

# Influence of slope aspect on Mediterranean woody formations: Comparison of a semiarid and an arid site in Israel

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This study investigates the effects of slope aspect on plant community characteristics such as plant cover, species composition and above-ground biomass production in Mediterranean trees and shrubs in two climatological regions. Two experimental sites were selected in a climatic gradient that runs from the foothills of the Judean Hills to the northern Negev desert in Israel. In each site, 16 quadrats of 10 m × 10 m (eight south-facing and eight north-facing slopes) were established and the vegetation was recorded. Dominant tree and shrub species were measured using allometric parameters of area and volume, and representative branches were cut and weighed. Species studied were *Quercus calliprinos*, *Phillyrea latifolia*, *Pistacia lentiscus*, *Cistus creticus*, *Coridothymus capitatus*, and *Sarcopoterium spinosum*. The results showed that slope aspect had significant effects on the composition, structure and density of the plant communities developing in both sites. Vegetation structure within a site changed significantly in the short distance separating the north and south-facing slopes, and that pattern remained generally constant when comparing the two sites along the rainfall gradient. The data collected here provides new insight into the slope aspect effects on biomass allocation of different woody life forms of eastern Mediterranean plant communities.

**Key words:** above-ground biomass; aridity; plant cover; productivity; rangelands; species composition.

## INTRODUCTION

Despite the importance of the Mediterranean vegetation to earth atmosphere energy budgets (Running *et al.* 1995; Sellers *et al.* 1996) and to ecosystem functioning, there is not much empirical data regarding its spatial distribution properties and its biomass characteristics. This situation is, to a large extent, due to technical difficulties in collecting detailed plant biomass data in the field and in producing regional data sets. A new field methodology is presented here combining detailed measurements of individual branches and the

extrapolation of this data to the whole plant by utilizing generalized descriptors of the canopy structure and geometrical models.

The vegetation dynamics of most Mediterranean ecosystems can be described as a shifting mosaic of patches in different stages of development (Quezel 1981; Kruger *et al.* 1986). This patchwork may result from the interactions between differential timing of local disturbances, spatial and temporal heterogeneity or result from competitive interaction between species (Henkin *et al.* 1998a; Schimel *et al.* 1991; Patten & Ellis 1995). The level of spatial heterogeneity is related to the patchy distribution of resources, whereas temporal heterogeneity is largely linked to high seasonality in the availability of resources (Goldberg & Novoplansky 1997). Within this regional characterization, the influence of slope aspect has an important effect on the spatial distribution characteristics of the vegetation (Kutiel 1992). In the Mediterranean basin region, south-facing slopes receive higher solar

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radiation thus affecting temperature, soil moisture, nutrients and soil aggregation processes which, in turn, affect the vegetation (Klemmedson & Wienhold 1992; Olivero & Hix 1998; Kutiel & Lavee 1999). In contrast, north-facing slopes generally receive lower solar radiation flux density, resulting in lower evapotranspiration rates and lower daily maximal temperatures during summer water stress periods. These differences are significant in Mediterranean plant communities where water availability is an important limiting factor. In view of favorable growing conditions in north-facing slopes in Mediterranean basin ecosystems, it is possible to hypothesize that plant community characteristics such as percentage cover, biomass, volume and density would be greater in this aspect than in opposing slopes.

Plant structure and composition also change along climatic gradients (Whittaker 1975; Whittaker & Niering 1975). The gradient that runs in Israel from the Judean Mountains to the Negev Desert shows important changes in the structure and composition of the vegetation (Danin & Orshan 1999; Kadmon & Danin 1999), which are associated with climate changes, land use and a long history of human intervention through fire and grazing of domestic herbivores (Naveh 1990). Despite its importance, there is much uncertainty regarding the biomass of vegetation types and its regional distribution.

In the present study, we investigated the effects of slope aspect on above-ground biomass production in Mediterranean trees and shrubs in two climatological regions in Israel. We hypothesize that habitat conditions (reflected through slope aspect) will affect the biomass, structure and composition of the plant communities developing at the sites.

The questions addressed were: (i) Are the structure and composition of the woody plant communities affected by slope aspect in two different climatological sites? (ii) Does slope aspect affect above-ground biomass productivity in woody life forms at two contrasting rainfall sites? (iii) Are these differences expressed at the level of individual species?

Data gathered through this study will facilitate the research of vegetation variations due to slope aspect differences which, in turn, may contribute to the understanding of Mediterranean ecosystem

responses to disturbance and potential climate changes at a regional scale.

