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Aboveground biomass allocation and water content relationships in Mediterranean trees and shrubs in two climatological regions in Israel

Marcelo Sternberg[2,*] and Maxim Shoshany[1]
*[1]Department of Geography, Bar-Ilan University, Ramat Gan, 52900, Israel; [2]Department of Plant Sciences, Faculty of Life Sciences, Tel Aviv University, Tel Aviv, 69978, Israel; *Author for correspondence (e-mail: sterenm@mail.biu.ac.il; fax: +972 3 6409380)*

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Abstract

This study investigated the variation along basipetal gradients of the relationships between the foliage/wood allocation ratios of biomass and of water content, in Mediterranean trees and shrubs, at two different locations along a climatic gradient. Understanding of the biomass allocation and water relations in Mediterranean trees and shrubs provides useful information on growth patterns of these species, and on resource dynamics of these plant communities. Two experimental sites were selected along a climatological transect that runs from the foothills of the Judean Hills to the northern Negev desert in Israel. At each site, 16 quadrats of 10 × 10 m (eight on south-facing slopes and eight on north-facing slopes) were marked. The aboveground biomass of dominant tree and shrub species were estimated. Main branches of trees and shrubs were cut, their foliage and wood biomass were separately weighed, and their respective water contents were determined. The species studied included the evergreen sclerophylls, *Quercus calliprinos, Phillyrea latifolia* and *Pistacia lentiscus*, and the semi-deciduous species, *Cistus creticus, Coridothymus capitatus* and *Sarcopoterium spinosum*. The results indicated that the foliage/wood ratio decreased from the periphery of the crown to the interior of the trees and shrubs: foliage biomass and water were mainly limited to the top 30 cm of the crown in all studied species. Leaves had higher relative water contents than woody tissues in the upper part of the crown. However; when the whole tree or shrub was considered, the relative water content was found to be mostly allocated to the woody structures. The results are discussed in terms of biomass allocation in various life forms of the eastern-Mediterranean plant communities and how they are affected by slope aspect and climatic conditions.

Introduction

The spatial distribution of leaf area in trees and shrubs is a primary element of crown architecture; it exerts a strong influence on light availability within the crown and potentially affects growth (Beaudet and Messier 1998). The assessment of vertical and horizontal distributions of foliage, and their relationship to tree dominance, crown size, tissue water content, and habitat characteristics provides important insights into the mechanisms by which the crown uses solar energy in producing biomass, into nutrient cycles, and into the release of trace gases to the atmosphere (Belsky et al. 1989; Carreira et al. 1994). Among the major aspects of crown morphology, the foliage/wood biomass ratio, i.e., the ratio of leaf biomass to branch and stem biomass, is considered central (Assman 1970; Armand et al. 1993). Trees and shrubs with differing foliage/wood biomass ratios differ in their ability to respond to changes in environmental factors such as increased light intensity resulting from the removal or reduction of competing neighbors (Velazquez-Martinez et al. 1992; Vila and Terradas 1998). Foliage/wood ratio and water content can also serve as good indicators of the growth potential of individual trees and shrubs, and as an index of carbohydrate balance (i.e., the ratio of photosynthesizing tissue to aboveground respiring tissue) (Givnish

1995). The masses and surface areas of leaf and woody tissues are determinant factors in processes depending on: water loss by transpiration, photosynthesis rate, precipitation retention, evapotranspiration, light penetration into the crown, and soil shading. These parameters are also important in the dynamics of ecosystems, and particularly in the Mediterranean region, characterized as it is by high temperatures, excessive radiation and water stress (Mooney 1981; Nahal 1981). Studies have been conducted in forests and shrublands to quantify foliage and woody biomass distributions of individual trees (Vose 1988; Gillespie et al. 1994) and shrubs (Uso et al. 1997). However, few studies have been carried out in the eastern-Mediterranean region (Orshan 1983). This region is characterized by steep climatic gradients, leading to changes in composition and structure in the plant communities over short distances (Kutiel et al. 1995). In particular, the gradient along the transect through Israel, from the Mediterranean hills to the Negev desert, shows important variations in the structure and floristic composition of the vegetation (Kadmon and Danin 1997, 1999; Danin and Orshan 1999). The vegetation along this gradient is dominated by evergreen sclerophylls and semi-deciduous drought-tolerant species, which differ in their physiological and structural adaptations to abiotic stresses. Despite its importance for community structure and function, there is much uncertainty regarding the variation in the spatial distribution and quality of aboveground biomass in different types of vegetation, and also regarding regional variations in these parameters.

