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ORIGINAL PAPER

Understory woody vegetation in manmade Mediterranean pine forests: variation in community structure along a rainfall gradient

Yagil Osem · Ela Zangy · Eitan Bney-Moshe · Yosi Moshe

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Abstract Natural regeneration that occurs in the understory of Mediterranean pine monocultures provides the basis for the transition of these simply structured systems toward a more complex and sustainable state. However, the course and consequences of this process, and its relationships with environmental and silvicultural variables, are still inadequately understood. We investigated the relationship between rainfall amount and understory woody vegetation (UWV) structure in mature (40–50 year) *Pinus halepensis* plantations in the Mediterranean zone of Israel, where rainfall ranges from 280 mm/year in the south to 900 mm/year in the north. We measured abundance, diversity and species composition on south- and north-facing slopes, in forest sites distributed along the rainfall gradient. UWV abundance, as measured by cover percentage and height, increased with rainfall amount along the entire gradient (2–113% and 0.1–3.4 m, respectively), more rapidly on north-facing slopes. Species composition varied along the rainfall gradient, with ranges of species occurrences corresponding to those in unforested habitats. The relationship between rainfall and UWV species richness was positive throughout most of the rainfall gradient, possibly with a shift in pattern at the highest rainfall levels. UWV richness increased sharply with increasing abundance, up to a certain point with no further increase in richness as abundance increased further. We concluded that UWV structure in the studied forest environment and climatic range is strongly determined by rainfall and suggested that the design and management of Mediterranean forests should focus more on optimizing water availability for the various components.

Keywords *Pinus halepensis* · Precipitation · Productivity · Diversity · Israel

Introduction

Although small in size, the Mediterranean zone of Israel encompasses a wide climatic range, with a steep rainfall gradient from 250 to nearly 1,000 mm × year^{-1} (Kadmon and Danin 1999). Within this region, formations of the native vegetation vary along the climatic gradient from dwarf shrublands (Batha) to dense woodlands (Maquis) (Rabinowitch 1985; Kadmon and Danin 1997, 1999). The highly degraded state of these vegetation communities at the beginning of the twentieth century may have provided the basic motivation for the conifer-based afforestation enterprise that has been pursued in Israel since the 1930s. Preparation of forest-planting sites and post-planting treatments caused further destruction of the remnant native vegetation and may account for what has been considered for some time as "pine deserts". However, under the protection and, possibly, the facilitation of the planted forests, the native vegetation slowly recovered and developed as a woody understory layer of vegetation (Lev-Yadun et al. 1999; Osem et al. 2009). The pace of this

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Y. Osem (✉) · E. Zangy · E. Bney-Moshe · Y. Moshe
Department of Natural Resources, Institute of Plant Sciences,
ARO, The Volcani Center, P.O. Box 6, 50250 Bet Dagan, Israel
e-mail: yagil@agri.gov.il

E. Zangy
e-mail: elaz@agri.gov.il

E. Bney-Moshe
e-mail: eitanbm@agri.gov.il

Y. Moshe
e-mail: yosi@agri.gov.il

process varies strongly among forest sites because of variations in habitat conditions, disturbance regimes and landscape history (Maestre and Cortina 2004).

Forest understory vegetation is increasingly being recognized as a major component in the structure and function of forest ecosystems (VanderSchaaf et al. 2000, 2004; Barbier et al. 2008; Hart and Chen 2008). Regenerating vegetation that develops beneath the canopy of coniferous monocultures can now be seen as providing the basis for the transition of these simply structured systems toward a more complex and sustainable state (Osem et al. 2008). Furthermore, the capacity of native species to regenerate and to develop within the *pine* plantations is considered as a key factor regarding afforestation as a means for restoring degraded ecosystems in semiarid Mediterranean areas (Maestre and Cortina 2004; Gomez-Aparicio et al. 2009). However, the course and consequences of this process, and its relationships with environmental and silvicultural variables, are still inadequately understood (Maestre and Cortina 2004). The present study aimed to investigate the relationship between rainfall amount and the structure of regenerating understory woody vegetation (UWV) in *Pinus halepensis* plantations distributed across the Mediterranean zone of Israel. We focused on the woody vegetation because it represents the major structural constituent of the understory vegetation as well as the potential for the future forest formation. This is not to underestimate the importance of the understory herbaceous component at various aspects.