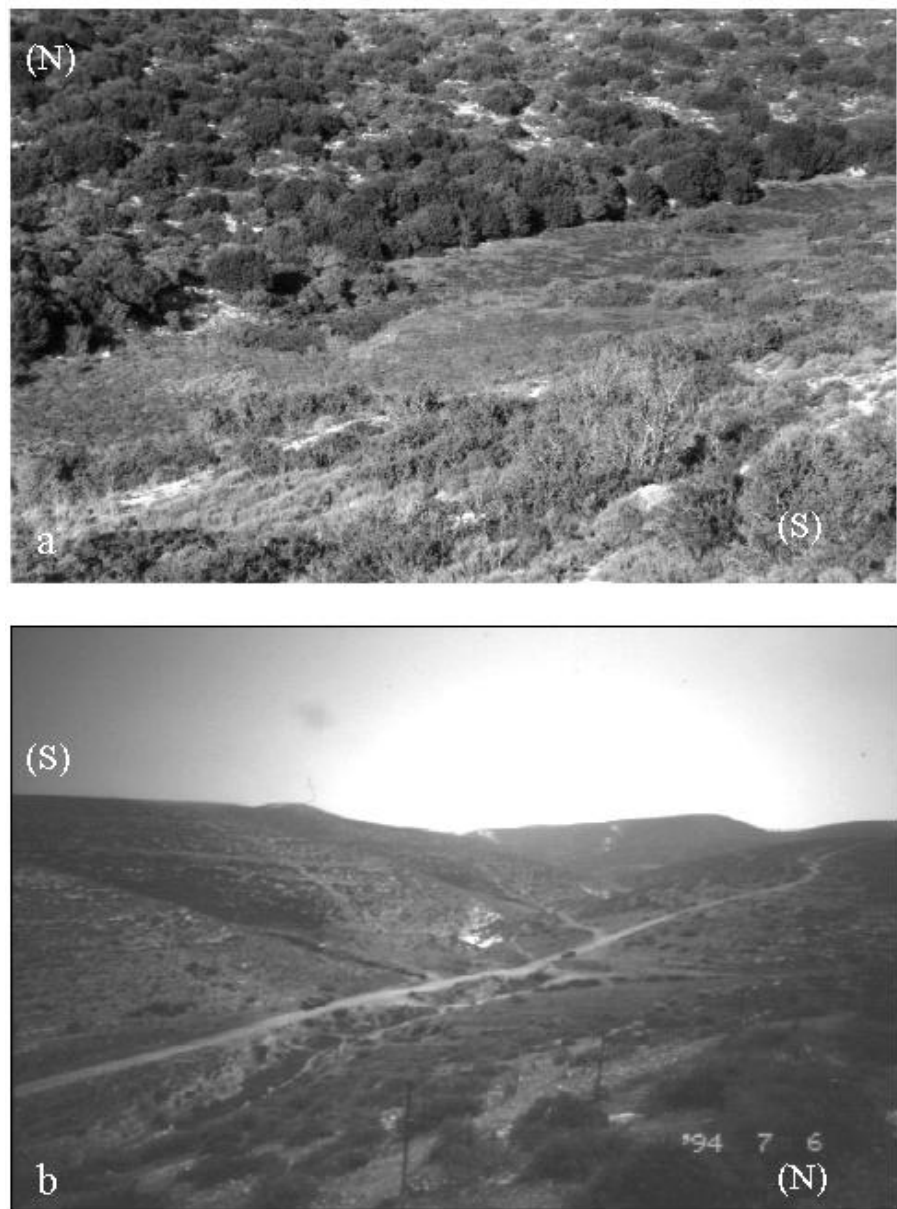
## METHODS

### The study sites

The study was conducted in two sites, which differed in climatic and edaphic conditions. The first site was at Ramat Avisur ( $34^{\circ}55'E$ ,  $31^{\circ}39'N$ ; Fig. 1a), which is located at the foothills of the Judean Hills, Israel, at 388 m a.s.l., on brown rendzina soil on Eocene chalk (Dan *et al.* 1970). The climate is Mediterranean, with a mean annual temperature of  $19.8^{\circ}C$  (mean maximum  $24.9^{\circ}C$  and mean minimum  $14.7^{\circ}C$ ) and a total annual rainfall of 450 mm, which falls mostly in winter (October/November to April). Summers are hot and dry. The site is in the Mediterranean phytogeographical region (Zohary 1973), and the vegetation developing in this area varies from maquis (evergreen sclerophyllous trees and semideciduous shrubs with herb associations) to dwarf shrublands. The growing season of the vegetation in the climatic gradient is closely associated with the distribution of rainfall. Germination of annuals and the regrowth of most perennials occur soon after the first rain.

