

Root biomass of *Quercus ilex* in a montane Mediterranean forest

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Biomass allocation to roots was studied in holm oak (*Quercus ilex* L.), a dominant evergreen tree in broad-leaved sclerophyllous Mediterranean forests. The root systems of 32 single-stemmed holm oaks growing in shallow soils on largely unfissured bedrock were excavated in a mesic site and a xeric site in the Montseny Mountains (northeast Spain). Individual root:shoot biomass ratios (roots with diameter < 1 cm not included) of single-stemmed trees were significantly higher in the xeric site (mean 0.45) than in the mesic site (mean 0.37), probably reflecting the lower water availability and higher light availability in the xeric site. It is concluded that single-stemmed holm oaks have higher root:shoot ratios than most temperate forest trees, particularly so when growing on a xeric site. Root:shoot ratios of single-stemmed trees were not linearly correlated with dbh. Allometric regressions of root biomass on dbh did significantly differ between sites. Roots < 1 cm in diameter were sampled with soil cores in the mesic site. Holm oaks ≥ 5 cm dbh in a stand dominated by single-stemmed trees on the mesic site had an aboveground biomass of 160 t/ha and a belowground biomass of 63 t/ha. The belowground biomass was composed of 30 t/ha of root crowns plus roots > 5 cm in diameter, 17 t/ha of roots 1-5 cm in diameter, and 16 t/ha of roots < 1 cm in diameter. The xeric stand was dominated by multistemmed holm oaks with massive root crowns developed after repeated coppicing. Three multistemmed trees were excavated, yielding a mean root:shoot ratio of 1.2. Through resprouting from root crowns, managed or disturbed holm oak forests can accumulate a belowground biomass greater than that displayed aboveground: 91 t/ha (excluding roots < 1 cm in diameter) and 79 t/ha, respectively, in our xeric stand.

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L'allocation de biomasse vers les racines a été étudiée chez le chêne vert (*Quercus ilex* L.), un feuillu dominant à feuilles persistantes des forêts sclérophylles méditerranéennes. Le système racinaire de 32 chênes verts à tige unique croissant dans des sols minces sur une assise rocheuse peu fissurée fut excavé dans des stations mésique et xérique dans les montagnes de Montseny situées dans le nord-est de l'Espagne. Les ratios racine:tige individuels de biomasse (les racines avec un diamètre < 1 cm n'étaient pas incluses) des arbres à tige unique étaient significativement plus élevés dans la station xérique (moyenne de 0,45) que dans la station mésique (moyenne de 0,37) reflétant probablement la moins grande disponibilité en eau et la plus forte disponibilité de lumière dans la station xérique. En conclusion, les chênes verts à tige unique ont un ratio racine:tige plus élevé que la plupart des arbres en forêt tempérée, particulièrement lorsqu'ils croissent dans une station xérique. Le ratio racine:tige des arbres à tige unique n'était pas linéairement corrélé avec le dhp. Les régressions allométriques entre la biomasse racinaire et le dhp étaient significativement différentes selon la station. Les racines < 1 cm de diamètre ont été échantillonnées en prenant des carottes de sol dans la station mésique. Les chênes verts > 5 cm dbh dans un peuplement dominé par des arbres à tige unique dans la station mésique avaient une biomasse aérienne de 160 t/ha et une biomasse racinaire de 63 t/ha, comportant 30 t/ha de collets et de racines > 5 cm de diamètre, 17 t/ha de racines 1-5 cm de diamètre et 16 t/ha de racines < 1 cm de diamètre. La station xérique était dominée par des chênes verts à tiges multiples avec d'importants collets qui se sont développés suite à des recépages répétés. Les trois arbres à tiges multiples excavés avaient un ratio moyen racine:tige de 1,2. Même si le chêne vert rejette à partir du collet, les forêts aménagées ou perturbées peuvent accumuler une biomasse racinaire plus importante que la biomasse aérienne : soit respectivement 91 t/ha (excluant les racines < 1 cm de diamètre) et 79 t/ha dans la station xérique.

[Traduit par la rédaction]

Introduction

Mediterranean-type ecosystems are characterized by summer drought and the concomitant scarcity of available soil water during the warm season (Specht 1982). As well, these ecosystems have a long history of recurrent fires and, at least in the Mediterranean basin, have been subjected to heavy grazing since ancient times. Under such conditions, the possession of a large root system could be advantageous for the sclerophyllous, evergreen trees and shrubs that often dominate the vegetation of Mediterranean-type ecosystems. Precious stores of water, photosynthate, and nutrients are best protected from desiccation, fire, aboveground herbivores if placed in belowground biomass. In addition, two other

factors could favour plants with well-developed root systems under Mediterranean conditions. First, a high belowground biomass could result from nutrient availability stress, a widespread situation in the nutrient-poor soils common in some of the Mediterranean-type regions of the world (Kruger et al. 1983). Second, coppicing for firewood or charcoal production has long been practised in the woodlands of the Mediterranean basin. As a result, resprouting trees and shrubs can develop massive root crowns (lignotubers or burls, James 1984). This can also happen with other recurrent disturbances that kill only the aboveground parts of plants, as is often the case with fire.