Mediterranean ecosystems are commonly regarded as water limited (Sabate et al. 2002; Hoff and Rambal 2003), and in these regions, the rainfall amount is widely recognized as a fundamental environmental factor in determining vegetation structure (Kadmon and Danin 1999; Kutiel et al. 2000). However, there has been little study of the extent to which woody vegetation structure in these systems is related to rainfall amount or of the pattern of such a relationship. Furthermore, although patterns of variation of vegetation structure along productivity gradients have been studied quite extensively in various parts of the world (Jennings et al. 2005; Partel et al. 2007), including the Mediterranean region (Kadmon and Danin 1999; Kutiel et al. 2000; Casado et al. 2004), the variation in forest understory structure along natural productivity gradients has been addressed far less. Understanding variations in forest understory structure along climatic gradients is often complicated because climatic factors are usually confounded with other factors such as silvicultural strategy and history (Maestre and Cortina 2004; Takafumi and Hiura 2009) and overstory characteristics (Barbier et al. 2008; Gomez-Aparicio et al. 2009). The comprehensive afforestation activities of the Israeli Forestry Organization (KKL) during the last 60 years, which established a uniform forest structure with regard to tree density and species composition using uniform silvicultural methodologies over a wide range of environmental conditions, have provided a unique opportunity to investigate the extent to which rainfall amount determines understory vegetation structure in Mediterranean forest systems.

Patterns of vegetation structure along semiarid Mediterranean rainfall gradients are not expected to be obvious, because the primary determinants of species existence and abundance have been hypothesized to vary along these productivity gradients (Milchunas and Lauenroth 1993; Milchunas et al. 1988; Osem et al. 2002). Previous studies within the same climatic range have already shown that effects of rainfall variations on vegetation structure were stronger in relatively dry regions than in more mesic ones (Kutiel et al. 1995; Kadmon and Danin 1999). Rabinowitch (1985) hypothesized that the woody vegetation in the Mediterranean zone of Israel is mainly rainfall limited only up to a certain rainfall level, above which bedrock type and soil mineral composition become more important. In forest systems, identification of a predominant limiting factor for understory regeneration and abundance is even more complicated because (1) light availability is strongly reduced and may become a crucial limiting factor (Kirby 1988; Bazzaz 1990; Jennings et al. 1999; Rodriguez-Calcerrada et al. 2008; VanderSchaaf 2008) even at the lower end of the rainfall gradient and (2) the availability of underground resources to the understory and its efficiency of using them may depend strongly on consumption by and microclimatic effects of the overstory (Devine and Harrington 2008; Rodriguez-Calcerrada et al. 2008). Furthermore, the intensity of the effects of the overstory on resources and, therefore, the proportion of these resources available exclusively to the understory layer should also be expected to vary along the rainfall gradient (Ludwig et al. 1999; Coomes and Grubb 2000). Such variations in overstory–understory interactions may result in shifts in the balance between facilitation and competition (Lortie and Callaway 2006; Gomez-Aparicio et al. 2009), and the nature of these shifts may also vary among species, depending on the balance between their drought and shade tolerance (Guerrero and Bustamante 2009; Rodriguez-Calcerrada et al. 2010).

In light of these issues we asked: To what extent is the structure of understory woody vegetation (UWV) in semiarid Mediterranean forest systems determined by rainfall amount? We hypothesized that, within the studied climate range, UWV structure would be strongly determined by rainfall amount in the drier regions whereas in the more mesic regions other potentially limiting biotic and abiotic factors, e.g., competitive interactions, bedrock and soil characteristics, and disturbances, would increase in importance. We thus expected UWV abundance, diversity and composition to be strongly dependent on rainfall amount where rainfall was relatively low and to become less dependent on it as rainfall increased.

This study should contribute to a better understanding of water-limited forest systems and possibly lead to improved management schemes for enhancement of forest diversity, complexity and sustainability, as well as landscape restoration, in Mediterranean climatic regions. Furthermore, it may provide insights regarding possible consequences of climate change in Mediterranean forest systems.