It has long been recognized that topography affects the solar radiation intensity at the surface; this, in turn affects temperature, habitat, soil moisture and nutrients, and all of these factors may affect the structure and composition of the vegetation (Pickett and Kempf 1980; Kirby et al. 1990; Klemmedson and Wienhold 1992; Oberhuber and Kofler 2000). In Israel, northern slopes receive lower solar radiation flux density than other aspects, resulting in lower evapotranspiration rates and lower daily maximal temperatures during summer water stress periods. In view of these differences, vegetation properties such as percentage cover, biomass, species composition and recovery rates after disturbance, differ among aspects (Kutiel 1992; Kadmon and Harari-Kremer 1999). In the present study of Mediterranean trees and shrubs at two different locations along a rainfall gradient, we investigated the variations in the relationships between slope aspect and crown biomass allocation, along basipetal gradients of foliage/wood biomass and water content ratios. We hypothesized that slope aspect would affect the patterns of crown biomass allocation and water content relations in Mediterranean trees and shrubs, and that these patterns remain constant along a climatic gradient.

The questions posed in this study were: 1) What are the distribution patterns of foliage and woody biomass, and of their respective water contents, within the crowns of Mediterranean trees and shrubs? 2) Does slope aspect affect foliage/wood ratios in various woody life form species in a climatic gradient?

A better understanding of biomass allocation and tissue water relations in Mediterranean trees and shrubs will provide useful information on the growth patterns of these species and on the resource dynamics of their communities. Furthermore, this information is important for biomass mapping, remote sensing and regional estimations of primary productivity in these areas.

Methods

The study sites

The study was carried out in two sites in Israel, differing in climatic and edaphic conditions. The first was in the foothills of the Judean Hills, at Ramat Avisur (34 ° 55′ E, 31 ° 39′ N), 388 m above sea level, on brown rendzina soil on Eocene chalk (soil nomenclature follows Dan et al. (1970)). The climate is Mediterranean, with a mean annual temperature of 19.8 °C (annual maximum 24.9 °C, annual minimum 14.7 °C) and mean annual rainfall of 450 mm. Winters are mild and rainy, summers hot and dry (at least five months of no rainfall). The vegetation in this area ranges from maquis (evergreen sclerophyllous trees and semi-deciduous shrubs with herb associations) to dwarf shrublands. Dominant species on the north-facing slopes are the tree *Quercus calliprinos* Webb., the shrub *Pistacia lentiscus* L. and the dwarf shrubs, *Cistus creticus* L. and *Sarcopoterium spinosum* (L.) Spach. On the south-facing slopes, the dominant species are the shrubs *Phillyrea latifolia* L. and *P. lentiscus*, and the dwarf shrub *C. creticus*.

The second study site was in the Goral Hills, near Lehavim (34° 45′ E, 31° 20′ N), 280 m above sea level, on light lithosol on Cenoman hard limestone and chalk (Dan et al. 1970). The mean annual temperature is 20.5 °C (annual maximum and minimum, 27.5 and 12.5 °C, respectively) and the mean annual rainfall, 250 mm. A dwarf-shrub type community has developed on the site, forming a steppe-like landscape with diffuse vegetation. Dominant species on the south-facing slopes are *Coridothymus capitatus* (L.) Lk. et Hoffm and *Thymelaea hirsuta* (L.) Endl., while *S. spinosum* and *Salvia dominica* L. were dominants in the north-facing slopes.

Species nomenclature follows Feinbrun-Dothan and Danin (1991).

Experimental design and sampling

Two south-facing slopes and two north-facing slopes were selected at each site. Within each slope, four 10 × 10 m quadrats were randomly selected by throwing a marker to fix the center of each quadrat. The quadrats were then marked, leading to total of eight sampling quadrats per aspect and a total of 16 quadrats per experimental site. The distance between quadrats was approximately 30 m. Similar sampling designs were applied at the Ramat Avisur and Lehavim study sites.

