Ann. For. Sci. 57 (2000) 803–810

Original article

Biomass of root and shoot systems of *Quercus coccifera* shrublands in Eastern Spain

Isabel Cañellas Rey de Viñas[a,*] and Alfonso San Miguel Ayanz[b]

[a] Dpto Selvicultura, CIFOR-INIA, Ap.8.111, 28080 Madrid, Spain
[b] Dpto. Silvopascicultura, E.T.S.I. Montes, Ciudad Universitaria, 28040 Madrid, Spain

(Received 12 October 1999; accepted 14 February 2000)

Abstract – Belowground and aboveground biomass of kermes oak shrublands (*Quercus coccifera* L.), an evergreen sclerophyllous species common in *garrigue* communities in Spain, have been studied by controlled excavation and harvesting. Aboveground biomass has been measured on 320 1-m^2 plots. Total biomass varies with age and ranges between 0.4 (7 months) to 2.8 kg m^{-2} D.M. (> 40 year), and leaf biomass increases with age until 6–8 years (0.56 kg m^{-2} D.M.) and then decreases and reaches a steady state around 0.35 kg m^{-2} D.M. (> 40 year). Total belowground biomass ranges from 34 to 81 mg ha^{-1} D.M., including rhizomes and lignotubers. Roots and rhizomes were concentrated in the uppermost 15 to 35 cm of the soils. The root area always exceeded the shoot area. The average dry weight root:shoot ratio was 3.5, ranging from 2.61 to 4.73. It is quite higher than that of other Mediterranean ecosystems.

Kermes oak / productivity / *Quercus coccifera* / shoot biomass / root biomass / root:shoot ratio

Résumé – **Biomasses des systèmes souterrains et aériens des garrigues de *Quercus coccifera* de l'Est de l'Espagne.** Les biomasses souterraines et aériennes de *Quercus coccifera*, espèce arbustive et persistante assez courante dans les garrigues espagnoles, ont été mesurées au moyen de techniques d'excavation et de coupe. La biomasse aérienne a été mesurée sur 320 placettes de 1 m^2 chacune. La biomasse totale change avec l'âge, en prenant des valeurs qui varient entre les 0.4 kg m^{-2} M.S. (à l'âge de 7 mois) à 2.8 kg m^{-2} (> 40 années). De même, la biomasse foliaire augmente avec l'âge jusqu'à 6–8 ans (0.56 kg m^{-2} M.S.), et diminue ensuite en prenant des valeurs très proches de 0.35 kg m^{-2} M.S. (> 40 années). La biomasse souterraine, y compris les rhizomes, varie entre 34 et 81 mg ha^{-1} M.S. Les racines et les rhizomes étaient concentrés dans la partie la plus superficielle du sol (jusqu'à 15–35 cm d'épaisseur). L'extension des racines débordait toujours de la projection au sol de la partie aérienne. La moyenne du rapport poids sec biomasse souterraine/biomasse aérienne était égale à 3.5 en variant de 2.71 à 4.73 ; ces valeurs sont un peu supérieures à celles trouvées pour d'autres écosystèmes méditerranéens.

chêne Kermès / production / *Quercus coccifera* / biomasse aérienne / biomasse souterraine / rapport biomasse souterraine/biomasse aérienne

1. INTRODUCTION

An accurate assessment of shrub biomass is important for the evaluation of the productivity of ecosystems, and their cycling of nutrients and carbon. In shrubland Mediterranean ecosystems, information on aboveground biomass, shrub size and structure is scarce, and relevant estimation methods are not very well known. There are only a few studies of this type in Spain [6, 7, 9, 37]. In contrast, there is more information in other countries and

---

* Correspondence and reprints
Tel. (34) 913 476 867; Fax. (34) 913 572 293; e-mail: canellas@inia.es

similar ecosystems [4, 5, 24, 35, 42]. This research concentrates on tree communities [12, 13, 38, 43, 44].

Compared with the relative abundance of information on aboveground standing crops, belowground information is limited. Root systems are an important fraction of plant biomass and play a significant role in forest net primary production [27]. This component is frequently more important than aboveground biomass in the mineral turnover process [15]. Although plant roots have been studied in their morphological and physiological aspects for a long time, little is known about characteristics such as the size of the roots systems, root growth rates under field conditions, interrelations among root systems of different plants species, root turnover rates, and so on.

Although scientists recognise the important role of these biomass fractions, the studies are scarce. This is at least partially due to the fact that roots, but even more so, entire root ecosystems, are difficult to observe, that has made it difficult to develop a reliable methodology of study. Comparison, generalisation and modelling of root systems, are very difficult to study due to the scarcity of data, and lack of precision in the methodology used. Thus there is no global theory which explains the dynamic and structural relations of root systems in natural ecosystems.

