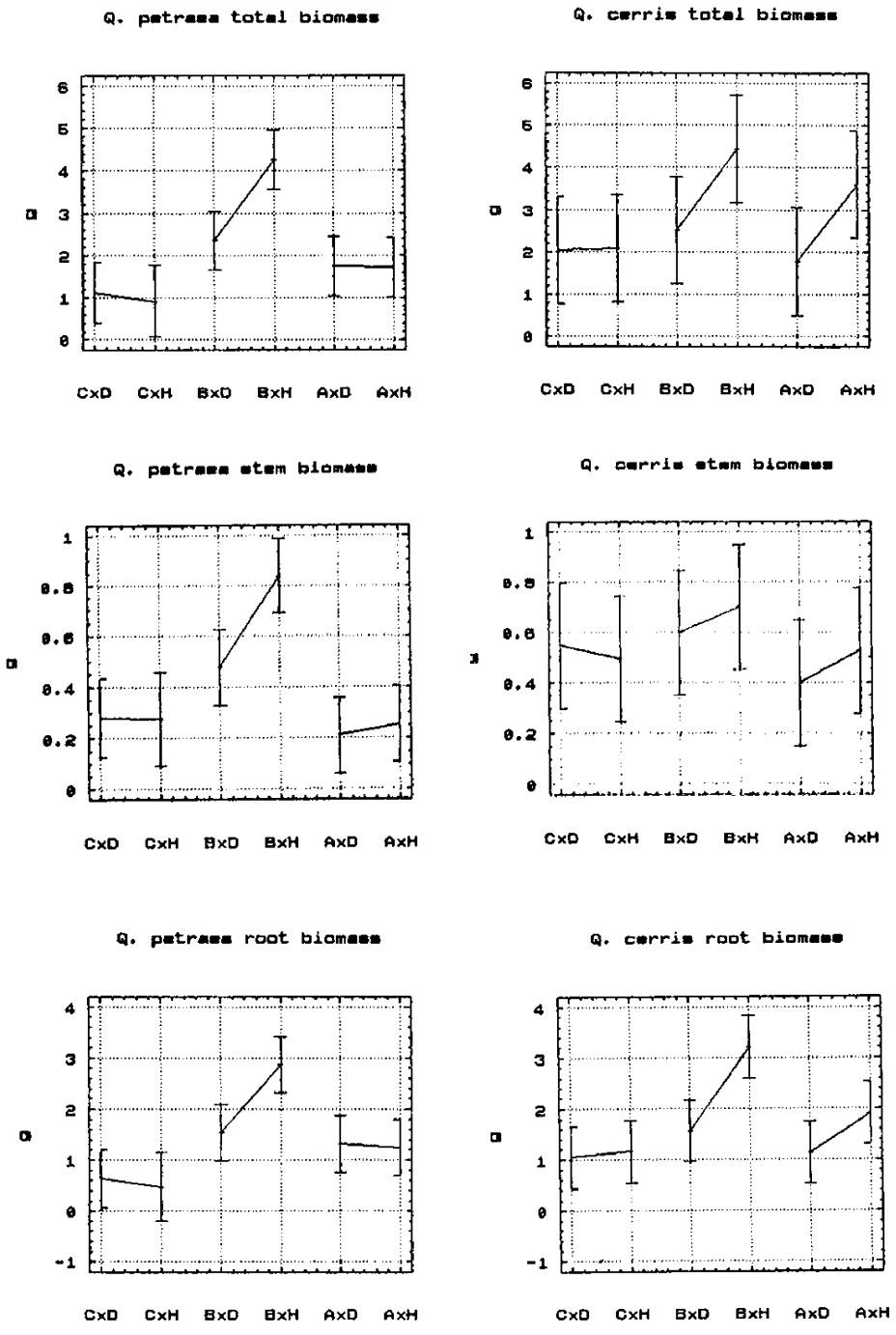

Figure 1. Means and confidence intervals (99%, Tukey's HSD test) of total, stem and root seedling biomass (in grams). Letters code: A = 50%, B = 30% and C = 5% of incident solar radiation; D = dry and H = humid soil moisture levels.

bined actions of light and soil moisture on growth are not additive, since the interaction terms are often statistically significant (particularly in sessile oak).