The vegetation was monitored in spring (mid-April), during the peak primary production season. The woody vegetation was classified and sampled according to physiognomic categories: dwarf shrubs (height < 0.5 m), shrubs (height 0.5–2.5 m) and trees (height > 2.5 m). Aboveground biomass and water content measurements were carried out in randomly selected shrubs and tree branches within each quadrat. Woody plant biomass of dominant species was measured by direct procedures. At Ramat Avisur, the dominant species studied on the south-facing slopes aspect were the evergreen sclerophylls, *P. latifolia* and *P. lentiscus*, and the semi-deciduous dwarf shrub *C. creticus*. The dominant species studied on the north-facing slopes included the evergreen sclerophylls *Q. calliprinos* and *P. lentiscus*, and the semi-deciduous dwarf shrub *C. creticus*. At Lehavim, the semi-deciduous dwarf shrub *C. capitatus*, was studied as dominant on the south-facing slope and the semi-deciduous dwarf shrub *S. spinosum* on the north-facing slope. Full descriptions of plant cover characteristics of the studied species will be presented elsewhere, but it is relevant to mention here that at Ramat Avisur the studied species on north-facing slopes formed 81.6% of the woody plant cover, while those on the south-facing slopes formed 92% of the total relative plant cover. At the Lehavim site, important differences were noted between the dominant species on the respective slopes: *S. spinosum* on the north, *C. capitatus* on the south.

Direct aboveground biomass estimations were obtained as follows: in each quadrat in Ramat Avisur, a representative main mature branch of each dominant tree and shrub species was harvested. Eight main branches (one per quadrat) were collected from *Q. calliprinos* (north-facing slope) and eight from *P. latifolia* (south-facing slope), and 16 main branches of *P. lentiscus* and *C. creticus*, which were present on both aspects (8 branches from north and 8 from south-facing slope, respectively) In Lehavim, a representative branch from each of three shrubs of the same species was harvested within each quadrat, i.e., from eight quadrats per aspect, 24 *S. spinosum* shrubs were harvested on the north-facing slopes and 24 *C. capitatus* shrubs on the south-facing slopes.

After harvest, the branches were brought to the laboratory and each was tightly enclosed in a big plastic bag, except for its base that was put in water for 24 hours at room temperature. Before putting the branches into the water containers, the first 3 cm of each base was re-cut to prevent the introduction of any air bubbles into the vessels. The plastic bag reduced evapotranspiration, enabling the branch and leaf tissues to reach full turgor. Afterwards, the plastic bags were removed and each branch was cut into 20-cm segments, starting from its upper end (Figure 1). The foliage and woody fractions of each segment were hand separated and their fresh weights measured to the nearest 0.01g. The samples were then dried for 3 days in an oven at 80 °C, and the dry weights of the foliage and woody samples were recorded at room temperature.

In the case of the dwarf shrubs, fresh and dry weights of leaf and woody biomass were recorded for the whole plant, as their canopy heights ranged between 20 and 60 cm.

Data analysis

Differences among species for biomass allocation and water content were studied by considering three different ratios and one estimate: The foliage/wood biomass ratio was based on the relationship between dry foliage biomass to dry wood biomass calculated for every 20 cm segment. Each ratio was estimated as the mean of eight branches as follows:

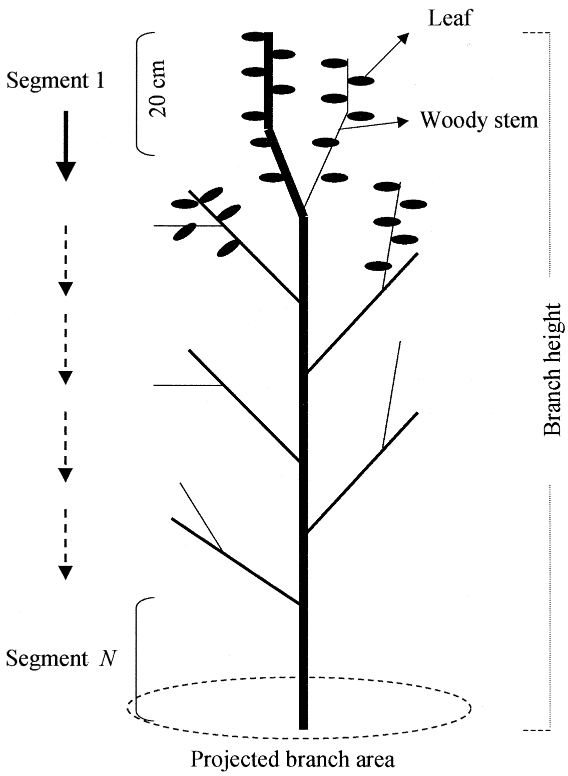

Figure 1. Schematic representation of a cut branch of a tree or shrub, and segments taken for biomass analyses.