The second site was located 35 km south at the Goral Hills, near Lehavim ( $34^{\circ}45'E$ ,  $31^{\circ}20'N$ ; Fig. 1b). The site was located at 280 m a.s.l., on light lithosol on Cenoman hard limestone and chalk (Dan *et al.* 1970). The mean annual temperature is  $20.5^{\circ}C$  (mean maximum and minimum,  $27.5^{\circ}C$  and  $12.5^{\circ}C$ , respectively) and the total annual rainfall is 250 mm. The site is in the Irano-Turanian phytogeographical region, but the vegetation is also represented by species from the Mediterranean and the Saharo-Arabian (desert) regions (Zohary 1973; Danin & Orshan 1999). A dwarf shrub type community has developed on the site, forming a steppe-like landscape with scatter vegetation.

Predominant wind direction is similar in both study sites. Winter winds are cool and humid, generally coming from the north-west direction (Mediterranean sea), whereas summer winds are dry and hot, predominantly arriving from the south-east direction (desert).



**Fig. 1.** Photographs of the study sites showing vegetation differences between slope aspects. (a) Ramat Avisur, representing Mediterranean maquis and (b) Lehavim, characterizing dwarf shrublands. (N) North-facing slope; (S) south-facing slope.

### Sampling design

The study was conducted by selecting two opposing hills at each site. Each hill included a south- and a north-facing slope. Within each slope, four 10 m × 10 m quadrats were randomly selected by throwing a mark that served as the center of each quadrat. The distance separating each quadrat was approximately 30 m. Quadrats were marked and led to a total of eight sampling quadrats per aspect and to a total of 16 quadrats per study site.

Vegetation was monitored in spring (mid April), during the peak season of primary produc-

tion. Within each quadrat, plant cover was estimated and perennial species composition inventoried by using four 10 m length transects placed on the edges of the quadrat. In each transect, a point was read every 20 cm, adding up to 50 points per transect, and a total of 400 points per quadrat. A point was read using a slender bar positioned exactly vertical to the ground (Müeller-Dombois & Ellenberg 1974). Relative plant cover (%) was calculated by excluding rock and bare ground cover. Woody vegetation was sampled according to life form categories; that is, dwarf shrubs (<0.5 m height), shrubs (>0.5 m <2.5 m height) and trees

(> 2.5 m height). Within each quadrat, tree and/or shrub density was estimated by the direct counting of all individuals present per category and species. Annual species were grouped into one category and considered in plant cover terms only.

Woody plant biomass of dominant species (higher plant cover) was measured by indirect and direct procedures. Indirect techniques included allometric variables, which were measured on randomly sampled dominant tree/shrub individuals. The variables included:

- 1 Total height, defined as the maximum vertical distance from the ground level to the highest point of the plant.
- 2 Crown diameter or crown width is the mean of the maximum crown diameter (horizontal) and the horizontal diameter orthogonal to the maximum diameter. Crown diameter is assumed as an estimator of the assimilative architecture (photosynthetic potential) of the tree/shrub.
- 3 Crown volume was determined for each species by using the formula of a solid (e.g. spheroids, inverted cones, etc.), which appeared to give the best fit of the natural shape of the crown (Fig. 2).
- 4 Basal diameter of the main shoot.
- 5 Branch height, defined as the maximum vertical distance from ground level to the height point of the selected branch. This branch was used for direct biomass estimation.
- 6 Maximal branch width, defined as the maximal distance formed by secondary branches within the main branch.

Direct tree and shrub biomass measurements were carried out in each quadrat from randomly selected main branches of shrubs and trees. A total of eight main branches were collected in Ramat Avisur from *Quercus calliprinos* Webb (north-facing slope) and *Phillyrea latifolia* L. (south-facing slope), and 16 branches of *Pistacia lentiscus* L. and *Cistus creticus* L. as they were present on both north- and south-facing slopes. Although *Quercus calliprinos* and *P. latifolia* were dominants (high plant cover) in their respective aspects, they were not dominant in opposite slopes (south- and north-facing slopes, respectively). At the Lehavim site, a representative branch from three dwarf shrubs of the same dominant species was harvested in each quadrat. Con-

sidering eight quadrats per facing slope, a total of 24 shrubs of *Sarcopoterium spinosum* (L.) Spach were harvested from the north-facing slopes. Similar number of individuals of the dwarf shrub *Coridothymus capitatus* (L.) Lk. et Hoffm were collected from the south-facing slope. *Sarcopoterium spinosum* and *C. capitatus* were almost exclusive dominants on their respective aspects (north- and south-facing slopes, respectively). Therefore, only one species per aspect was considered.