There is qualitative evidence that in some cases Mediterranean trees do possess a large root system. For instance, the roots of some species of California oak trees can reach, under favorable conditions, a depth of 26 m (Lewis and Burghy 1964), and sinker roots of jarrah trees (*Eucalyptus*

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marginata) in Western Australia descend more than 40 m into weathered granite (Abbott et al. 1989). However, reliable quantitative data of either individual root:shoot biomass ratios or stand belowground biomass are distinctly lacking for Mediterranean forest trees. Root biomass studies are available for Mediterranean shrubs, which often exhibit rather high root:shoot biomass ratios (Kummerow 1981), but trees should allocate proportionally more biomass to shoots than shrubs do (Rundel 1980). As most Mediterranean woody plants are resprouters (Naveh 1974), a large root:shoot ratio at a given site could arise from genetically determined constraints on growth form, from water or nutrient availability stress, or from the effects of repeated resprouting after disturbances. It is not known whether seed-derived (i.e., not resprouted) Mediterranean trees do indeed have a high root:shoot ratio, and how this ratio is affected by site conditions.

Our studies in holm oak (*Quercus ilex* L.) forest ecosystems in northeast Spain provide a suitable framework to address such questions. Holm oak is an evergreen, sclerophyllous tree with a circum-Mediterranean distribution. It resprouts abundantly and vigorously when burned or cut. The main objective of this paper is to determine whether seed-derived (single-stemmed) holm oaks allocate a higher proportion of biomass to belowground organs than do other temperate forest trees, even in a mesic site with relatively high availabilities of water and nutrients that has not been affected by burning, grazing, or coppicing. In addition, we (i) derive allometric regressions for root biomass in holm oak, (ii) compare root:shoot ratios of single-stemmed trees in a mesic and a xeric site, (iii) compare root:shoot ratios of seed-derived trees versus resprouted multi-stemmed ones, and (iv) compare patterns of root biomass distribution in two stands of contrasting structure.

Study area

This study was carried out at La Castanya Biological Station in the Montseny Mountains (northeast Spain), 40 km north-northeast from Barcelona and 27 km inland from the Mediterranean coast. Climate is montane Mediterranean. Annual precipitation at La Castanya, at an elevation of 700 m, averages 870 mm, falling mostly as rain. There is a large year to year variability in both the annual amount and the monthly distribution of precipitation. On average, rainfall is highest in spring and autumn and lowest in summer. However, the intensity and duration of summer drought are often mitigated by convective storms. Owing to the strong relief of the area, temperatures are highly dependent on aspect. Mean annual air temperature at this elevation is estimated to be 9–10°C on north-facing slopes and 13–14°C on south-facing slopes.

The bedrock is composed of low-grade metamorphic schists. Slopes are very steep (30°–35°). The soils are Dystric Xerochrepts of sandy-loam texture and high stone content. On north-facing slopes, soils are shallow, the compact bedrock lying at only 0.4–1.5 m from the surface. On south-facing slopes, soils are usually somewhat deeper. Pure holm oak stands cover most of the area below an elevation of 1000–1200 m. These forests were intensively coppiced for charcoal production until about 35 years ago, and multistemmed trees make up a large fraction of the present tree population of most stands.

Holm oaks were sampled from a mesic and a xeric site at La Castanya. The mesic site is a high-quality stand on a permanent plot of 0.23 ha, where intensive studies on biomass, primary production, and nutrient cycling have been conducted (Ferrés et al. 1984; Terradas et al. 1980). The plot lies at the base of a north-west-facing slope, at an elevation of 665 m. Slopes within the plot

TABLE 1. Characteristics of holm oak stands from the mesic site and the xeric site

	Site	
	Mesic*	Xeric
Canopy height (m)	9–12	6–8
Density (stems/ha)	2010	1814
Proportion of single-stemmed trees (%)	80	7
Basal area (m ² /ha)	26.6	16.3
Aboveground biomass (t/ha)	160	79

NOTE: Data refer to trees of dbh \geq 5 cm, tallied in a 0.23-ha plot in the mesic site and a 0.03-ha plot in the xeric site.

*From Ferrés et al. (1984).

are 7°–23°, gentler than the surrounding hillslopes. The plot is covered by a pure, closed stand of holm oak, whose major characteristics are shown in Table 1. The understory is very sparse. Part of the plot was cultivated in the past and, in contrast with most other stands in the area, about 80% of the trees are single-stemmed. Age of the canopy trees was unknown but was estimated at 60–90 years from current diameters and radial growth rates. The mesic character of the site was derived from the plot lying at the base of a steep slope, having a relatively high water availability, and with the eastern, southern, and western horizons at angles close to 30° from horizontal. The annual energy flux in global solar radiation measured above the canopy of this plot was only 65% of what would be received by an unobstructed horizontal surface at this location (Gracia 1983). In fact, ecophysiological studies in this plot did not find any strong water stress in holm oak leaves, even on hot summer days (Savé 1986).