$$(DLW/DWW)$$

where: DLW is dry leaf weight and DWW dry wood weight. The absolute foliage/wood water content ratio was assessed by considering the absolute difference in water content (g) between fresh and dry foliage, and that between fresh and dry woody structures, for each segment. Each ratio was also calculated as the mean over eight branches as follows:

$$[(FLW-DLW)/(FWW-DWW)]$$

where: FLW is the fresh leaf weight and FWW the fresh wood weight. The relative foliage/wood water content ratio, based on the proportions of water contained in leaves and woody structures in each biomass segment. The comparison between fresh and dry material provided an estimation of the relative water contents in live tissues. Each ratio was calculated as the mean over eight branches, as follows:

$$[(FLW-DLW)/FLW]/[(FWW-DWW)/FWW]$$

The relative water allocation to woody tissues was estimated as the proportion of the water content of each biomass segment contained in its woody structures. The estimate was obtained by multiplying the relative water content in the woody structures by their relative biomass in each biomass segment. Each segment was the result of the mean of 8 branches and calculated as follows:

$$\frac{[(FWW-DWW)/FWW]*[DWW/(FWW+DWW)]}{\{[(FLW-DLW)/FLW]*[DLW/(FLW+DLW)]+[(FWW-DWW)/FWW]*[DWW/(FWW+DWW)]\}}$$

Analyses of variance (ANOVA) were used to determine differences between relative water content and allocation in foliage and woody structures of the studied species (Sokal and Rohlf 1995). The analyses of data for each site were carried out with respect to two sampling sites (slopes), with eight quadrats as replicates.

Results

Relationships between foliage/wood biomass ratios and water content

Differences in biomass allocation between foliage and woody structures of the studied species are presented in Table 1. Most of the aboveground biomass of the species growing in both sites was allocated to the woody structures (from 72.4% to 90.9%), regardless of the aspect. At Ramat Avisur, *Q. calliprinos* and *P. latifolia*, the dominant trees on the north- and south-facing slopes, respectively, showed similar relations between foliage and woody structures. In *P. lentiscus* and *C. creticus* the allocation to leaves was about twice that in other species, but was not affected by the slope aspect. In Lehavim, similar allocations to those of *Q. calliprinos* and *P. latifolia* were noted for the dominant dwarf shrubs *S. spinosum* and *C. capitatus* (Table 1).

The results of analysis of variance for relative water content (RWC) differences and relative allocation of water content between foliage and woody structures of the studied species are presented in Table 2. The water distribution between leaves and woody parts was also studied for the main woody species that were collected (Figure 2). The results showed that relative water content (%) was significantly higher in leaves than in woody tissues in *S. spinosum*, *C. capitatus* and *Q. calliprinos* (Table 2, Figure 2a). A similar trend, although not significant, was noted in the remaining species studied. However, when the rela-

Table 1. Comparison between means of dry foliage and wood (%) for dominant species in north and south-facing slopes (mean ± standard error).

Species	North-facing slope		South-facing slope	
Ramat Avisur	Foliage biomass	Wood biomass	Foliage biomass	Wood biomass
Quercus calliprinos	12.0 ± 1.5	88.0 ± 1.5	—	—
Phillyrea latifolia	—	—	9.1 ± 0.7	90.9 ± 0.7
Pistacia lentiscus	21.8 ± 3.5	78.2 ± 3.5	21.0 ± 5.1	79.0 ± 5.1
Cistus creticus	21.6 ± 3.6	78.4 ± 3.6	27.6 ± 3.6	72.4 ± 3.6
Lehavim				
Sarcopoterium spinosum	12.0 ± 1.4	88.0 ± 1.4	—	—
Coridothymus capitatus	—	—	10.2 ± 0.7	89.8 ± 0.7

tive water content was considered in relation to the total tree or shrub biomass, we found that the proportion (%) of water allocated to woody tissues was significantly greater than that to leaves, as most of the biomass was invested in the former (Table 2, Figure 2b). This trend was common to all species studied, regardless of the aspect and site in the climatic gradient. In *C. creticus* and *P. lentiscus*, relative water content and allocation were jointly considered as no important differences between aspects were found (Table 1). Indeed, the relative water allocation to woody structures steadily increased from the periphery to the interior of the crown (Figure 3), and the relative proportion of water allocated to woody structures increased with the segment order (i.e., from the tip to the base).