Although the results of these experiments do not highlight particular differences in growth of the two species, the Turkey oak is able to maintain good levels of growth under lower light conditions. The higher biomass of sessile oak seedlings under intermediate light levels (B = 30%) confirms the clear preference of this species for intermediate light conditions, at least in the early development phases (Jarvis 1964, Igboanugo 1990).

Different light and soil moisture conditions modify the characteristics of oak seedlings, including average leaf area, SLA, and the biomass distribution between above-ground and below-ground biomass, as previously observed in sessile oak (Ovington & MacRae 1960, Jarvis 1964) and other oak

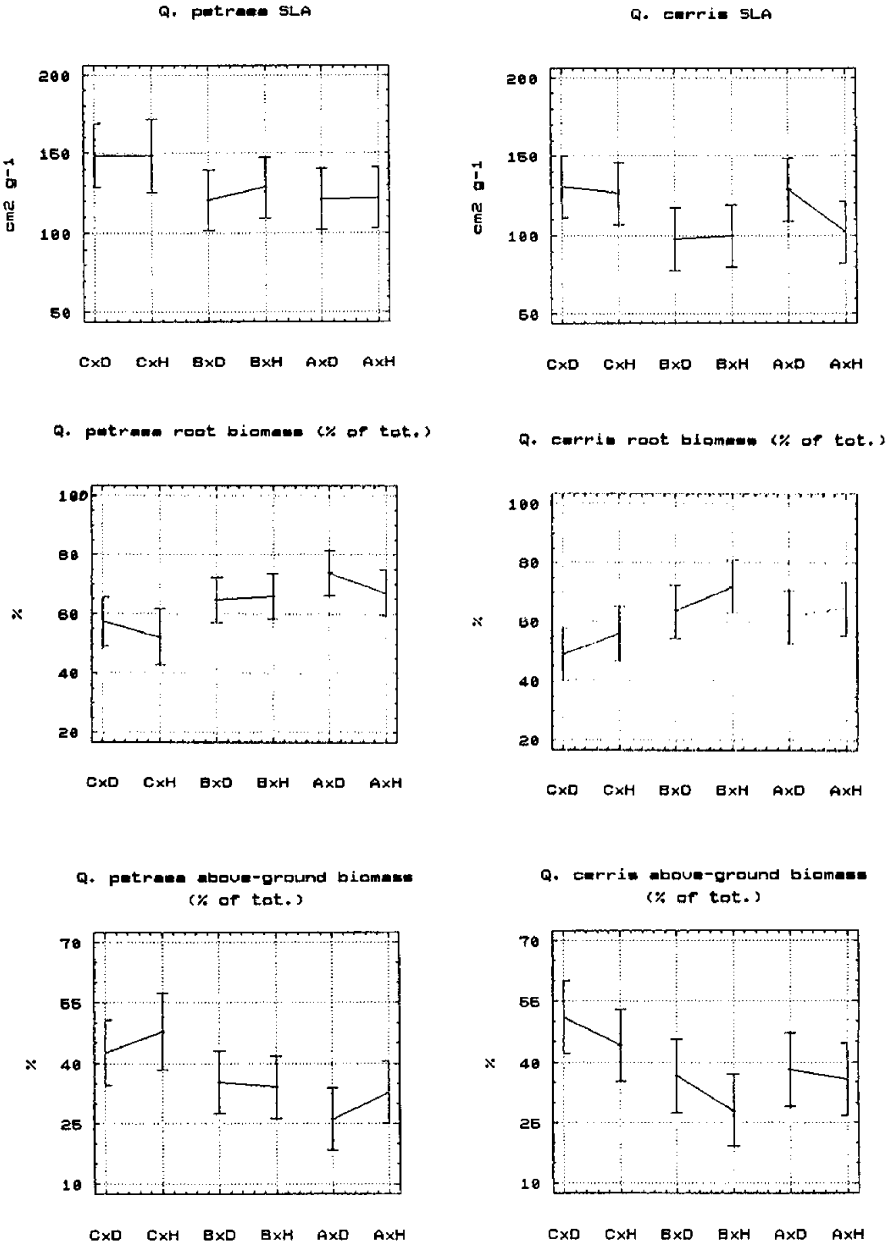

Figure 2. Means and confidence intervals (99%, Tukey's HSD test) of specific leaf area (SLA), percent root biomass, and percent above-ground biomass. Letters codes as in Fig. 1.