The xeric site is located in a midslope position on a south-facing slope, at the same elevation as the mesic site. The xeric site is very steep (38°) and has a lower southern horizon (10°) than the mesic site. Tree density and basal area are lower than in the mesic site (Table 1). The tree layer (i.e., all trees \geq 5 cm dbh) of a 0.03-ha plot has a density of 1814 stems/ha, a basal area of 16.3 m²/ha, and an aboveground biomass of 79 t/ha. The stand is dominated by multistemmed trees, only 7% of the stems of the tree layer belonging to single-stemmed trees. The understory is more developed than in the mesic site, and it is dominated by *Erica arborea* shrubs 2–3 m high. Age of the resprouted holm oak stems was unknown, but the last thinning took place more than 25 years ago, as indicated by dating the resprouted stems of *E. arborea*. Though, as stated earlier, average soil depth is greater in the xeric than in the mesic site, this probably did not compensate for the much higher solar radiation received on the xeric site. Water stress is indeed higher in the xeric site, as revealed by the lower water potentials in holm oak leaves compared with the mesic site (R. Prat, personal communication).

Methods

The root systems of 32 single-stemmed holm oaks were excavated in the winter of 1985, and were a subset of an extended sample of 71 holm oaks from the same sites, all of which were processed for aboveground biomass data. Allometric equations for aboveground biomass were developed by Canadell et al. (1988) using this extended sample.

Twenty trees were excavated near the permanent plot in the mesic site, and 12 in the xeric site. Only those trees that had no neighbours of dbh $>$ 5 cm within a radius of 1 m were chosen, in order to

facilitate the identification of the root system of individual trees. Sample trees were selected to cover as wide a range as possible of dbh, tree height, and crown radius (Table 2).

We placed the emphasis on single-stemmed trees because the root systems of single-stemmed trees are free from the effects of repeated resprouting. Although, in principle, a single-stemmed tree could result from resprouting, we feel confident that our single-stemmed sample trees were derived from seed, since they lacked any enlargement of the stem base or the root crown, which occurs in resprouted trees. As the xeric site was dominated by multistemmed holm oaks, we also excavated the root systems of three such trees in that site, chosen to represent small, medium, and large individuals. This limited number of multistemmed sample trees is a reflection of the huge amount of labour needed to excavate their massive root crowns.

For each sample tree we measured dbh, diameter of the stem at 50 cm from the ground (d_{50}), tree height, and crown projection radius taken as the quadratic mean of two perpendicular radii. Sample trees were felled, fractioned into major components, and weighed in the field. Root systems were manually excavated up to an end diameter of 1 cm, to a soil depth of 1 m, or down to bedrock, whichever came first. The root systems were fractioned into roots thicker than 5 cm in diameter (root crown included) and roots between 1 and 5 cm in diameter, and their fresh weights were recorded. Subsamples of both above- and below-ground components were oven-dried at 60°C until constant weight.

Small roots were lost during the excavation process. Total biomass (living plus dead) of roots thinner than 1 cm were obtained by core samples of the soil in the mesic site. Thirteen random samples were taken in October 1984 with a cylindrical steel corer of 4 cm internal diameter hammered into the soil to a depth of 60 cm. Soil samples were first divided into 20 cm depth intervals and then bulked by depths. Roots were manually separated in the laboratory into three diameter classes: (i) <2 mm, (ii) 2–5 mm, and (iii) 5–10 mm. Dry weight was determined as described earlier. As the sampling method did not allow assigning the roots to individual trees, only a stand estimate of small-root biomass was possible.

The power (log–log) regression model was used to develop allometric equations for single-stemmed trees. Between-site differences in the various components of belowground biomass of single-stemmed trees were tested by an analysis of covariance (ANCOVA) (Abacus Concepts Inc. 1989). When the interaction was not significant ($p > 0.05$), the model was recalculated without it (adjusted ANCOVA). The differences in root:shoot biomass ratios between sites were tested by the Mann–Whitney test (SPSS Inc. 1986).

Results

Structure of the root system

A description of the rooting patterns of holm oak at the study sites can be derived from data obtained during the excavation of the root systems of 32 single-stemmed trees. A major portion of the belowground biomass in the sampled trees was located just below the trunk, in the root crown. This is a mass of woody tissue resulting from the more or less complete anastomosis of the basal parts of the main roots. Root crowns reached down to a variable depth, but they usually did not exceed a depth of 50–60 cm. Most of the excavated trees did not have a prominent taproot. Most of the roots that emerged from the root crown lay roughly parallel to the soil surface at depths from 20 to 60 cm, making up a well-defined rooting layer. This arrangement was most clearly seen in holm oaks from the mesic site that were rooted in shallow soils (Fig. 1A). At both sites, the root system was highly asymmetrical because most roots grew