After harvesting, branches were brought to the laboratory. The samples were then dried in an oven at 80°C for three days. After removing them from the oven, foliage and woody samples were weighed at room temperature on an electronic balance to the nearest 0.01 g. Biomass estimation of total individual weight was carried out by considering the dry weight of the sampled branch in relation to its respective volume. Thereafter, individual biomass was estimated by extrapolating the branch weight to the whole individual volume.

Total above-ground biomass estimations were calculated by considering the mean biomass weight of the dominant species by their relative densities.

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

### Statistical analysis

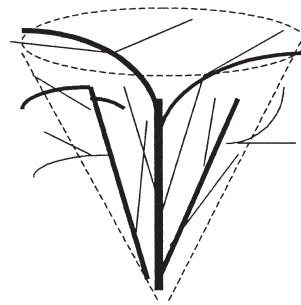
Each plant cover observation in the analysis consisted of the mean of four transects per quadrat. The relative cover of woody species in a quadrat was transformed by arcsine square-root transformation, while density counts were square-root transformed (Sokal & Rohlf 1995). Analyses of variance (ANOVA) were used to determine differences between hills and slopes. The analyses at each study site were carried out in respect to a randomized design with two hills and two slopes as replicates. The Tukey–HSD (honestly significant difference) test was used to compare differences of density means between slopes (Tukey 1953).

## RESULTS

### Vegetation characteristics at the sites

A total of 25 woody species (trees, shrubs and semishrubs) were recorded at the Ramat Avisur

*Quercus calliprinos*  
*Phillyrea latifolia*

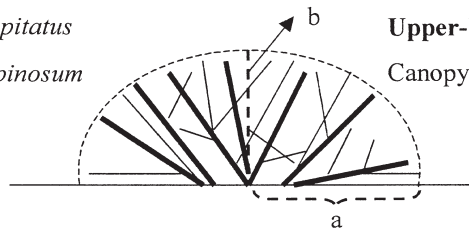


**Inverted cone**

Canopy volume =  $\frac{\pi}{3} r^2 h$

Canopy area =  $\pi r^2$

*Pistacia lentiscus*  
*Coridothymus capitatus*  
*Sarcopoterium spinosum*

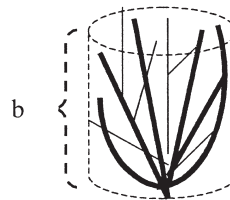


**Upper-half spheroid**

Canopy volume =  $\frac{4}{3} \pi a^2 b$

Canopy area =  $\pi r^2$   
 (a = r, r = radius)

*Cistus creticus*



**Cylinder**

Canopy volume =  $\pi r^2 b$

Canopy area =  $\pi r^2$

Fig. 2. Canopy shapes and the geometric formulae used to fit the shapes of the studied species. (a) Crown radius and (b) total height.

site, and 12 woody species (shrubs and semishrubs) were recorded at the Lehavim site. Differences in bare ground and rock cover percentages between north- and south-facing slopes were much more pronounced in the Lehavim site, with bare ground in southern slopes being greater by 30% in relative terms (Table 1). At the Ramat Avisur site, plant cover on the south-facing slope was slightly higher (3.9%) than on the north-facing slope. However, the opposite trend was observed at the drier site (Lehavim), where plant cover on the north-facing slope was 9.5% higher than on the opposing slope. Relative plant cover at Ramat Avisur on the south- and north-facing slopes was dominated by woody species (93% and 95%, respectively), which were mostly trees and shrubs. At the Lehavim site, the relative plant cover of annuals was more important, whereas that of perennial species at the north- and south-facing

slope was much lower, with 35% and 52%, respectively. When comparing the two sites, plant cover was almost equal on the south-facing slopes, while on the north-facing slopes vegetation cover was much higher at the Lehavim site.