Methods

The study sites

The study was constructed along Israel's Mediterranean zone that extends from the semiarid northern Negev desert in the south to the subhumid Upper Galilee in the north. The climate in this region is defined as east Mediterranean, with winter rains occurring mainly during December through March, and a relatively long, dry, hot summer. A comprehensive UWV survey was conducted during 2006–2008 in 10 planted *Pinus halepensis* forests, in areas with rainfall amounts representative of the range (280–900 mm × year^{-1}) that occurs within the studied region (Fig. 1). The surveyed stands were selected to minimize variations in other factors, such as bed rock and soil type, altitude and topography, and silvicultural history (Table 1). Among these, we prioritized the importance of the forest overstory structure, i.e., species composition (90–100% *Pinus halepensis*), and tree age (40–50 years) and density (300–350 trees ha^{-1}). Table 1 presents data on basal area and tree average height in the studied forest sites. The following positive linear relationships were found between these parameters and rainfall amounts.

North-facing slopes:

$$\text{basal area}\,[\text{m}^2\,\text{ha}^{-2}] = 2.7 + 0.015 \times \text{rainfall}\,[\text{mm}]\ (R^2 = 0.70, N = 9, P = 0.005)$$

South-facing slopes:

$$\text{basal area}\,[\text{m}^2\,\text{ha}^{-2}] = 3.1 + 0.011 \times \text{rainfall}\,[\text{mm}]\ (R^2 = 0.59, N = 9, P = 0.016)$$

North-facing slopes:

$$\text{tree height}\,[\text{m}] = 4.36 + 0.018 \times \text{rainfall}\,[\text{mm}]\ (R^2 = 0.77, N = 9, P = 0.002)$$

South-facing slopes:

$$\text{tree height}\,[\text{m}] = 5.69 + 0.012 \times \text{rainfall}\,[\text{mm}]\ (R^2 = 0.59, N = 9, P = 0.015)$$

Fig. 1 Distribution of the studied forest sites along the Mediterranean zone of Israel

We present these overstory characteristics separately for north and south as we intend to analyze and present understory structure in the same way.

The following relationship was found between basal area (BA; m^2 ha^{-2}) and leaf area index (LAI; m^2 × m^{-1}) in typical *Pinus halepensis* plantations in Israel:

$$\text{LAI} = 0.27 \times \text{BA}\ \left(R^2 = 0.37, N = 26,\ P = 0.001\right)$$

Experiment design and sampling

The forest locations were chosen to provide a continuum of rainfall levels within the range of 250–900 mm × year^{-1}. Forests growing in different rainfall levels were selected from two distinct and quite widely separated districts (Fig. 1). In each forest, sampling sites were selected on

Table 1 The studied forest sites

Forest	Longitude latitude	Elevation m	Average annual rainfall mm	Basal area m^2 ha^{-1}	Tree average height m	Predominant bedrock type	Predominant soil type
Yatir	203–204 583–584	550–600	276	9.0 N 5.3 S	10.00 N 7.50 S	Hard and semi-hard limestone and nari (Turonian)	Mediterranean brown forest soils and loess soils
Lahav	189 584	350–450	315	4.8 N 5.4 S	8.75 N 7.00 S	Hard and semi hard limestone and nari (Turonian)	Mediterranean brown forest soils and loess soils
Shaharia	183 612	200–250	435	10.3 N 11.2 S	15.00 N 14.00 S	Limestone chalk, calcareous sandstone (Eocene)	Mediterranean brown forest soils and mountain Rendzina soils
Eshtaol	199–200 633–635	300–350	519	9.6 N 7.0 S	13.00 N 12.00 S	Limestone and chalk (Eocene)	Mediterranean brown forest soils and mountain Rendzina soils
Natheret	233–234 733–735	350–400	573	10.7 N 10.5 S	13.00 N 12.50 S	Limestone chalk, calcareous sandstone (Eocene)	Terra Rossa soils
Natheret	233–234 733–735	350–400	573	8.9 N 9.6 S	12.00 N 12.00 S	Hard limestone (Ceno-manian, Turonian)	Terra Rossa soils
Kdoshim	204–206 632–633	350–450 500–550	628	12.9 N 9.7 S	17.00 N 15.00 S	Limestone and dolomite (Ceno-manian, Turonian)	Terra Rossa and Mediterranean brown forest soils
Yaaranim	204–205 738–739	450–500	687	12.7 N 13.3 S	16.50 N 14.00 S	Limestone, dolomite and chalk (Ceno-manian)	Terra Rossa, Mediterranean brown forest soils and mountain Rendzina
Maalot	227–228 767	500–550	777	14.7 N	19.00 N	Limestone, dolomite and chalk (Ceno-manian Turonian)	Terra Rossa
Sasa	233 773–774	700–750	894	11.8 S	14.00 S	Limestone, dolomit and chalk (Ceno-manian)	Terra Rossa