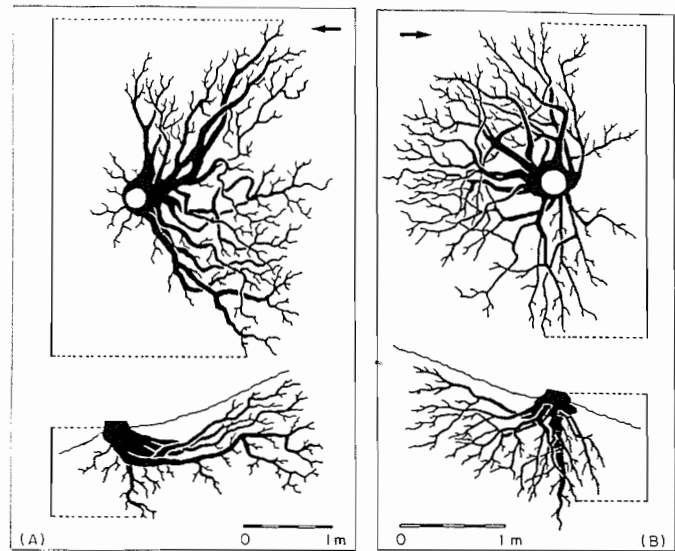


FIG. 1. Root systems (roots <1 cm in diameter) of single-stemmed holm oaks from (A) the mesic site and (B) the xeric site.

TABLE 2. Average, range, and standard error of dbh (stem diameter at 1.3 m), d_{50} (stem diameter at 50 cm), tree height (H), crown projection radius (CPR), and total aboveground biomass (TAB) for single-stemmed holm oaks for the two sampling sites at La Castanya

Variable	Mesic site ($n = 20$)			Xeric site ($n = 12$)		
	Range	Mean	SE	Range	Mean	SE
dbh (cm)	7.2–23.1	14.3	0.90	8.8–19.8	13.8	1.04
d_{50} (cm)	8.7–25.0	15.9	0.94	11.4–21.4	16.0	0.91
H (m)	4.4–12.8	7.8*	0.58	5.5–9.0	6.7†	0.31
CPR (m)	1.0–2.6	1.7‡	0.11	1.5–2.7	2.0†	0.11
TAB (kg)	15.6–237.4	81.7‡	12.78	28.3–195.5	83.6	13.94

* $n = 17$.

† $n = 11$.

‡ $n = 18$.

upslope (Fig. 1). Roots with a diameter >1 cm did not usually extend more than 2.5 m away from the trunk, but sometimes we found them up to 4.5 m from the trunk. The horizontal extension of the whole root system, i.e., including roots thinner than 1 cm, is unknown.

Vertically oriented roots tapered quite rapidly. Thus we feel that only a minor part of the root system was left out by restricting the excavation to 1 m depth, particularly so on the mesic site. On the xeric site some trees had a few roots beyond 1 m depth (Fig. 1B). While such roots probably accounted for only a few percent of total belowground biomass, they could have an important role in providing the tree with water during drought periods. Roots extending out horizontally from the root crown were often highly contorted and convoluted, probably due to the high stone content of these soils.

Root grafts were occasionally observed between roots of the same tree, but never between roots of different trees. However, only trees that had no neighbours in a radius of about 1 m were excavated. The lack of root grafts in holm oak is consistent with Keeley's (1988) hypothesis that root grafts would be adaptative in sites where physical support is not adequate, and are thus not expected to be common in Mediterranean-type ecosystems. Hoffmann and Kummerow

TABLE 3. Large-root biomass (y) allometric equations for single-stemmed holm oak trees at La Castanya

Equation No.	y^*	x	a	b	r^2	$S_{y,x}$	n
Total trees							
1	Total [†]	dbh	-1.047	2.191	0.73	0.166	32
2	Roots > 5 cm [‡]	dbh	-1.188	2.139	0.64	0.192	31
3	Roots 1-5 cm	dbh	-1.145	1.897	0.67	0.162	31
4	Total [†]	d_{50}	-1.687	2.623	0.79	0.145	32
5	Total [†]	TAB	-0.212	0.894	0.83	0.118	30
Mesic site							
6	Total [†]	dbh	-1.393	2.451	0.81	0.159	20
7	Roots > 5 cm [‡]	dbh	-1.563	2.422	0.70	0.201	19
8	Roots 1-5 cm	dbh	-1.417	2.093	0.75	0.150	19
Xeric site							
9	Total [†]	dbh	-0.448	1.734	0.71	0.136	12
10	Roots > 5 cm [‡]	dbh	-0.714	1.790	0.70	0.146	12
11	Roots 1-5 cm	dbh	-0.835	1.688	0.63	0.159	12

NOTE: The model is $\log y = a + b \log x$. Log indicates logarithm to base 10. dbh, stem diameter at 1.3 m (cm); d_{50} , stem diameter at 50 cm (cm); TAB, total aboveground biomass (kg).

*Large-root biomass was measured as kilograms dry weight. Sizes of roots refer to diameter.

[†]Biomass of roots with diameter > 1 cm plus root crown.

[‡]Root crown included.