On the north-facing slopes, dominant species were represented by the tree *Q. calliprinos*, the shrubs *P. latifolia* and *P. lentiscus*, and the dwarf shrubs *C. creticus* and *S. spinosum* (Table 1). On the south-facing slopes, dominant species included the shrubs *P. lentiscus* and *P. latifolia*, and the dwarf shrub *C. creticus*. These species are representative of the maquis formation (evergreen sclerophyll trees and semideciduous shrubs with herb associations) dominating the region. At the Lehavim site, dominant species of the south-facing slope were *C. capitatus* and *Thymelaea hirsuta* (L.) Endl., whereas *S. spinosum* and *Salvia dominica* L. were dominant on the north-facing slope (Table 1).

**Table 1** Comparison between site characteristics in cover (%), slope gradient (%) and relative plant cover (%) of dominant woody species in north and south-facing slopes at Ramat Avisur and Lehavim sites

	Ramat Avisur		Lehavim	
	North aspect	South aspect	North aspect	South aspect
Bare ground cover	12.6±1.5	10.4±1.8	15±1.6	22±2.4
Rock cover	23.5±1.7	21.8±1.9	8±0.9	10.5±0.9
Plant cover	63.9±4.5	67.8±5.7	77±4.9	67.5±4.1
Slope gradient	10.3±0.9	9.5±0.8	13.5±0.9	12.2±0.7
Woody species				
<i>Cistus creticus</i> ‡	33±2.9	31±3.3	–	–
<i>Coridothymus capitatus</i> ‡	–	–	–	35±3.9
<i>Phillyrea latifolia</i> †	14±2.5	23±1.5	–	–
<i>Pistacia lentiscus</i> †	14±1.8	38±3.3	–	–
<i>Pistacia palaestina</i> †	5±0.9	+	–	–
<i>Quercus calliprinos</i> *	18±1.6	+	–	–
<i>Rhamnus lycioides</i> †	3±0.7	+	–	–
<i>Salvia dominica</i> ‡	3±0.6	1±0.3	5±1.0	–
<i>Sarcopterium spinosum</i> ‡	5±0.9	+	33±2.9	+
<i>Thymelaea hirsuta</i> ‡	–	–	+	6±1.1

\*Tree; †shrub; ‡dwarf shrub. (–), Species not recorded; (+), species with plant cover lower than 1%. Mean ± SE.

### Effects of aspect on plant density, biomass, height, canopy volume and area

In Ramat Avisur, *Q. calliprinos* and *P. latifolia* were dominant on the north- and south-facing slopes, respectively. Their presence in opposite slopes (south-facing slope for *Q. calliprinos* and north-facing slope for *P. latifolia*) was relatively less important (Table 2). *Pistacia lentiscus* and *C. creticus* were jointly considered as they were abundant on both slopes. Total above-ground biomass of *Q. calliprinos*, *P. lentiscus* and *C. creticus* for the north-facing slope was 12.8 ton ha<sup>-1</sup>, and represented 81.6% of the woody plant cover (17.4 ton ha<sup>-1</sup> when considering 100% of woody plant cover). Total above-ground biomass of the southern slope including *P. latifolia*, *P. lentiscus* and *C. creticus* was lower, with 11.8 ton ha<sup>-1</sup>, and represented 92% of total relative plant cover (13.4 ton ha<sup>-1</sup> when considering 100% of woody plant cover). At the Lehavim site, density and biomass of dwarf shrubs were higher in the southern slope. Total above-ground biomass of *S. spinosum* for the northern slope was 4.6 ton ha<sup>-1</sup>, whereas total above-ground biomass of *C. capitatus* was 5.4 ton ha<sup>-1</sup>.

Significant differences in numbers of shrubs and dwarf shrubs were found at the Ramat Avisur site

when the north and south-facing slopes were compared (Table 3). Significantly higher numbers of individuals of *Q. calliprinos*, *Pistacia palaestina* Boiss., *S. dominica* and *Phagnalon rupestre* (L.) DC. were present in the north-facing slope. On the opposite slope, *Fumana thymifolia* (L.) Webb and *P. lentiscus* were significantly higher in numbers of individuals. No significant effects of hill or interaction with slope aspect were found for density of individuals of woody species. At the Lehavim site, differences in composition and density were strongly marked as *S. spinosum* was dominant in north-facing slopes, while almost absent in south-facing slopes. The opposite phenomenon occurred for the distribution of *C. capitatus*, as its presence was almost restricted to the south-facing slopes.

Figure 2 describes the relationships among structural properties of woody plants in two dimensions: (i) the aspect contrast (north *vs* south); and (ii) the geographical comparison between sites (Ramat Avisur *vs* Lehavim). This graphical representation is critical for understanding the importance of slope aspect differences to local and regional climatic variations. These relationships can be generalized as discussed below.