N North-facing slopes, *S* South-facing slopes

north- and south-facing slopes, with the aid of the GIS (Geographic Information System) database of the Israeli Forest Service (KKL). After GIS selection, the sites were examined on the ground to verify that they matched the desired criteria of tree species composition, age and density. Sites that had been exceptionally heavily disturbed by human activity, such as intensely used picnic areas, or by grazing, such as areas that served as livestock paddocks, were avoided. In each forest, six randomly distributed sites that exhibited the required characteristics were sampled along 50-m transects, which were further divided into 10-m subtransects to enable spatial analyses. Because of all the aforementioned limitations, sites representing the highest rainfall level could be found in only two forests, each presenting only one topographic aspect: north-facing slopes in Maalot Forest and south-facing slopes in Sasa Forest. Thus, a total of 108 sites were sampled, distributed among 10 forests, covering two aspects in all except two of the forests and comprising six replicates (sites). In each site, the surface cover and heights of understory woody species were recorded by the line intercept method (Boyd et al. 2007).

Parameters and definitions

We used three parameters for quantifying UWV abundance: (1) surface cover—the proportion of the transect covered by vegetation; (2) average height (weighted by cover); and (3) specific volume—the product of surface cover [proportion] × area [m^2] × average height. A vegetation patch was defined as a unit of continuous cover by a single woody species, and by measuring all such patches separately, we could calculate surface cover for any single species or species group, as well as for the total UWV. Average patch height was the average of the highest points (intercepting the line transect) taken at 1-m intervals along the transect within each patch. Average understory height was the weighted (by relative cover) average of the individual-patch averages. Woody species richness was determined as the number of woody species intercepting the transect (50 m). For species diversity, we used the Shannon–Weiner Diversity Index. In order to examine variations in the floristic composition along the rainfall gradient, we looked at the relative cover of species and life-form groups (i.e., trees, shrubs, dwarf shrubs and vines).

Statistical analysis

We performed GLM (General Linear Model) analyses to investigate the effects of rainfall amount (Rainfall), topographic aspect (Aspect) and their interaction. Post hoc comparisons were used to analyze the effect of Aspect within a given forest and to compare similar aspects among forests. The relationship between rainfall amount and understory community structure was subjected to regression analysis, separately for each topographic aspect. In these analyses, we compared linear models with log (x) models to test whether changes in community structure were gradual throughout the entire rainfall gradient (linear fit) or moderated as rainfall level increased (log (x) fit). Variations in the floristic composition of woody species with respect to rainfall amount and topographic aspect were subjected to Canonical Correspondence Analysis (CCA). The statistical significance of the relationship was determined with the Monte Carlo permutation test (ter Braak and Smilauer 1998). Alpha level used for all statistical tests was 0.05.

Results

Understory woody vegetation abundance

We used surface cover (hereafter "cover"), weighted average height (hereafter "height") and their product, specific volume (hereafter "volume") as indicators of UWV abundance. All three parameters increased with rainfall along the entire rainfall gradient (Table 2): cover ranged from 2 to 113%; height from 0.1 to 4.4 m; and volume from 0.18 to 3.87 $m^3 \times m^{-2}$ (Fig. 2). Rainfall versus abundance relationships were generally best fitted by a linear model except in case of rainfall versus cover on south-facing slopes, for which a slightly better fit was achieved with the log (x) model (Table 2). GLM analyses showed that the Rainfall × Aspect interaction was significant for all three abundance parameters (Table 3), indicating that the increase in UWV abundance along the rainfall gradient was significantly steeper on north-facing than on south-facing slopes. It is worth mentioning, however, that the two forest sites located on the high end of the rainfall gradient (i.e., Maalot and Sasa) may have played a significant role in determining the observed rainfall–abundance relationships. We, thus, conducted separated analyses after excluding these two points. According to these analyses, rainfall–abundance relationships remained highly significant ($P < 0.0001$) for all three abundance parameters. However, the effect of aspect was no longer that clear (i.e., not significant for volume and height, but still significant for cover and specifically tree cover, results not shown).