Changes in the foliage/wood ratio, from the tip to the base of the branch, were studied for the dominant species in Ramat Avisur. In all species, the proportion of leaf biomass was greater in the upper 20 cm of the branch (segment 1; foliage/wood biomass ratio > 1), than in any other segment (Figure 4). In contrast, from segment 2 downwards (foliage/wood ratio < 1) the proportion of woody structures steadily increased. *Q. calliprinos* and *P. latifolia* showed similar patterns of foliage/wood ratio distribution, with the higher proportion of foliage biomass concentrated in the upper 20 cm of the canopy (Figure 4a, b). For example, *P. lentiscus* on north-facing slopes, showed a much higher proportion of leaf biomass in the upper 20 cm of the crown (segment 1) than those in *Q. calliprinos* and *P. latifolia*, with a ratio of 2.8 (Figure 4c). Similar results were observed in *P. lentiscus* growing on opposite slopes, although individuals were taller than on north-facing slopes (larger number of segments) (Figure 4d).

The relative foliage/wood water content ratio in *Q. calliprinos*, showed that foliage and woody structures

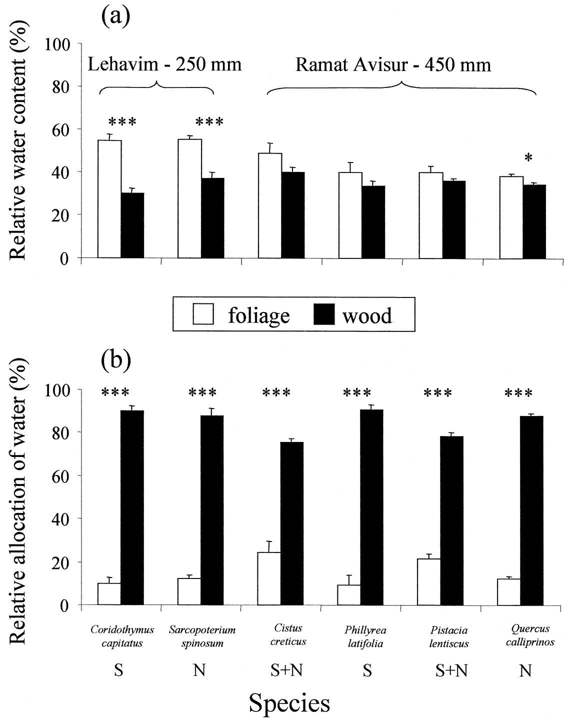

Figure 2. Differences in relative water content (%) in foliage and woody biomass (a) and their relative water allocation with respect to total biomass (%) (b), in woody species collected from Lehavim (*C. capitatus* and *S. spinosum*) and Ramat Avisur (*C. creticus, P. latifolia, P. lentiscus* and *Q. calliprinos*). Mean annual rainfall in Lehavim, 250 mm and Ramat Avisur, 450 mm. N, north-facing slope; S, south-facing slope. Error bars: ± s.e.m. Significance: $^{*}P < 0.05$, $^{***}P < 0.001$.

had similar proportions of water in the upper 160 cm of the crown (segments 1 to 8), the ratios being close to 1 (Figure 5a). The proportion of water in woody tissues increased from segment 8, towards the base of the tree. The foliage/wood absolute water content ratio showed a similar pattern to that observed for the foliage/wood biomass ratio, with a higher proportion of the absolute water content concentrated in the up-

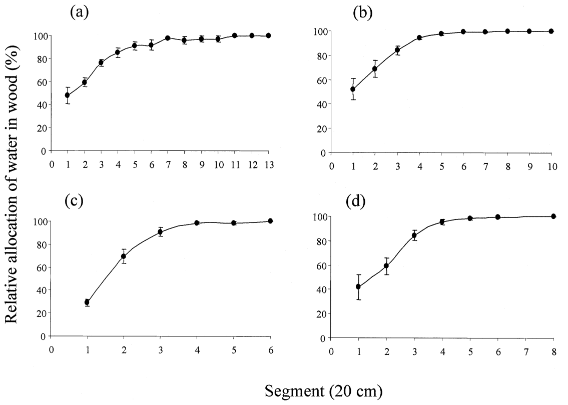

Figure 3. Changes with height in relative water allocation in woody structures, in *Q. calliprinos* (a), *P. latifolia* (b) and *P. lentiscus* (c and d) in north- and south-facing slopes, respectively. Error bars: ± s.e.m.