The shrubland Mediterranean American ecosystems are among the most studied [16, 19, 29, 30]. In Spain, studies about root biomass and its productivity were made on grasslands [18], and some forests [14]. However there is not much information on root systems in shrubland ecosystems [27, 28].

Kermes oak (*Quercus coccifera* L.) is undoubtedly one of the most important shrub species in the Mediterranean Basin, which covers more than 2 million hectares. It grows under typical Mediterranean climates, with a considerable summer drought period and on a great variety of soil types, either on acidic or basic parent materials [6]. In Spain, it is widely distributed along the Mediterranean coastal provinces and also in the interior. It plays a very important role in erosion control, especially after fire, as a fundamental fodder source for wildlife and livestock (mostly sheep and goats). It is also an important habitat for small game species, such as rabbits (*Oryctolagus cunniculus*) and red legged partridge (*Alectoris rufa*), which are often the most useful natural resources of these plant communities from the economic point of view [6, 7].

There is not very much information on above- and belowground biomass of Spanish *Q. coccifera* shrublands but there are more abundant data in other Mediterranean countries. Long et al. [23] and Rapp and Lossaint [34] presented the first data about biomass (shoot and root) and root and shoot ratios in the *garrigue* of Southern France. Kummerow et al. [22], Rambal [32] and Rambal and Leuterne [33] evaluated and analyzed the characteristics of the root systems of these French communities. Christodoulakis and Psaras [10] studied the root anatomy characteristic of Greek kermes oak shrublands; and Arianoutsou [1] and Tsiouvaras [41] have published some data about shoot and browse biomass.

The purpose of the present study is to contribute with quantitative data to the generally scarce knowledge of *Q. coccifera* root and shoot systems and their ratio.

2. MATERIALS AND METHODS

2.1. The study site

Our study was carried out in Valencia (eastern Spain) on eight kermes oak shrublands of different ages. The precise location of our experimental plots, and their main characteristics are shown in *table I.*

The climate could be included in the lower meso-Mediterranean belt and dry ombrotype, according to the Rivas Martínez bioclimatic typology [36]. The mean

Table I. Main characteristics of *Quercus coccifera* experimental plots at Valencia (Eastern Spain).

Plot	Age at ground base (years)	Longitude	Latitude	Elevation (m)	Height (m)	Slope (%)
Acentinela	0.6	0º43' W	39º29' N	360	0.10	15
Moratilla	3.2	0º54' W	39º27' N	805	0.38	5
La Nevera	4.2	0º47' W	39º32' N	450	0.50	30
Requena	4.8	1º00' W	39º25' N	830	0.40	5
La Parra	5.0	0º47' W	39º26' N	600	1.20	30
Venta Moro	7.7	1º20' W	39º28' N	950	0.60	10
Yátova	10.8	0º51' W	39º23' N	605	0.60	10
Hortunas	16.67	1º10' W	39º35' N	600	1.10	25
Buñol	> 40	0º45' W	39º24' N	725	1.55	5

annual rainfall is 500 mm, and the average temperature is 11.1 ºC. There is a possible frost period from late fall (November) to early spring (March), with an absolute minimum temperature of –12 °C. The soil belongs to the Calcic Cambisol–Calcaric Regsol association [11]. The potential vegetation is an evergreen sclerophyllous forest: *Bupleuro-Quercetum rotundifoliae* with *Pistacia lentiscus* [36]. However, due to fire, browsing and other human impacts, the current vegetation type is a continuous kermes oak *garrigue* (*Rhamno lycioidis-Quercetum cocciferae*).

2.2. Aboveground biomass

Aboveground biomass was measured on 160 (20 samples × 8 plots) 1-m^2 sub-plots for two years. Each plot was harvested to ground level and separated into different categories: kermes oak leaves, kermes oak stems and biomass of other species. Some additional variables were also measured: age (through the date of the last fire, number of kermes oak stems and dominant height). Oven dry matter percentage in a fraction was also determined (48 hours at 105 °C).

The annual increment of aboveground biomass was calculated dividing the corresponding total biomass by the years since the last fire.

The dependent variable was tested for normality of distribution using the Shapiro-Wilk statistic [39]. Data were used to select biomass equations through non-linear regression techniques (Marquardt method). The independent variable used was age. We considered the age of shrubland as a number of years since the last fire. The difference of aboveground biomass of the sites was tested by analysis of variance. Duncan’s test of range multiple has been used when there were significant differences between sites (95% confidence intervals). The statistical package SAS [39] was used for analysis.