First, similar trends in vegetation structure differences were found when comparing both slope

Table 2 Comparison between north- and south-facing slopes for means of density, above-ground biomass, height, volume and area per individuals of monitored species

Species	North				South					
	Density (indiv. m <sup>-2</sup> )	Biomass (kg indiv.)	Height (cm)	Volume (m <sup>3</sup> )	Area (m <sup>2</sup> )	Density (indiv. m <sup>-2</sup> )	Biomass (kg indiv.)	Height (cm)	Volume (m <sup>3</sup> )	Area (m <sup>2</sup> )
Ramat Avisur										
<i>Quercus calliprinos</i> *	0.017 ± 0.002	49.3 ± 2.62	294.2 ± 25.8	17.6 ± 0.22	16.3 ± 1.31	0.003 ± 0.002	6.95 ± 0.89	173 ± 12.8	2.31 ± 0.19	3.6 ± 0.4
<i>Phillyrea latifolia</i> †	0.05 ± 0.03	7.15 ± 1.1	87.5 ± 10.1	3.91 ± 0.25	5.06 ± 0.9	0.05 ± 0.025	6.19 ± 0.61	103.3 ± 9.76	4.04 ± 0.76	5.06 ± 0.7
<i>Pistacia lentiscus</i> †	0.07 ± 0.04	0.28 ± 0.15	56.8 ± 4.90	0.31 ± 0.09	0.49 ± 0.07	0.093 ± 0.03	0.52 ± 0.23	70.2 ± 5.85	0.38 ± 0.03	0.53 ± 0.06
<i>Cistus creticus</i> ‡	0.27 ± 0.06					0.39 ± 0.09				
Lehavim										
<i>Sarcopoterium spinosum</i> ‡	0.39 ± 0.08	1.17 ± 0.30	47.8 ± 3.55	0.51 ± 0.06	1.28 ± 0.18	—	—	—	—	—
<i>Coridothymus capitatus</i> ‡	—	—	—	—	—	0.98 ± 0.05	0.55 ± 0.06	23.6 ± 1.2	0.11 ± 0.05	0.55 ± 0.03

\*Tree; †shrub; ‡dwarf shrub. (—) No individuals observed; blank entry, not measured. Mean ± SE. Volume and area are calculated by using the formulae in Fig. 1.

and geographical differences. North-facing slopes and northern sites had, in general, higher biomass, volume and area values than south-facing ones. However, exceptions to this generalization were found in the drier site (Lehavim), where the opposite was true for north versus south aspects for biomass and area estimations (in brackets in Fig. 3). Furthermore, higher density values were noted for the southern slopes in both sites.

Second, above-ground biomass was significantly higher on north-facing slopes in Ramat Avisur, whereas the opposite trend was observed in Lehavim. When comparing biomass differences between sites on similar facing slopes, the maquis formation on the north-facing slope was more than three times greater in biomass than the dwarf shrubland formation in Lehavim (17458 vs 4607 kg ha<sup>-1</sup>; Fig. 3). Similarly, biomass was greater in south-facing slopes in Ramat Avisur than in Lehavim (13389 vs 5417 kg ha<sup>-1</sup>; Fig. 3).

Third, plant volume was the most pronounced difference between sites.

Fourth, plant area was higher on the north-facing slopes in Ramat Avisur, whereas the opposite trend was noted in the Lehavim site.

Finally, in contrast to most of the other parameters measured, plant density increased from north to south both between slope aspects and sites.

## DISCUSSION

To the best of our knowledge the present study provides, for the first time, data concerning above-ground biomass estimations of woody formations in Israel and for eastern Mediterranean basin plant communities.

A prominent finding in the study is that the vegetation structure within a site changes significantly despite the short distance separating the north- and south-facing slopes, and that pattern remains generally constant when comparing the two sites of contrasting climatic and edaphic characteristics.