Species diversity

Altogether, 51 woody species were listed in the UWV survey. Rainfall amount and Aspect interacted significantly in determining UWV species richness (Table 3), which, in the various sets of forest sites, ranged between 0.4 and 6.6 species per 10 m (subtransect); 1.3 and 13.5 species per 50 m (transect); and 4 and 23 species per 300 m (pull of six transects; Table 4). When analyzed separately for each topographic aspect, the rainfall–richness relationship could be fitted to either a linear model, polynomial model (hump-shaped relationship, on north-facing slopes: $R^2 = 0.721$, $N = 9$, $P = \mathbf{0.022}$; on south-facing slopes: $R^2 = 0.524$, $N = 9$, $P = 0.108$) or a log (x) model, with the latter being slightly better (Table 2; Fig. 3). Both linear and log (x) models depicted species richness increasing with rainfall amount throughout the entire rainfall gradient on both north- and south-facing slopes, with sharper increases on north-facing slopes. Trends in species diversity, as indicated by the Shannon–Weiner Index, were similar to those found for richness (Tables 2, 3).

Abundance–richness relationship

We analyzed the relationship between UWV abundance (cover, height and volume) and species richness. UWV richness was strongly and positively related to abundance (Table 5). The cover–richness relationships were best fitted with a linear model (Fig. 4), whereas the height–richness and volume–richness relationships were clearly better fitted with the log (x) model (Table 5; Fig. 5), which indicates that species diversity increased sharply with increasing volume and increasing height up to certain points—volume $\approx 1\ m^3\ m^{-2}$; height ≈ 1 m—with no further increase in species diversity as volume or height increased further (Fig. 5). Cover–richness relationships were also found significantly linearly positive when analyzed separately for trees, shrubs, dwarf shrubs and vines (Table 5).

Species composition

Canonical Correspondence Analysis revealed significant linear relationship between woody understory species

Table 2 Regression analyses: The relationship between rainfall and understory woody vegetation structure

Parameter	Aspect	Linear fit			Log (x) fit		
		R^2	*N*	*P*	R^2	*N*	*P*
Richness	North	0.572	9	**0.018**	0.643	9	**0.009**
	South	0.485	9	**0.037**	0.504	9	**0.032**
Shannon index	North	0.562	9	**0.02**	0.664	9	**0.008**
	South	0.360	9	0.088	0.384	9	0.075
Trees richness/Total richness	North	0.759	9	**0.002**	0.626	9	**0.011**
	South	0.662	9	**0.008**	0.631	9	**0.011**
Shrub richness/Total richness	North	0.334	9	0.103	0.378	9	0.078
	South	0.520	9	**0.028**	0.534	9	**0.025**
	All	0.398	10	0.051	0.428	10	**0.040**
Dwarf-shrub richness/Total richness	North	0.458	9	***0.045***	0.421	9	0.059
	South	0.137	9	0.327	0.103	9	0.399
	All	0.390	10	0.053	0.363	10	0.066
Vine richness/Total richness	North	0.197	9	0.231	0.301	9	0.126
	South	0.001	9	0.933	0.000	9	0.987
Total cover	North	0.934	9	**<0.0001**	0.909	9	**<0.0001**
	South	0.431	9	0.055	0.482	9	**0.038**
	All	0.596	10	**0.0089**	0.656	10	**0.0045**
Trees cover/Total cover	North	0.641	9	**0.009**	0.523	9	**0.028**
	South	0.629	9	**0.011**	0.592	9	**0.015**
Shrubs cover/Total cover	North	0.275	9	0.1468	0.300	9	0.127
	South	0.443	9	**0.050**	0.481	9	**0.038**
	All	0.304	10	0.099	0.344	10	0.075
Dwarf-shrub cover/Total cover	North	0.409	9	0.0636	0.382	9	0.076
	South	0.140	9	0.3209	0.108	9	0.388
	All	0.382	10	0.057	0.363	10	0.065
Vine cover/Total cover	North	0.011	9	0.791	0.045	9	0.582
	South	0.186	9	0.246	0.168	9	0.273
Weighted height	North	0.749	9	**0.003**	0.649	9	**0.009**
	South	0.781	9	**0.002**	0.737	9	**0.003**
Specific volume	North	0.660	9	**0.008**	0.542	9	**0.024**
	South	0.620	9	**0.012**	0.594	9	**0.015**