2.3. Belowground biomass

The roots were harvested on 24 (3 samples × 8 plots) 1-m^2 plots subdivided into three soil layers: 0–15 cm, 15–30 cm and 30–45 cm, although reaching the last layer was not always possible by the frequent presence of large rocks. At 45 cm depth, further excavation proved to be nearly impossible. At this depth, fine roots were very rare and thicker roots were not very common. Rocks generally inhibited further vertical penetration.

Roots were extracted from the soil samples by means of sieving (2 mm) and sorted into diameter classes of small and fine roots (diameter < 5 mm) and of large roots (diameter > 5 mm) with rhizomes and lignotubers. We did not intend to separate living from dead fine roots because the criteria for such decision was not clear in field and the live-dead fine root percentage changes along the year [20, 22]. For this reason the percentage given by Kummerow et al. [22] about live and dead fine root biomass has been used. Finally, dry weight for each root fraction was measured and recorded.

The difference of belowground biomass of the sites was tested by analysis of variance. Duncan’s test of range multiple has been used when there were significant differences between sites (95% confidence intervals). The statistical package SAS [39] was used for analysis.

Roots of *Brachypodium retusum* Boiss., a grass frequent in the repeatedly burned plots, can be distinguished morphologically quite well from *Q. coccifera* fine roots, and thus be eliminated from the samples.

3. RESULTS AND DISCUSSION

3.1. Aboveground biomass

Results are presented and summarised in the *figures 1, 2* and *3* (where each point is the average of 20 data from 1-m^2 plots) and in the *table II.*

Table II. Predictive equations for total and leaf biomass (n = 20) filled by non linear regression in kermes oak shrublands.

Fraction	Parameter	SE(a)	SE(b)	SE(c)	*RMS*
Total biomass $Pt = a \cdot X^b$	a = 0.8339 b = 0.3406	0.0648	0.0290	-	0.0378
Leaf biomass $Pf = a \cdot X^b \cdot \exp(c \cdot X)$	a = 0.3189 b = 0.2866 c = –0.0253	0.0385	0.0889	0.0078	0.0044
Mean annual total biomass increment $IB = a \cdot X^b$	a = 0.5522 b = –0.4305	0.0283	0.0375	-	0.0025

*P*t: total biomass (kg m^{-2} D.M.); *P*f: leaf biomass (kg m^{-2} D.M.); *IB*: mean annual total biomass increment (kg m^{-2} yr^{-1} D.M.); *X*: Age (yr); *RMS*: residual mean square; SE(a), SE(b), SE(c): standard deviation of parameters.

Total aboveground biomass varies with age (*figure 1*) and ranges between 0.4 kg m^{-2} D.M. (7 months) and 2.8 kg m^{-2} (> 40 year). Our data basically behave like those presented by Arianoutsou [1], Long et al. [23], Mooney and Kummerow [21] and Rapp and Lossaint [34]. However, a faster initial biomass increase has been observed in our case, and though our maximum limit of total biomass accumulation (asymptote) seems to be somewhat smaller, maybe due to our lower rainfall and rocky calcareous soil.

Mean annual total biomass increment (*figure 2*) is high (about 0.6 kg m^{-2}) immediately after fire and during the next 6–8 years. Later it decreases and reaches a minimum of 0.006 kg m^{-2} at 40 years after fire.

Leaf biomass also increases with age (*figure 3*) until 6–8 years after fire (0.56 kg m^{-2} D.M.) and then decreases and reaches a steady state around 0.35 kg m^{-2}. These data are in agreement with those of Malanson and Trabaud [26] and those of Specht [40], thus confirming the possible interest of using rejuvenation treatments