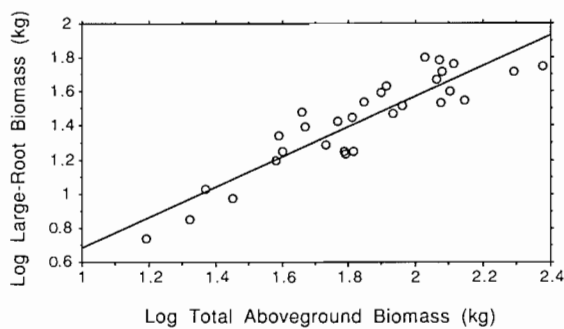


FIG. 2. Regression of large-root biomass (LRB) on total aboveground biomass (TAB) for single-stemmed holm oaks. The equation is $\log \text{LRB} = -0.212 + 0.894 \log \text{TAB}$; $r^2 = 0.83$.

(1978) found root grafts in only one out of nine shrub species excavated in the Chilean matorral.

Tree dimensions

Aboveground dimensions of the excavated single-stemmed holm oaks are summarized in Table 2. The range of dbh for these trees was 7–23 cm. Mean dbh did not differ between the mesic and xeric sites (Student's t , $p = 0.74$). Mean tree height was 1.1 m higher in trees from the mesic site, though the difference was not significant (Student's t , $p = 0.14$), even after removing the effect of dbh by ANCOVA (adjusted ANCOVA, $p = 0.23$). Mean crown projection radius was slightly higher in the xeric site (Student's t , $p = 0.09$), a difference that became highly significant when the effect of dbh was removed (adjusted ANCOVA, $p = 0.011$). Broader crowns in the xeric site probably resulted from the more open canopy in this stand, a condition reflected in its lower stem density and, particularly, in its lower basal area than those of the mesic stand.

Allometric equations for single-stemmed trees

Predicting large-root biomass

Large-root biomass (i.e., roots with diameter > 1 cm plus root crowns) of the excavated single-stemmed holm oaks was

regressed against aboveground biomass and stem diameters (dbh and d_{50}).

The best prediction of large-root biomass was obtained using the total aboveground biomass of the tree as the independent variable; the corresponding allometric equation is given in Table 3. The log-log scatterplot between both variables shows a slight curvature (Fig. 2). A quadratic term added to the log-log regression is indeed significant ($p = 0.019$), though it only increases r^2 from 0.83 to 0.86 and it becomes nonsignificant ($p = 0.21$) if the two trees with the higher aboveground biomass are excluded. As medium-sized trees show substantial variation in their relationship of belowground to aboveground biomass (Fig. 2), it is possible that the significant quadratic equation results from the two larger trees in the sample having a relatively low large-root biomass for their dbh.

Though aboveground biomass was the tested variable with the highest predictive power for root biomass, its usefulness is limited because the aboveground biomass of an unfelled individual tree is unknown. Therefore, regressions (log-log) were developed using stem diameter as the independent variable. For all trees combined, both d_{50} and dbh gave a good fit to root biomass, d_{50} yielding a slightly higher coefficient of determination than dbh (Table 3). In an extended sample of holm oaks from the same sites, Canadell et al. (1988) also found d_{50} to be a better predictor of aboveground biomass than dbh. It is likely that d_{50} was more closely related to both above- and below-ground biomass than dbh because of the moderate stature of these trees (Table 2). In spite of this, we used the allometric regressions based on dbh to compute large-root biomass in holm oak stands because only dbh was available for every tree in our plot inventories.

Effects of site

Between-site differences in the various components of belowground biomass of single-stemmed trees were tested by ANCOVA using dbh as the covariate. For large-root biomass, trees from the mesic and xeric sites were different

TABLE 4. Dimensional characteristics of the three multistemmed excavated holm oak trees

Root crown perimeter (m)	Living stems		Belowground biomass (kg dry wt.)				Total aboveground biomass (kg)	Root:shoot ratio
	No. of stems (dbh > 5 cm)	Total basal area (cm ²)	Root crown	Roots > 5 cm diam.	Roots 1–5 cm diam.	Total		
3.60	7	548.3	317.4	81.9	71.3	470.6	244.9	1.92
2.08	4	371.1	89.4	30.8	23.4	143.6	171.5	0.84
1.55	3	247.6	51.2	9.2	31.2	91.6	106.9	0.86

after removing the effect of dbh (adjusted ANCOVA, $p = 0.022$). For trees of dbh < 20 cm, large-root biomass predicted from site-specific allometric regressions on dbh was higher in the xeric than in the mesic site (Fig. 3, Table 3; only one sample tree had a dbh > 20 cm). Differences between sites appeared to be restricted to small trees (Fig. 3). When the ANCOVA was repeated using only trees with dbh > 12 cm (i.e., those that contributed most of the stand biomass; $n = 24$), sites did not differ ($p = 0.21$).

Despite the significant between-site differences in the allometric regressions for large-root biomass and roots 1–5 cm in diameter, their predicted biomass for a given dbh were only moderately different. Therefore, we have included for simplicity a general allometric equation in Table 3, pooling all sample trees irrespective of site.