Cells in bold indicate statistical significance. Cells in italics indicate negative relationship

composition and rainfall amount (Eigenvalue = 0.43, $F = 2.17$, $P = 0.016$), and better fitting of the relationship between species composition and rainfall was achieved using a log transformation of the rainfall data (Eigenvalue = 0.45, $F = 2.26$, $P = 0.006$). The effects of topographic aspect (Aspect) and of the Rainfall × Aspect interaction on species composition were found not significant. The ranking of the 32 most common understory woody species according to their relationship with rainfall amount as revealed by the CCA (Table 6) corresponded to the commonly known natural distribution of these species in unforested areas. We evaluated the relative contributions of four life-form groups—trees, shrubs, dwarf shrubs and vines—to the surface cover and species richness of UWV, as they varied along the rainfall gradient. The contributions of tree species ranged from 0 to 71% of the total understory surface cover and from 0 to 54% of the species richness. Rainfall and topographic aspect interacted in determining the relative contributions of trees to surface cover and species richness (Table 3). When analyzed separately for north- and south-facing slopes, the relative contributions of trees were found positively linearly related to rainfall throughout the rainfall gradient on both topographic aspects (Table 2), and the Rainfall × Aspect interaction reflected steeper increases on north-facing than on south-facing slopes. GLM analyses of the relative contributions of shrubs and dwarf shrubs to the UWV cover and richness revealed significant effects of rainfall amount (Table 3) in both groups, but the effects of topographic aspect and of the Aspect × Rainfall interaction were not significant. Shrub relative cover and richness increased with rainfall, whereas the contributions of dwarf shrubs to understory cover and richness decreased as rainfall increased. The relationship between rainfall amount and the contribution

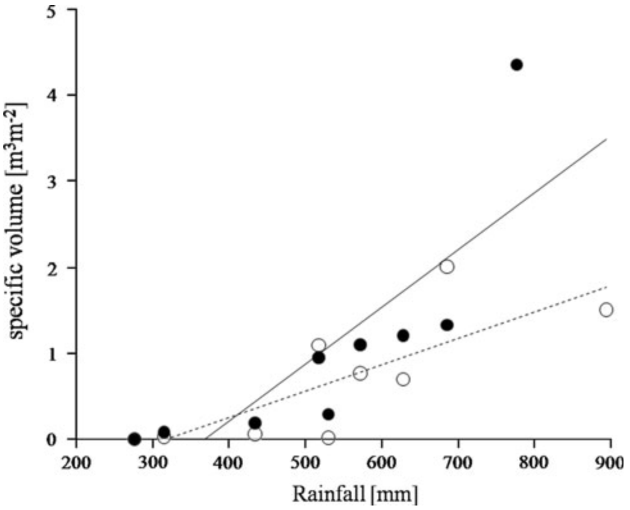

Fig. 2 Variation along the rainfall gradient in the specific volume of the forest understory woody vegetation (*closed circle*) north-facing slopes; (*open circle*) south-facing slopes

of vines to UWV was unclear; however, the contribution of vines was found to be significantly higher on north-facing than on south-facing slopes (Table 3).

Discussion

Understory abundance

The present results show that the abundance of UWV in mature *Pinus halepensis* plantations was determined by rainfall amount throughout the studied climatic gradient, where annual rainfall ranged from 280 to 900 mm. The finding that rainfall–abundance relationships were usually better fitted by linear models than by log (x) models indicates that the increase in UWV abundance with increasing rainfall was continuous and did not moderate at higher rainfall levels. The increase in UWV abundance with increasing rainfall amount paralleled the increases in overstory tree basal area and height, and intensity of light interception (LAI). This finding contradicts our research hypothesis. It highlights the importance of water availability as a predominant limiting factor also at the wetter end of the studied rainfall range and under conditions of severe shading by the forest overstory. Further support for water availability being the main limiting factor could have been provided by a clear advantage of north-facing over south-facing slopes throughout the rainfall range. Although such trend was evident in some cases (e.g., total cover, tree cover,) it was not as clear in other cases (e.g., specific volume, height). The prevalence of better water regimes on north- than on south-facing slopes is well known in Mediterranean (Carmel and Kadmon 1999; Sternberg and Shoshany 2001) and also other systems (Coble et al. 2001). However, Kutiel et al. (1998), in a study conducted within a similar climatic range in unforested habitats, found that this effect disappeared at the wetter end of the rainfall gradient, i.e., where annual rainfall exceeded 700 mm. Furthermore, in forested habitats, the positive influence of the north-facing compared with the south-facing aspect should be even less obvious because, for a given overstory cover level, solar radiation to the understory is more restricted on the former (Fyllas et al. 2008). Thus, it may be argued that water availability in the understory of planted pine forests is highly restricted. This is in agreement with Maestre et al. (2003), who found pine plantations to have a negative effect on water balance in semiarid Mediterranean habitats, because of both rainfall interference (Schiller 1979) and water uptake by the pines (Schiller and Cohen 1998).