per 20 cm of the canopy (Figure 5b). Results for the foliage/wood water content ratio in *P. latifolia* showed a higher proportion of water in foliage in the upper 80 cm of the crown (Figure 5c), with the proportion of water in woody structures increasing from segment 4 downwards, towards the base of the shrub. The foliage/wood absolute water content ratio also showed more water in the upper 20 cm, but decreasing towards the base of the shrub (Figure 5d).

The effects of slope aspect on the foliage/wood relative and absolute water content ratios of *P. lentiscus* were compared (Figure 6). Individuals of this species on the south-facing slopes were bigger than those on north-facing slopes, as indicated by the larger number of segments (eight vs. six). The foliage/wood water content ratios showed similar patterns in individuals from both aspects (Figure 6a, c). The proportion of water in leaves decreased from the top to the base of the shrub, but showed a peak within the top 60 cm of the crown (Figure 6a, c). The foliage/wood absolute water content ratio showed similar patterns to those for the foliage/wood biomass ratio, regardless of their aspect (Figure 6b, d). However, the absolute amount of water found in leaves of the upper crown of shrubs on north-facing slopes, was greater than that in those on south-facing slopes (2.8 vs. 0.9; Figure 6b, d).

Discussion

This is the first study which provides data on foliage/wood biomass and water ratios in woody species, of eastern-Mediterranean plant communities, growing at two climatically differing sites in Israel. In contrast to our original hypothesis, the results showed that foliage/wood biomass and water ratios in woody species remained generally constant regardless of any effects of the slope aspect. Previous studies in the Mediterranean region, have found that plant cover, and species composition and richness significantly differed between north- and south-facing slopes (Nevo 1995; Kutiel 1992; Kadmon and Harari-Kremer 1999; Kutiel and Lavee 1999). The higher solar radiation on south-facing slopes induced changes in soil properties such as soil surface temperature, soil moisture and evapotranspiration and consequently influenced the vegetation developing at the sites. This phenomenon was also found true in the Alps, where the interaction between soil condition and topography affected tree growth (Oberhuber and Kofler 2000). However, our present results show that certain morphological parameters such as the relations between foliage and wood, and their distribution through the crown were similar for the various studied species and slope directions. The results also showed that the foliage/wood biomass ratio provided a good estimator of the foliage distribution within the crowns of the studied species. In most species, a greater proportion of leaves was found within the outermost 20 cm of the crown, and this peripheral foliar layer around the crown is the main converter of solar energy in forming aboveground biomass. The foliage/wood biomass ratio was inversely related to the distance from the outer part of the crown towards the base of the tree or shrub, which suggests that trees and shrubs tend to maximize the light availabile to the lower crown foliage by minimizing self-shading, as light intensity steadily declined from the periphery to the interior of the crown.

The higher relative content of water in leaves than in woody tissues, observed in the upper part of the crown, provided an important insight into the distribution of water within the crown. However, for the whole tree or shrub, the water content was mostly concentrated in the woody structures and was inversely allocated from the peripheral foliar layer to the interior of the crown (Figure 3).

These results are also important for interpreting reflected radiation from vegetation layers as recorded in satellite images. Understanding the pattern of leaf height distribution allowed significant improvement in modeling radar backscattering from these layers and wide regional mapping of biophysical vegetation properties from satellite data (Shoshany 2000). Such

Table 2. Results of one-way ANOVA for relative water content differences and relative water allocation between foliage and woody structures of dominant species at Ramat Avisur and Lehavim sites. Significant differences ($P < 0.05$) are indicated in boldface type.