Regressions of aboveground biomass on dbh (log–log) also differed ($p < 0.05$) between the mesic and xeric sites (Canadell et al. 1988). At both sites, regressions of aboveground biomass on dbh changed little if only excavated trees were used instead of the full extended sample. Using the excavated trees, i.e., the same trees for which root biomass was known, aboveground biomass predicted from dbh was also higher in the xeric site for trees of dbh < 20 cm. Thus, for a given dbh, both aboveground biomass and large-root biomass were higher on average in the xeric site. The differences between both sites were smaller for aboveground biomass than for large-root biomass. In the mesic site, the regression coefficients (mean \pm SE) were 2.36 ± 0.16 for aboveground biomass and 2.45 ± 0.28 for large-root biomass; in the xeric site, respective values were 1.94 ± 0.27 and 1.73 ± 0.35 . Hence, these holm oaks do not display differences in the allometry of growth between roots and shoots at either site. As a consequence, root:shoot ratios should not vary markedly with increasing dbh, an expectation confirmed later.

Biomass of roots 1–5 cm in diameter was different, after removing the effect of dbh, between trees of the mesic and xeric sites (adjusted ANCOVA, $p = 0.038$), while differences in the biomass of roots > 5 cm in diameter (plus root crowns) were close to statistical significance (adjusted ANCOVA, $p = 0.060$).

Belowground biomass of multistemmed trees

Since only three multistemmed trees were excavated, allometric regressions were not derived for this kind of holm oak. Relevant characteristics for these three multistemmed trees are summarized in Table 4. The most prominent feature of the root systems of these trees was their huge root crowns. Root crowns accounted for 56, 62, and 67% of the large-root biomass of, respectively, the small, medium, and large multistemmed holm oaks. The largest tree had a root

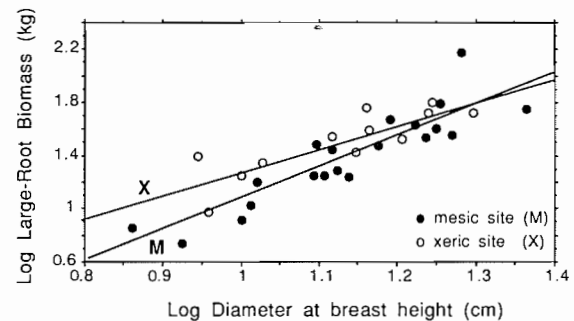


FIG. 3. Regression of large-root biomass (LRB) on dbh for single-stemmed holm oaks. Mesic site regression: $\log \text{LRB} = -1.393 + 2.451 \log \text{dbh}$. Xeric site regression: $\log \text{LRB} = -0.448 + 1.734 \log \text{dbh}$.

crown with a dry weight of 317 kg; such a weight has never been reported before for an individual root crown.

Root:shoot biomass ratios

Root:shoot ratios of single-stemmed trees were not linearly correlated with either dbh or d_{50} ($p > 0.22$ in both cases, pooling all sample trees; Fig. 4). When we pooled together all single-stemmed trees their mean root:shoot ratio was 0.41 (SE = 0.02, $n = 30$). In contrast, the three multistemmed holm oaks excavated had much greater root:shoot ratios, ranging from 0.86 and 0.84 for the small- and medium-sized trees, respectively, to 1.92 for the largest one (Table 4).

In the mesic site, root:shoot ratios (roots < 1 cm in diameter not included) of single-stemmed trees ranged from 0.23 to 0.66, with a mean of 0.37 (SE = 0.03, $n = 18$). In the xeric site, they ranged from 0.27 to 0.59, with a mean of 0.45 (SE = 0.03, $n = 12$). The root:shoot ratio was different between sites (Mann-Whitney test, $p = 0.031$).

Root biomass of the stands

Large-root biomass in the mesic stand was obtained from the allometric regression for this site (eq. 6 in Table 3), applied to the dbh inventory of the permanent plot for all stems with dbh > 5 cm. To obtain the stand biomass of roots 1–5 cm in diameter, eq. 8 of Table 3 was similarly used. Stand biomass of roots > 5 cm in diameter plus root crowns was found by determining the difference between the preceding stand estimates.

Large-root biomass for the permanent plot was 46.6 t/ha, of which 30.0 t/ha were roots > 5 cm in diameter plus root crowns and 16.6 t/ha were roots with a diameter of 1–5 cm. On average, bark accounted for 17.3% of the dry weight of roots > 5 cm in diameter plus root crowns, and 33.7% of roots in the 1–5 cm diameter class. Total (living plus dead) biomass of small roots (i.e., > 1 cm in diameter) was

TABLE 5. Small-root biomass (SRB, t/ha) (living plus dead) of the permanent plot at La Castanya

Soil depth (cm)	SRB for roots with a diameter of			Total SRB
	<2 mm	2-5 mm	5-10 mm	
0-20	2.0	2.2	3.8	8.0
20-40	1.3	3.1	2.5	6.9
40-60	0.7	0.8	0.0	1.5
Total	4.0	6.1	6.3	16.4

NOTE: Values are composite means of 13 soil cores taken in October 1984.