The results also show that slope aspect has a significant effect on the composition, structure and density of the plant communities developing at both sites. These results are in agreement with other studies in Israel, in which species

**Table 3** Results of analysis of variance for density of commonly occurring species at the Ramat Avisur site

Species	Hill		Slope		Hill × Slope	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
<i>Asphodelus microcarpus</i>	0.539	0.477	0.124	0.731	0.996	0.338
<i>Cistus salviifolius</i>	0.004	0.951	0.857	0.372	0.398	0.540
<i>Fumana thymifolia</i>	0.229	0.641	<b>12.40*</b>	<b>0.004<sup>1*</sup></b>	4.169	0.064
<i>Micromeria nervosa</i>	0.010	0.922	0.813	0.385	0.676	0.427
<i>Osyris alba</i>	0.134	0.721	1.866	0.197	0.134	0.721
<i>Phagnalon rupestre</i>	1.267	0.282	<b>11.10*</b>	<b>0.006<sup>2*</sup></b>	1.267	0.282
<i>Phillyrea latifolia</i>	0.001	0.971	0.001	0.972	0.064	0.804
<i>Pistacia lentiscus</i>	4.10	0.066	<b>5.571*</b>	<b>0.036<sup>1*</sup></b>	2.38	0.148
<i>Pistacia palaestina</i>	4.492	0.056	<b>6.545*</b>	<b>0.025<sup>2*</sup></b>	0.001	0.997
<i>Quercus calliprinos</i>	0.62	0.446	<b>4.81*</b>	<b>0.048<sup>2*</sup></b>	0.04	0.840
<i>Rhamnus lycioides</i>	0.102	0.755	0.951	0.348	0.783	0.394
<i>Salvia dominica</i>	0.187	0.673	<b>13.16*</b>	<b>0.003<sup>2*</sup></b>	0.187	0.673
<i>Sarcopoterium spinosum</i>	0.464	0.509	0.246	0.629	0.161	0.695
<i>Teucrium divaricatum</i>	0.297	0.596	1.916	0.191	0.047	0.832

\*Significant differences ( $P > 0.05$ ) are indicated in boldface type; <sup>1</sup>Higher density in south-facing slope; <sup>2</sup>Higher density in north-facing slope. Degrees of freedom: 1,12.

composition and richness significantly differed between north- and south-facing slopes (Kutiel 1992; Nevo 1995; Kadmon & Harari-Kremer 1999; Kutiel & Lavee 1999). The decrease in plant biomass from the Mediterranean site (open maquis) to the northern Negev Desert site (dwarf shrubland), corresponded to the decrease in the amount of rainfall and the increase in water potential deficit (Kadmon & Danin 1999).

Relative changes in vegetation traits, such as biomass, density, volume and area, between the two sites were of different scales. These changes were more important than we could have expected simply due to the addition of differences in rainfall and radiation density between the sites. Although not directly measured in the present study, it is assumed that the underlying differences in vegetation characteristics are related to differences in resource availability, particularly soil water temporal availability. The vegetation that developed in the north-facing slopes and sites, compared to that of the south-facing slopes and location, undergo phases of higher resources availability, particularly through soil moisture. These periods are longer in north-facing slopes and sites, thus explaining the important differences between the parameters studied. Results from other investigations carried out in similar areas as the present

study, and where solar radiation and soil water condition were measured, support our assumptions (Kutiel 1992).

When resource levels are too low for most plants to utilize, mortality takes place in annual species and perennial plant growth is restricted (Henkin *et al.* 1998b). We should expect that in the Mediterranean basin area this phenomenon occurs first in south-facing slopes. In the Mediterranean climate, the 'two-phase resource dynamics' (Henkin *et al.* 1998a) between the wet and dry seasons create transition periods during which available soil water can be erratic and varies from year to year (Hiernaux & Gerard 1999). Inter-annual variation in rainfall in Mediterranean ecosystems also has important consequences in the distribution of plant functional types (Noy-Meir & Sternberg 1999; Sternberg *et al.* 2000), soil organic carbon (Burke *et al.* 1989), and above-ground net primary productivity (ANPP) and its distribution throughout the year (Sala *et al.* 1988; Sternberg & Shoshany 2001).

A study done by Osem *et al.* (1999) showed that biomass production in annuals in the north-facing slopes at the Lehavim site during an average rainfall year was 0.72 ton ha<sup>-1</sup>, whereas in the south-facing slopes biomass production of annual species was 0.45 ton ha<sup>-1</sup>. Considering the proportions of