		Relative water content		*Rel. water allocation*	
Species	df	*F*	*P*	*F*	*P*
Ramat Avisur					
Cistus creticus	1,15	2.55	0.125	**189.8**	**< 0.001**
Phillyrea latifolia	1,15	1.43	0.259	**5113**	**< 0.001**
Pistacia lentiscus	1,15	2.24	0.148	**184.8**	**< 0.001**
Quercus calliprinos	1,15	**6.23**	**0.032**	**1326**	**< 0.001**
Lehavim					
Coridothymus capitatus	1,23	**54.3**	**< 0.001**	**6075**	**< 0.001**
Sarcopoterium spinosum	1,23	**33.1**	**< 0.001**	**1475**	**< 0.001**

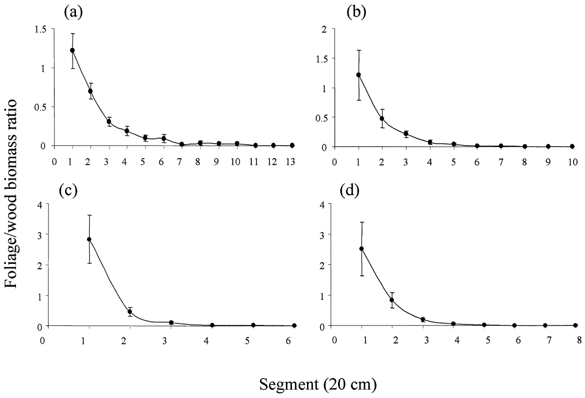

Figure 4. Changes with height in foliage/wood biomass ratio, in *Q. calliprinos* (a), *P. latifolia* (b) and *P. lentiscus* (c and d) in north and south-facing slopes, respectively. Error bars: ± s.e.m.

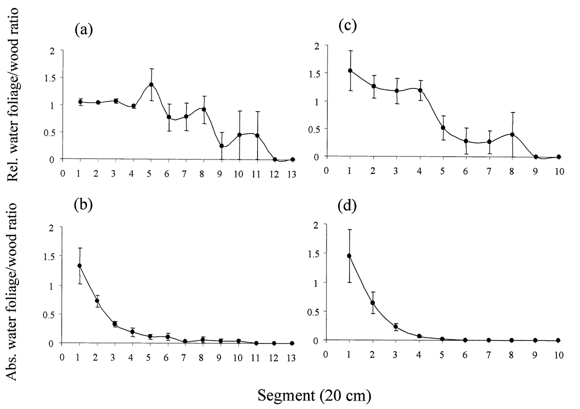

Figure 5. Changes in relative and absolute water foliage/wood ratio with height in *Q. calliprinos* (a and b) and in *P. latifolia* (c and d), respectively. Error bars: ± s.e.m.

application may contribute to the understanding of relationships between ecosystems structure and their functioning (Running et al. 1994; Asner et al. 1998a; Shoshany et al. 2000).

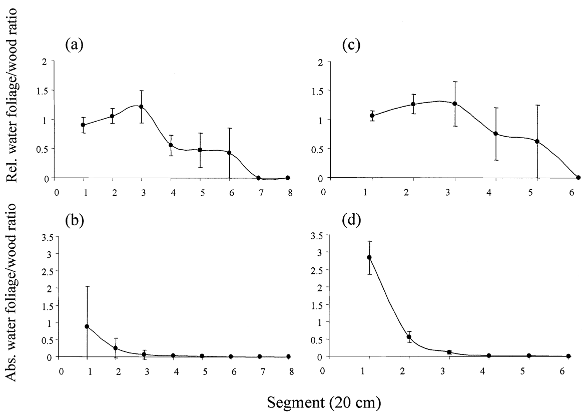

Figure 6. Changes in relative and absolute water foliage/wood ratio with height in *P. lentiscus* in south- (a and b) and north-facing slopes (c and d), respectively. Error bars: ± s.e.m.

In conclusion, the studied species showed similar patterns of biomass allocation and distribution within their canopies. These patterns were not affected by slope aspect nor by differences in location along the climatic gradient. We assume that this pattern of biomass and water allocation is "optimal" under water stress conditions such as those noted at the study sites. Since most of water is allocated to woody tissues, these could serve as water reservoirs for woody plants growing in water-deficit environments. Research on water content changes in leafy and woody structures through the seasons should provide further understanding of biomass production and water dynamics in plant tissues of Mediterranean woody species, and how variation in vegetation structure affects the functional characteristics of Mediterranean ecosystems. We are aware that water content at full turgor mainly indicates a physiological trait. Realized ecosystem processes such as photosynthesis strongly depend on seasonal variation in tissue and whole-plant water relations, particularly in water-limited regions such as the Mediterranean basin. However, the data presented in the present paper provide a basic idea of potential water relations under "optimal conditions" and should serve as a basis against which to compare the relationships under water-stress conditions.

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