Understory species composition

In addition to the above-mentioned patterns of understory abundance, the composition of UWV shifted throughout the rainfall gradient, with the relative contributions of larger life forms, i.e., trees and shrubs, increasing gradually with increasing rainfall and that of dwarf-shrub species decreasing. These observed changes in floristic composition corresponded to the shifts in vegetation physiognomy, from dwarf shrublands to dense woodlands (maquis) along the studied rainfall gradient, as typically observed in the natural, unforested, landscape. Moreover, specific examination of the ranges of species occurrence found in our UWV survey did not reveal any clear deviations from the natural distribution of species, as commonly found in unforested habitats. Thus, the shifts in species composition with increasing rainfall, from dominance by species typical of arid/semiarid habitats to domination by those typical of Mediterranean/mesic-Mediterranean habitats, as found in the present study, provide further evidence that water availability is the major determinant of UWV structure throughout the studied climatic range. Nevertheless, as previously found in unforested landscapes within the same climatic range (Kadmon and Danin 1999), application of CCA to the composition–rainfall relationship showed that the rate of compositional shift varied along the rainfall gradient, a somewhat more rapid shift in the drier than in the wetter zone, i.e., a log (x) model fitted the observations slightly better than a linear model.

Understory species diversity

Forms of the productivity–diversity relationship have been shown to vary among ecosystems for various causes, such as the type and range of the limiting resource (Casado et al.

Table 3 GLM analyses on the effects of rainfall amount (Rainfall) and topographic aspect (Aspect: north, south) on understory woody vegetation structure

Parameter	R^2	Factor	DF	SS	*F*	*P*
Richness	0.502	Rainfall	1	621.295	86.627	**<0.0001**
		Aspect	1	95.702	13.344	**0.0004**
		Aspect × Rainfall	1	40.950	5.710	**0.0188**
Trees richness/Total richness	0.617	Rainfall	1	1.592	152.582	**<0.0001**
		Aspect	1	0.046	4.373	**0.0391**
		Aspect × Rainfall	1	0.106	10.172	**0.0019**
Shrub richness/Total richness	0.395	Rainfall	1	1.210	52.709	**<0.0001**
		Aspect	1	0.051	2.225	0.1390
		Aspect × Rainfall	1	0.055	2.388	0.1256
Dwarf-shrub richness/Total richness	0.216	Rainfall	1	1.774	25.150	**<0.0001**
		Aspect	1	0.068	0.962	0.3291
		Aspect × Rainfall	1	0.219	3.101	0.0814
Vine richness/Total richness	0.170	Rainfall	1	0.097	3.740	0.0560
		Aspect	1	0.346	13.269	**0.0004**
		Aspect × Rainfall	1	0.123	4.720	**0.0323**
Total cover	0.601	Rainfall	1	8.159	133.586	**<0.0001**
		Aspect	1	0.881	14.422	**0.0003**
		Aspect × Rainfall	1	0.643	10.528	**0.0016**
Trees cover/Total cover	0.513	Rainfall	1	2.424	101.254	**<0.0001**
		Aspect	1	0.041	1.710	0.1941
		Aspect × Rainfall	1	0.101	4.230	**0.0424**
Shrubs cover/Total cover	0.299	Rainfall	1	1.412	35.195	**<0.0001**
		Aspect	1	0.068	1.694	0.1961
		Aspect × Rainfall	1	0.039	0.961	0.3294
Dwarf-shrub cover/Total cover	0.208	Rainfall	1	1.939	24.041	***<0.0001***
		Aspect	1	0.059	0.735	0.3934
		Aspect × Rainfall	1	0.254	3.144	0.0794
Vine cover/Total cover	0.140	Rainfall	1	0.003	0.114	0.7369
		Aspect	1	0.344	11.876	**0.0008**
		Aspect × Rainfall	1	0.100	3.451	0.0662
Weighted height	0.645	Rainfall	1	563378.63	171.509	**<0.0001**
		Aspect	1	22011.47	6.701	**0.0111**
		Aspect × Rainfall	1	25449.11	7.747	**0.0065**
Specific volume	0.562	Rainfall	1	6.951e11	111.647	**<0.0001**
		Aspect	1	5.627e10	9.038	**0.0034**
		Aspect × Rainfall	1	1.074e11	17.247	**<0.0001**
Shannon index	0.413	Rainfall	1	13.332	63.597	**<0.0001**
		Aspect	1	1.038	4.955	**0.0283**
		Aspect × Rainfall	1	1.206	5.753	**0.0184**