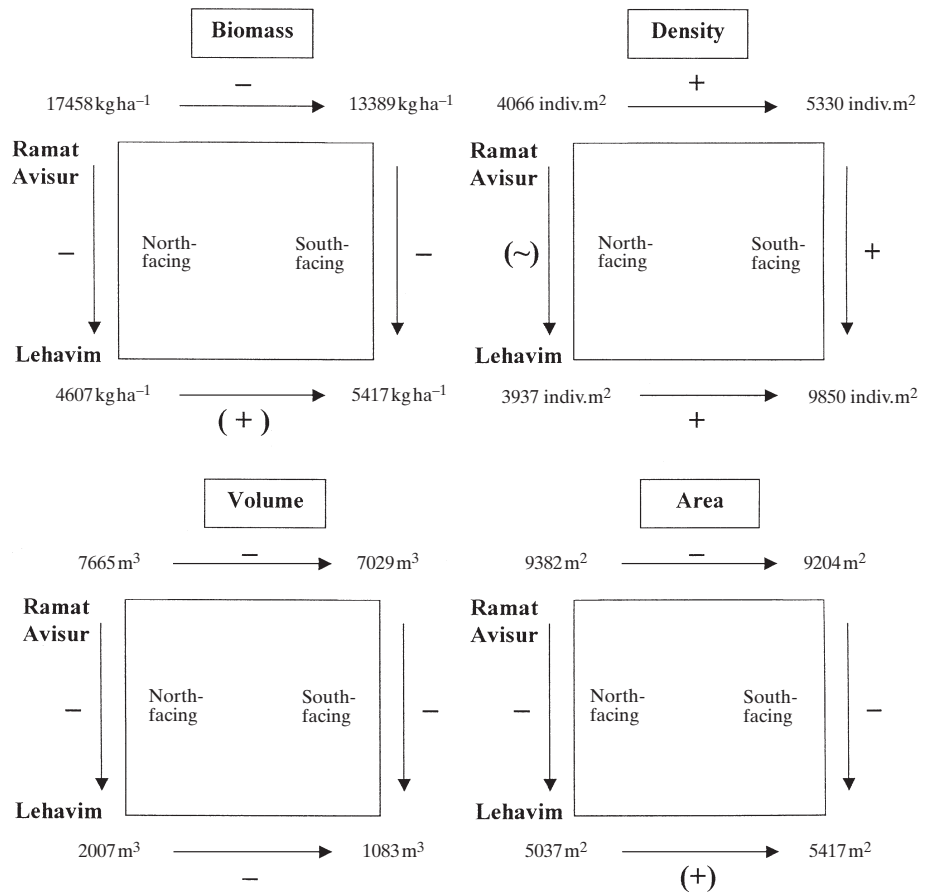


Fig. 3. Schematic comparison between slope aspect and study site differences for plant biomass (kg ha<sup>-1</sup>), density (No. individuals m<sup>-2</sup>), volume (m<sup>3</sup>) and area (m<sup>2</sup>). Results presented in the figure are calculated on the basis of density values for the dominant species. Arrows indicate a decreasing relationship (↔), an increasing relationship (↗), a similar relationship (≈) or an unexpected relationship (↘).

the biomass of annual species compared to that of woody plants, annual biomass production was almost double on the north-facing slopes (13.6%) compared to the south-facing slopes (7.6%). Nevertheless, the results concerning higher woody biomass production and covered area in the southern slope in Lehavim were surprising and unexpected, as indicated in Fig. 2. *Coridothymus capitatus*, which is dominant in the south-facing slope, was generally smaller than *Sarcopoterium spinosum*, which was dominant on the northern slopes. However, it was much more densely distributed than *S. spinosum* (0.98 individuals m<sup>-2</sup>–0.39 individuals m<sup>-2</sup>; Table 2). Considering that above-ground biomass and area estimates were calculated in relation to density of the species per unit area, the overall result showed higher woody biomass and area in the southern slopes. As mentioned earlier, plant volume was the most pronounced difference between sites. Vegetation in the northern and more humid site was higher than in the southern site. Although not directly measured in the

present study, it is inferred that this phenomenon is related to higher resource availability and to competition for light (Wilson & Tilman 1993).

In a study carried out by Kutiel and Lavee (1999) on slope aspect effects on soil and vegetation properties along an aridity gradient in Israel, they concluded that differences between slopes in the semiarid and arid zones were small and generally negligible. Our results disagree with their finding, as our study shows that significant differences between north and south hill slopes can be found in regions that have less than 400 mm of rainfall, as observed in the Lehavim area which has 250 mm mean annual precipitation. Indeed, it is in the semiarid or transitional regions where we might expect the strongest slope effects, as water in these areas is the critical limiting factor for the development of vegetation.

The information presented here should aid in the elaboration of management recommendations for conservation, prevention of fire hazards and sustainable production in Mediterranean rangelands.

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