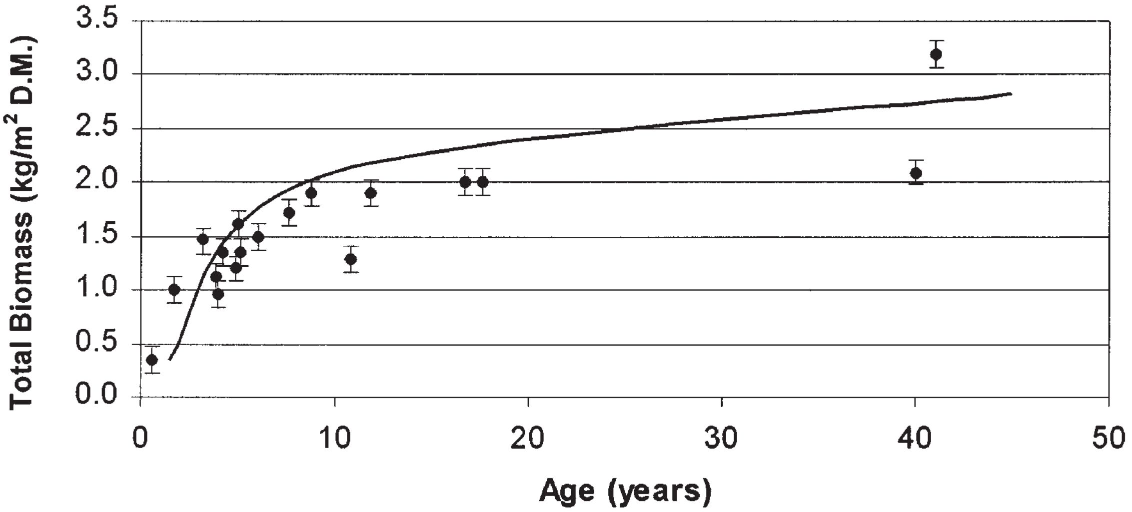

Figure 1. Relation between total biomass (kg m^{-2} D.M.) and age (years) of *Quercus coccifera* shrublands at Valencia (Eastern Spain). Vertical lines indicate mean confidence interval at 95%.

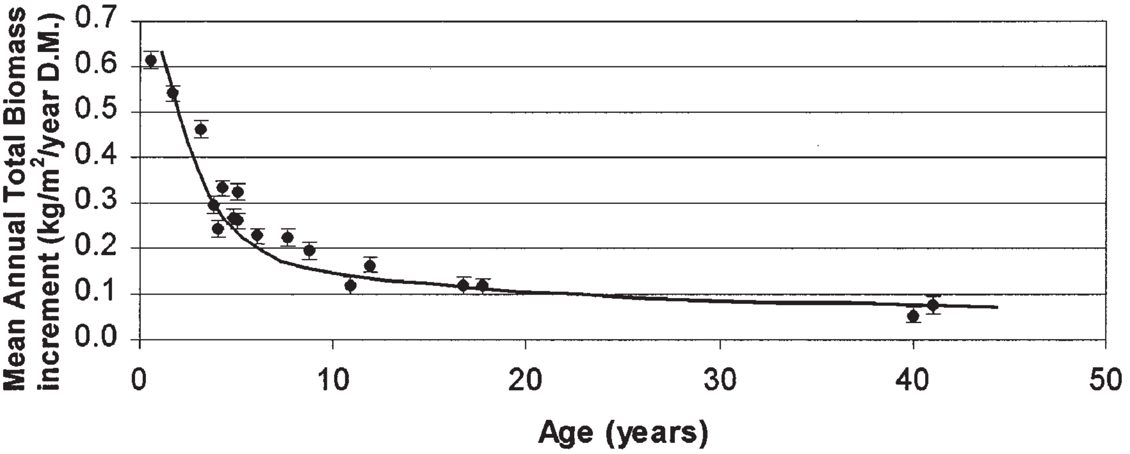

Figure 2. Relation between mean annual total biomass increment (kg m^{-2} yr^{-1} D.M.) and age (years) of *Quercus coccifera* shrublands at Valencia (Eastern Spain). Vertical lines indicate mean confidence interval at 95%.