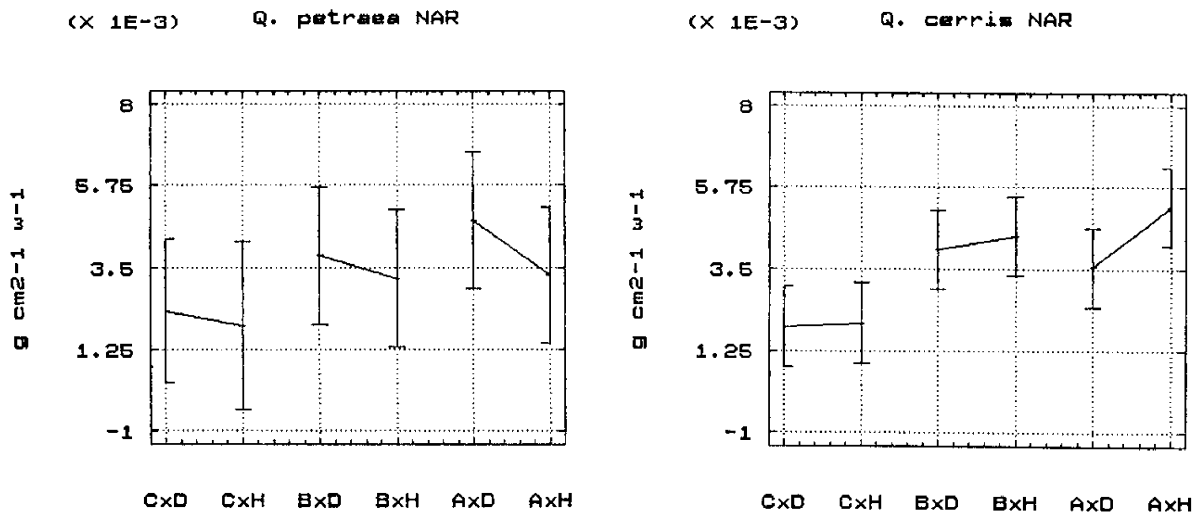

Figure 3. Means and confidence intervals (99%, Tukey's HSD test) of net assimilation rate (NAR). Letter codes as in Fig. 1.

species (Kolb et al. 1990). As light levels increase, the leaf area and the above-ground biomass are often reduced, to the advantage of the root system. In addition, the leaves thicken, confirming what has previously been observed in other oak species (Abrams & Kubiske 1990, Abrams 1996). The highest ecological efficiency (NAR, the produced biomass to leaf area per unit time) of seedlings of both species results from a reduction in the leaf system on the one hand and an increase in energy availability on the other.

On the whole, the two species responded in similar ways to the treatment combinations used in these experiments. The low mortality rates in these experiments (relative to rates obtained in previous experiments, see Cutini & Mercurio 1996), indicate that both species are adapted to light conditions varying between 5% and 50% of full sunlight. The Turkey oak is better able to resist water deficit conditions than is sessile oak, as shown by the lower death rate and the absence of partial drying up of the leaves.

The absence of clear differences in the responses of sessile and Turkey oak seedlings to various light and water deficit conditions do not allow us to discriminate between the two species from an autecological point of view, at least in the initial development stages. However, some differences between the two species are suggested from the results of the experiment, allowing us to generate hypotheses regarding the adaptive strategies of the seedlings. The Turkey oak appears to be a more adaptable species, capable of better growth under the treatment combinations tested and thus able to compete with sessile oak even under low light conditions. Nonetheless, the sessile oak is capable of stronger growth under clearly defined ecological conditions. The two species appear to differ mostly in their adaptive strategies, with Turkey oak pursuing a more stress-tolerant strategy and sessile oak a competitive one (cf. Grime 1979).

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