16.4 t/ha. Small-root biomass, split by soil depth and root diameter class, is shown in Table 5. Small-root biomass was dominated by the 2-5 and 5-10 mm diameter classes in nearly equal proportions, and it was concentrated in the 0-20 and 20-40 cm soil depths. Living plus dead fine roots (those with a diameter <2 mm) amounted to 4.0 t/ha (Table 5). Total belowground biomass in the permanent plot was 63.0 t/ha, 74% of which was large roots plus root crowns and 26% of which was small roots. Total above- and below-ground biomass was 223 t/ha, 28% of which was below ground.

The holm oak stand at the xeric site was dominated by multistemmed trees. As only three such trees were excavated, any estimate of the belowground biomass of this stand must be tentative. Our approach was to apply the mean root:shoot ratio (1.2) of the three excavated multistemmed trees to the predicted aboveground biomass of the multistemmed trees within the plot. The root biomass of the few single-stemmed trees was obtained through eq. 9 in Table 3 and added to that of multistemmed trees. Total large-root biomass (root crowns included) so estimated in the xeric site was 91.4 t/ha, compared with 79.1 t/ha of aboveground biomass. Assuming small-root biomass to be similar to that of the mesic site, total belowground biomass in the xeric site was 108 t/ha, or 58% of total tree biomass.

Discussion

Allometric relationships

Allometric regressions developed in this paper predict that single-stemmed holm oaks from the xeric site have a higher large-root biomass than trees from the mesic site, for a given dbh within the diameter range of sample trees. This finding is not necessarily related to a plastic response under increased water stress in the xeric site relative to the mesic site, since (i) this difference was due to the effect of the smaller trees, while the large-root biomass for trees of dbh > 12 cm did not differ significantly between sites and (ii) regressions for aboveground biomass also predict higher individual tree biomass in the xeric site.

Log-log regressions of tree biomass on dbh in the mesic site have a steeper slope and a more negative intercept than in the xeric site, for both above- and below-ground biomass. Hence, the regression lines predict a maximum difference between sites for the smallest trees (dbh = 7-11 cm), while they converge for trees of dbh 15-20 cm until crossing at a dbh of 21 cm. This holds true for both above- and below-ground biomass. The steeper slope of the regressions for trees of the mesic site means that a given change in dbh has a stronger effect on both the above- and below-ground

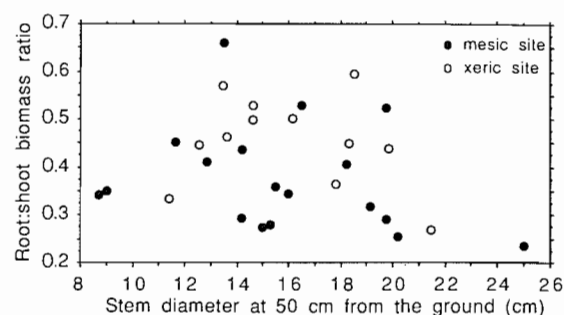


FIG. 4. Root:shoot biomass ratio against stem diameter at 50 cm for single-stemmed holm oaks.

biomass in a tree in the mesic than in the xeric site. This is mainly due to the smallest trees from the mesic site weighing less than those of the same dbh from the xeric site. Contrasting light conditions between both sites may be partly responsible for these findings. Small trees in the mesic site are more prone to be shaded out by dominant neighbours than their counterparts in the xeric site, because the mesic stand has a more closed canopy and receives much less solar radiation than the xeric stand. Light-starved suppressed trees are likely to have thin crowns and less above- and below-ground biomass than better illuminated trees of the same dbh, thus accounting for the differences between the mesic and xeric sites in weight of trees in this size class.

Santantonio et al. (1977) compiled allometric regressions (log-log) of large-root biomass (kg) on dbh (cm) for a number of tree species. From equations given in their Table 11, we have computed a mean slope of 2.44 (SD = 0.31) and a mean intercept of -1.34 (SD = 0.80) for 13 regressions of seven species of temperate coniferous trees (two other regressions were excluded because of their anomalous intercept values). Six regressions for temperate deciduous trees yielded a mean slope of 2.12 (SD = 0.22) and a mean intercept of -1.35 (SD = 0.35). Our general regression for holm oak (eq. 1 in Table 3) has a slope of 2.19 and an intercept of -1.05. Though arithmetic averaging of regression lines is not a sound statistical procedure, we think it is useful for the broad comparison we intend, particularly when the averaged regressions are rather similar, as is now the case. In the dbh range 10-20 cm, which contains most of our sample trees, values of large-root biomass predicted for holm oak are very close to those derived from the mean regression for coniferous trees, and about 2.5 times higher than those from the mean regression for deciduous trees.

Root:shoot biomass ratio

Single-stemmed holm oaks in our study had a mean root:shoot ratio of 0.41, with holm oaks from the xeric site having a significantly higher mean root:shoot ratio (0.45) than those from the mesic site (0.37). Thus, root:shoot values at both sites are higher than the range of 0.20-0.30 found in many temperate forest trees (Rodin and Bazilevich 1967; Santantonio et al. 1977), especially for the xeric site.