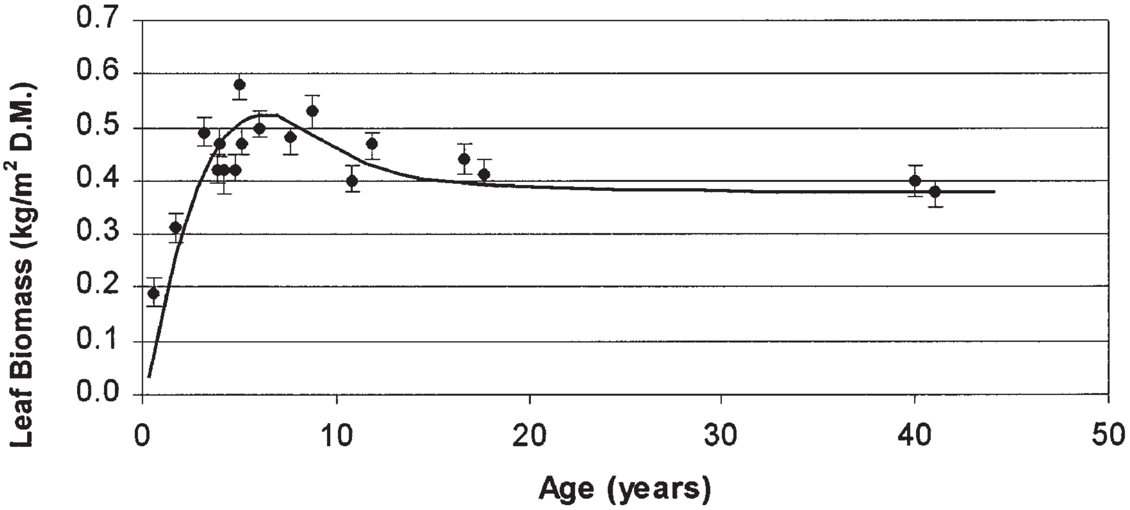

Figure 3. Relation between leaf biomass (kg m^{-2} D.M.) and age (years) of *Quercus coccifera* shrublands at Valencia (Eastern Spain). Vertical lines indicate mean confidence interval at 95%.

(prescribed fire, browsing, cutting) in order to increase the extent of browse production and nutritive value of kermes oak shrublands.

Statistically significant difference between the mean aboveground biomass and sites, at the 95% confidence level, has been founded. *Table V* shows the results of Duncan's test of differences between means of aboveground biomass.

3.2. Belowground biomass

Although our intensity sampling is bigger that the other studies carried out in this species [22, 34], the excavation of 24 m^2 plots of kermes oak shrublands is not enough to draw many far reaching conclusions. Nevertheless, the data obtained from this investigation elucidate the distribution of space between the roots of kermes oak and quantify its biomass.

The method used (direct excavation) allows us to determine the characteristics of roots and their colour, length, size and distribution in the soil stages, but this method needs a lot of physical work and time [3]. This makes it difficult to increase the study area.

The total root biomass for the excavated area is presented in *table III.* The dry weight values are subdivided into root size classes in each of the three soil layers. The standard deviation of mean is presented in brackets. Buñol plot, which is the oldest (> 40 years), has the highest value (81 mg ha^{-1} D.M.), while the youngest plot (2 years) has the lowest one (34 mg ha^{-1} D.M.). The average of the plots we analysed was 53 mg ha^{-1} D.M., next to some forest ecosystems [34]. The comparison of the contribution of the two biomass categories to the total demonstrates the relatively low biomass of small roots compared to that of larger roots, lignotubers and rhizomes. Small roots constituted 22.64% of total biomass and the large roots, including lignotubers and rhizomes, constituted 77.36% of total biomass.

While our data might look very high (*table IV*), they are in close agreement with studies in *Q. coccifera* shrublands of Kummerow et al. [22], Rambal [32] and Rapp and Lossaint [34].

The results of the analyses of variance for total belowground biomass show that there are significant differences between the youngest and oldest plots, so the biomass in Buñol was significantly greater than that in either of the most frequently burned stands. *Table V* shows the results of Duncan's test of differences between means of belowground biomass.

The small roots were concentrated near the surface. About 54 to 89% of this fraction was found in the uppermost 15 cm of the soil. Rambal [32] and Kummerow et al. [21] found that more than 50% of fine roots (diameter < 1 mm) were in the first 10 cm of the soil. Although the root distribution was mainly concentrated in the uppermost 20 cm, it also became clear that some roots penetrated even deeper through the cracks of the

Table III. Belowground biomass of *Q. coccifera* shrublands, in g m^{-2} (D.M.) (standard deviations in brackets).

Sites	Soil Depth cm	Diameter classes < 5 mm	> 5 mm	Total Biomass
Acentinela	0–30	632 (97)	2 823 (154)	3 455 (113)
Moratilla	0–15	844 (107)	3 815 (259)	4 659 (352)
	15–30	103 (42)	442 (81)	545 (106)
	total	947 (115)	4 257 (180)	5 204 (258)
La Nevera	0–30	961 (97)	4 151 (749)	5 112 (809)
Requena	0–15	897 (41)	1 930 (139)	2 827 (159)
	15–30	190 (36)	27 (22)	217 (15)
	30–45	68 (21)	394 (101)	462 (168)
	total	1 155 (72)	2 351 (252)	3 506 (313)
La Parra	0–15	1 513 (210)	2 574 (434)	4 087 (643)
	15–30	185 (30)	72 (30)	257 (39)
	30–45	58 (16)	86 (16)	144 (28)
	total	1 756 (223)	2 732 (461)	4 488 (684)
Venta Moro	0–15	795 (286)	3 914 (522)	4 709 (731)
	15–30	532 (255)	2 061 (384)	2 593 (633)
	30–45	137 (17)	242 (50)	379 (41)
	total	1 464 (521)	6 217 (940)	7 681 (1396)
Yátova	0–20	959 (65)	4 239 (818)	5 199 (851)
Buñol	0–15	985 (120)	5 735 (738)	6 720 (852)
	15–30	144 (17)	678 (65)	822 (75)
	30–45	192 (11)	395 (43)	587 (52)
	total	1 321 (146)	6 808 (825)	8 129 (961)

Table IV. Belowground biomass data in some Mediterranean shrublands.

Mediterranean communities	Belowground biomass mg ha^{-1} D.M.	References
Matorral (Chile)	20.0	[19]
Matorral (Chile)	113.0	[17]
Chaparral (California)	6.8	[17]
Chaparral (California)	18.8	[19]
Mallee (Australia)	13.7	[25]
Low shrublands (SW of Spain)	13.5	[27]
Garrigue (France)	72.0	[22]
Garrigue (France)	46.0	[34]
Garrigue (France)	80–120	[32]
Q. coccifera shrubland (Spain)	34–81	our data

Table V. Above- (S) and belowground (R) biomass and R/S ratios for *Quercus coccifera* shrublands at Valencia.

Sites	Aboveground biomass (S) mg ha^{-1} D.M.	Belowground biomass (R) mg ha^{-1} D.M.	Root/Shoot Ratio (R/S)
Acentinela	8.9^{a}	34.6^{a}	3.9
La Moratilla	11.0^{b}	52.0^{b}	4.7
La Nevera	13.0^{bc}	51.1^{b}	3.9
Requena	13.4^{c}	35.1^{a}	2.6
La Parra	14.8^{c}	44.9^{ab}	3.0
Venta Moro	17.2^{d}	76.8^{bc}	4.5
Yátova	19.4^{d}	52.0^{b}	2.7
Buñol	31.1^{e}	81.3^{c}	2.6
Average	15.1	53.5	3.5

$^{a\,b\,c\,d\,e}$: multiple comparison procedure (Duncan's test, 95%).

fissured limestone. Although these roots may be unimportant in their contribution to total biomass, physiologically they are probably highly important because they attenuate the effects of summer drought. The existence of a root system that exploits progressively deeper soil layers with the advance of summer drought has been reported for *Q. coccifera* by Kummerow et al. [21] and Rambal [32].

The larger conducting roots formed an intricate meshwork, and grafts were frequently observed at crossings not only between roots of the same shrub but also between individuals growing several meters apart from each other.

Table VI. Root:Shoot biomass ratios in some Mediterranean shrublands.

Mediterranean communities	root:shoot ratio	References
Matorral (Chile)	0.3–0.4	[17]
Matorral (Chile)	0.7	[30]
Frigana (Greek)	1.6	[25]
Chaparral (California, USA)	0.9–2.5	[30]
Chaparral (California, USA)	0.4–0.8	[21]
Garrigue ((Kermes oak) France)	2.0	[34]
Low shrublands (SW Spain)	2.3	[27]
Q. coccifera shrubland (Spain)	2.6–4.7	our data

3.3. Root:shoot biomass ratios

The importance of root:shoot biomass ratio for the assessment of carbon allocation to the root system is unquestionable [3, 30]. However, the root:shoot ratio is of questionable value in an environment that burns at more or less frequent intervals. Burls or lignotubers are clumps of secondary wood and development from a transition zone between hypocotyl and main root of seeding plant. The resprouting shrub species, like *Q. coccifera*, issued from large burls, are difficult to identify with respect to their age, and it is virtually impossible to define the proportions of contribution of root and stem issue.

With these restrictions in mind, root:shoot ratios from *Q. coccifera* shrublands were made (*table V*). Our data are in disagreement with Barbour's concept [2] that root systems from arid areas are not necessarily very large, but they agree with data on other *Quercus* shrubs like *Q. turbinella* (root:shoot ratio was 3.2) or *Q. dumosa* (3.8), both including lignotubers [20].

In other Mediterranean communities this ratio is usually smaller than ours (*table VI*). Perhaps this is the result of many years of wood-cutting for fuelwood and charcoal or repeated fires since the volume of burls increases with age and repeated harvesting of stems.

CONCLUSIONS

Total biomass varies with age and ranges between 0.4 (7 months) to 2.8 kg m^{-2} D.M. (> 40 year), and leaf biomass increases with age until 6–8 years (0.56 kg m^{-2} D.M.) and then decreases and reaches a steady state around 0.35 kg m^{-2} D.M. (> 40 year). Total belowground biomass ranges from 34 to 81 mg ha^{-1} D.M., including rhizomes and lignotubers. A comparison of the root densities in the soil beneath the eight stands reveals a surprising fact: quotas for small and large roots, the latter including lignotubers and rhizomes, did not seem to differ significantly between stands that are frequently burned, although the aboveground standing biomass differed widely (*table IV*).