The difference in root:shoot ratios between our xeric and mesic sites probably arises from the lower availability of water and higher irradiance at the xeric site. Limited availabilities of water or nutrients favour allocation of photosynthate to roots, resulting in high root:shoot ratios (Bray 1963; Hirose and Kitajima 1986; Whittaker and Marks 1975), while light limitation favours allocation to shoots, lowering root:shoot ratios (Fitter 1986).

Though root:shoot ratios often decrease with increasing plant age or size as result of differences in the allometric growth of roots and shoots (Rutherford 1983), we have not detected such a trend in single-stemmed holm oaks. Instead, holm oaks of any diameter class exhibit a large variability in root:shoot ratio (Fig. 4), the coefficient of variation pooling all sample trees being 27%. As we are dealing with single-stemmed trees, repeated resprouting is not involved in this variability. Sources of the observed variation can be genetical or phenotypical. Among the latter, local soil depth has been demonstrated to influence root density of chaparral shrubs at very small spatial scales (Kummerow and Mangan 1981). Past and present growth conditions, and particularly the number and size of neighbours, are expected to strongly influence both above- and below-ground development of a tree, and are likely to affect its root:shoot ratio at any given time.

We have found no reliable published information on either large-root biomass or root:shoot ratios for Mediterranean trees. In his review on Mediterranean-climate oaks, Rundel (1980) gave root:shoot ratios from literature sources for six *Quercus* species, three trees and three shrubs. Only one of these three oak tree species was from a Mediterranean climate, this being holm oak from Le Rouquet in southern France (Lossaint and Rapp 1978). But the root:shoot ratio of 0.18 given for this site was obtained by excavating two 1-m² pits, thus ignoring root crowns that are a major component of belowground biomass in holm oak forests, and more so in multistemmed stands as Le Rouquet (Table 5).

Westman and Rogers (1977) found a mean root:shoot ratio of 0.53 in a fire-affected subtropical *Eucalyptus* spp. forest in Queensland, Australia, located outside the area of Mediterranean-type climate. Whittaker and Woodwell (1968) determined root:shoot ratios for young (mean age 33–34 years), multistemmed deciduous oak trees in the Brookhaven Forest (New York) that had resprouted after repeated fires. *Quercus coccinea* Muenchh. had a mean root:shoot ratio of 0.47 and *Quercus alba* L. 0.91. The first value is close to the mean for our single-stemmed holm oaks in the xeric site (0.45), while the second is close to our small- and medium-sized multistemmed trees.

More information is available on root:shoot ratios of Mediterranean shrubs. Fifteen shrub species from the Californian chaparral and the Chilean matorral had a mean root:shoot ratio of 1.03 (Kummerow 1981). Several studies have dealt with the belowground biomass of resprouting shrub oaks in Mediterranean-type climates. A 17-year-old garrigue of *Quercus coccifera* L. in southern France had a stand root:shoot ratio of 2.0 (Rapp and Lossaint 1981). In southern California, *Quercus dumosa* Nutt., a deep-rooted evergreen shrub, had a mean root:shoot ratio of 4.5 if the burl was included and 1.9 if it was not (fine-root estimates were included in both cases; Kummerow and Mangan 1981). In Arizona, one individual of *Quercus turbinella* Greene, also an evergreen shrub, had a root:shoot ratio of 3.2 including the burl, and 1.9 excluding it (Davis and Páse 1977). However, high root:shoot ratios are not only found in Mediterranean shrubs. In the Brookhaven Forest, *Quercus ilicifolia* Wangerh., a deciduous shrub, whose stems were on average 9 years old and had resprouted after repeated fires, had a mean root:shoot ratio of 6.3 (Whittaker and Woodwell 1968). Our arboreal multistemmed holm oaks

exhibit root:shoot ratios similar to those of many Mediterranean shrubs, though lower than ratios of many shrub oaks.

Biomass distribution in stands

The proportion of biomass allocated to belowground tissues by perennial plants usually increases as the environment becomes more severe (Rundel 1980). Thus, root systems may account for up to 90% of total plant biomass in many arctic plants and some desert shrubs (Bliss 1988; Caldwell and Fernández 1975; Rodin and Bazilevich 1967).

In our mesic site, a holm oak stand dominated by single-stemmed trees had 28% of its total tree biomass below ground. This is a relatively high-figure, but it still falls within the range of 15–35% commonly found in temperate forest ecosystems (Rodin and Bazilevich 1967); though according to Harris et al. (1980), root biomass of forest ecosystems generally accounts for 15–25% of total biomass. Thus, single-stemmed holm oak forests are not strikingly different from temperate forest ecosystems in their pattern of biomass allocation to above- and below-ground structures, at least when growing on a mesic site without major hydric stress during the dry season, and where trees have not been affected by coppicing, burning, or grazing.

A very different picture emerges when the multistemmed holm oak stand in the xeric site is considered. Through repeated resprouting after coppicing, current stems are much younger than the stools bearing them. Holm oak, a long-lived species, develops massive root crowns under this management regime, and belowground biomass keeps accumulating while aboveground biomass is harvested at each rotation. Belowground biomass in these multistemmed stands can exceed that above the soil.

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