The mean dry weight root-shoot (R/S) ratio ranged from 2.6 to 4.7 (average 3.5). These figures are higher than those of other Mediterranean ecosystems. This shows us the important adaptation of the *Quercus coccifera* shrublands to the Mediterranean region and its capacity to live in hard climatic and edaphic conditions.

The continuity of belowground biomass after the fire in this vegetation probably plays an important role in determining the optimum tactics to be adopted during succeeding cycles. The retention of a considerable amount of minerals in the belowground plant compartment [6, 8] which could be partially mobilised after a fire, allows competing in ecosystems that are usually very poor.

Acknowledgements: This work was funded by the Spanish National Institute for Agricultural Research (INIA), Research Project 8147. We give our acknowledgements to Dr. Irena Trukova (teacher of English in the Forest School, UPM) for checking this manuscript.

REFERENCES

[1] Arianoutsou M., Post-fire successional recovery of a phryganic (East-Mediterranean) ecosystem, Acta Oecol. 5 (1984) 387-394.

[2] Barbour M.G., Desert dogma reexamined: root/shoot productivity and plant spacing, Ame. Midl. Nat. 89 (1973) 41-57.

[3] Bohm W., Methods of studying root systems, Springer-Verlag, New York, 1979.

[4] Brown J.K., Estimating shrub biomass from basal stem diameters, Can. J. For. Res. 6 (1976) 152-158.

[5] Buech R.R., Rugg D.J., Biomass relations of shrub components and their generality, For. Ecol. Manage. 26 (1989) 257-264.

[6] Cañellas I., Ecología, características y manejo de matorrales *de Quercus coccifera* L. en España, Ph.D. Thesis E.T.S.I. de Montes, Madrid, 1993.

[7] Cañellas I., San Miguel A., Structure and browse production of kermes oak shrublands in Spain, in: Gaston A., Kernick M., Le Hoerou H.N. (Eds.), Proc. IVth International Rangeland Congress, Vol. I, Association Française de Pastoralisme, Montpellier, 1991, pp. 518-520.

[8] Cañellas I., San Miguel A., Biomasa del sistema radical de los matorrales de *Quercus coccifera* L. en el este de España, Investigaciones Agrarias, Sistema y Recursos Forestales 5 (1996) 189-200.

[9] Cañellas I., San Miguel A., Litter fall and nutrient turnover in kermes oak (*Quercus coccifera* L.) stands in Valencia (eastern Spain), Ann. Sci. For. 55 (1998) 589-597.

[10] Christodoulakis N.S., Psaras G.K., A contribution to the root study of the evergreen sclerophyllous anatomy of the primary root of *Quercus coccifera* L., Flora Morphol. Geobot. Oekophysiol. 180 (1988) 445-453.

[11] Commission of the European Communities, Soil Map of the European Communities (1:1.000.000), D.G.A. Luxembourg, 1985.

[12] Crow T.R., Common regressions to estimate tree biomass in tropical stands, For. Sci. 24 (1978) 110-114.

[13] Ek A.R., A model for estimating branch weight and branch leaf weight in biomass studies, For. Sci. 25 (1979) 303-310.

[14] Escarre J., Gracia C., Roda F., Terradas J., Ecología del bosque esclerófilo mediterráneo, Investigación y Ciencia 95 (1984) 69-78.

[15] Fogel R., Root as primary producers in below-ground ecosystems, in: Fitter A.H. (Ed.), Ecological Interactions in soil, Special Publication No. 4 of the British Ecological Society, Blackwell Scientific Publication, 1985.

[16] Hellmers M., Horton J.S., Juhren G., O'keefe J., Root systems of some chaparral plants in southern California, Ecology 36 (1955) 667-678.

[17] Hoffmann A., Kummerrow J., Root studies in the Chilean matorral, Oecologia 32 (1978) 57-69.

[18] Joffre R., Leira M.J., Rambal S., Fernandez R., Dynamique racinaire et extraction de l'eau du sol par des graminées pérennes et annuales méditerranéennes, Oecologia Plantarum 8 (1987) 181-184.

[19] Kummerow J., Structure of roots and root systems, in: Castri F. di, Goodall D.W., Specht R.L. (Eds.), Ecosystems of the world 11. Mediterranean-type shrublands, Elsevier Scientific Publishing Company, New York, 1981, pp. 269-288.

[20] Kummerow J., Mangan R., Root systems in *Quercus dumosa* Nutt. dominated chaparral in southern California, Oecol. Plant. 2 (1981) 177-188.

[21] Kummerow J., Montenegro G., Krause D., Biomass, phenology and growth, in: Miller P. (Ed.), Resource use by chaparral and matorral, Springer-Verlag, Berlin, 1981, pp. 69-96.

[22] Kummerow J., Kummerow M. , Trabaud L., Root biomass, root distribution and the fine-root growth dynamics of *Quercus coccifera* L. in the *garrigue* of southern France, Vegetatio 87 (1990) 37-44.

[23] Long G., Fay F., Thiault M., Trabaud L., Essais de détermination expérimentale de la productivité d'une garrigue à *Quercus coccifera*, Montpellier CNRS-CEPE, Doc. 39, 1967.

[24] Ludwing J.A., Reynolds J.F., Whitson P.D., Size-biomass relationships of several Chihuahuan desert shrubs, Am. Midl. Nat. 94 (1975) 451-461.

[25] Margaris N.S., Structure and dynamics in a phryganic (east Mediterranean) ecosystem, J. Biogeogr. 3 (1976) 249-259.

[26] Malanson G.P., Trabaud L., Ordination analysis of components of resilience of *Quercus coccifera garrigue,* Ecology 68 (1987) 463-472.

[27] Martínez F., Merino J., Evolución estacional de la biomasa subterránea del matorral del Parque Nacioanl de Doñana, VIII Bienal Real Sociedad Española Historia Natural, 1987, pp. 563-570.

[28] Martínez F., Merino O., Merino J., Aspectos metodológicos de la estimación de la productividad del sistema radical en matorral mediterráneo, Congreso Mundial del Bosque y Matorral Mediterráneo, Sep. Cáceres, 1988.

[29] Miller P.C., Resource use by chaparral and matorral, in: Billings W.D. (Ed.), Vol. 39, Springer-Verlag, New York Inc., 1981.

[30] Miller P.C., Ng E., Root-shoot biomass ratios in shrubs in southern California and Chile, Madroño 24 (1977) 215-223.

[31] Mooney H.A., Kummerow J., Phenological development of plants in mediterranean climate regions, in: Castri F. di, Goodall D.W. and Specht R.L. (Eds.), Ecosystems of the world 11. Mediterranean-type shrublands, Elsevier Scientific Publishing Company, New York, 1981, pp. 249-255.

[32] Rambal S., Water balance and pattern of root water uptake *by Quercus coccifera* L. evergreen shrub, Oecologia 62 (1984) 18-25.

[33] Rambal S., Leuterne J., Changes in above ground structure and resistances to water uptake in *Quercus coccifera* along a rainfall gradient, in: Tehnunen J.D. (Ed.), Plant response to stress, Springer-Verlag, Berlin, 1987, pp. 191-200.

[34] Rapp M., Lossaint P., Some aspects of mineral cycling in the *garrigue* of southern France, in: Castri F. di, Goodall D.W., Specht R.L. (Eds.), Ecosystems of the world 11. Mediterranean-type shrublands, Elservier Scientific Publishing Company, New York, 1981, pp. 289-301.

[35] Rittenhouse L.R., Sneva F.A., A technique for estimating big sagebrush production, J. Range Manage. 30 (1977) 68-70.

[36] Rivas Martínez S., Mapa de las series de vegetación de España, ICONA, Madrid, Spain, 1987.

[37] Robledo A., Rios S., Correal E., Estimación de biomasa en los matorrales de albaida (*Anthyllis cytisoides*) del suroeste de España, Pastos 20-21 (1991) 107-129.

[38] San Miguel A., Fernández A., Yagüe S., Ecuaciones para estimar la biomasa en pie en tallares de chopo a turno corto, Investigación Agraria, Producción y Protección Vegetal 3 (1988) 85-97.

[39] SAS® Institute Inc., SAS/Stattm User's guide, Release 6.03, Cary, USA, 1988.

[40] Specht R.L., General characteristic of Mediterranean-type ecosystems, in: Conrad E.G., Oechel W.C. (Eds.), Dynamics and Management of Mediterranean-type ecosystems, USDA, Gen. Tech. Rep. PSW-58, Berkeley, California, 1981, pp. 13-19.

[41] Tsiouvaras C.N., Long-term effects of clipping on production and vigor of kermes oak (*Quercus coccifera*), For. Ecol. Manage. 24 (1988) 159-166.

[42] Vora R.S., Predicting biomass of five shrub species in northeastern California, J. Range Manage. 41 (1988) 63-65.

[43] Whittaker R.H., Branch dimensions and estimation of branch production, Ecology 46 (1965) 365-370.

[44] Whittaker R.H., Woodwell G.H., Dimension and production relations of trees and shrubs in the Brookhaven forest, New York, J. Ecol. 51 (1968) 1-25.