Numbers in bold indicate statistical significance. Numbers in italics indicate negative relationship

2004; Enica-Dominguez et al. 2007), species life history traits and nature of interspecific interactions (Adkison and Gleeson 2004; Hart and Chen 2008; Speziale et al. 2010) or the relative importance of other non-resource factors such as disturbances (Takafumi and Hiura 2009). Hence, the varied findings of the limited number of studies that have examined this issue in forest understory communities, some of which have found positive productivity–diversity relationships (Williams et al. 1996; Adkison and Gleeson 2004; Chen et al. 2004), whereas others have found negative (Enica-Dominguez et al. 2007) or unimodal (Casado et al. 2004; Gomez-Aparicio et al. 2009; Speziale et al. 2010) relationships. In our present study, a positive relationship between rainfall and UWV species richness was found throughout most of the rainfall gradient with, possibly, a moderate decrease in the rate of richness increase with increasing rainfall at the higher rainfall levels. The productivity range covered by our survey may need further extension toward higher rainfall levels, or longer succession periods, i.e., older forests, to enable a

Table 4 Understory woody vegetation species richness in different spatial scales (transect length)

Forest	Aspect	Richness		
		Forest (300 m)	Transect (50 m)	Subtransect (10 m)
Yatir	North	6	1.33	0.43
Yatir	South	6	2.33	0.60
Lahav	North	7	3.83	2.13
Lahav	South	12	4.33	1.37
Shaharia	North	13	4.67	2.13
Shaharia	South	4	2.00	1.10
Giv—ham	North	16	7.40	3.20
Giv—ham	South	5	2.40	1.04
Eshtaol	North	21	13.50	6.65
Eshtaol	South	13	7.33	4.23
Nathereth	North	13	7.83	3.60
Nathereth	South	16	8.33	3.20
Kdoshim	North	23	12.50	6.00
Kdoshim	South	21	9.17	3.43
Carmel	North	19	11.50	5.45
Carmel	South	14	8.20	4.04
Maalot	North	13	8.83	4.50
Sasa	South	14	8.00	3.80

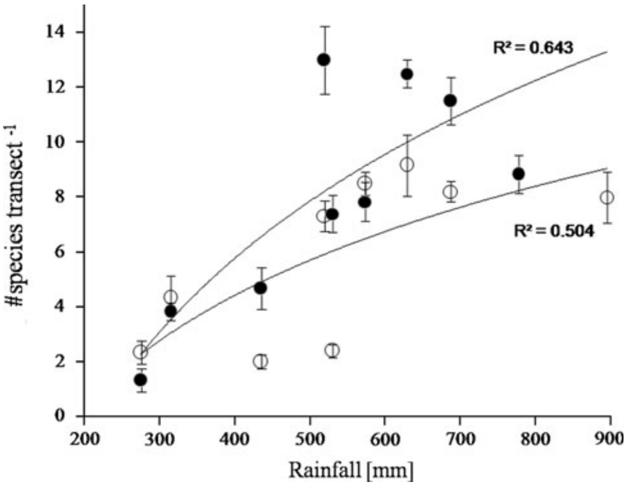

Fig. 3 Variation along the rainfall gradient in the species richness of the forest understory woody vegetation (*closed circle*) north-facing slopes; (*open circle*) south-facing slopes

Table 5 Regression analyses: The relationship between understory woody vegetation abundance and species diversity

Parameter	Linear fit			Log (x) fit	
	R^2	N	P	R^2	P
Total richness versus cover	0.719	18	<0.0001	0.702	<0.0001
Shannon index versus cover	0.621	18	0.0001	0.670	<0.0001
Tree richness versus cover	0.806	18	<0.0001	0.579	0.0025
Shrub richness versus cover	0.833	18	<0.0001	0.732	<0.0001
Dwarf-shrub richness versus cover	0.704	18	<0.0001	0.638	0.0001
Vine richness versus cover	0.887	18	<0.0001	0.771	<0.0001
Total richness versus specific volume	0.294	18	0.02	0.723	<0.0001
Total richness versus weighted height	0.413	18	0.004	0.683	<0.0001

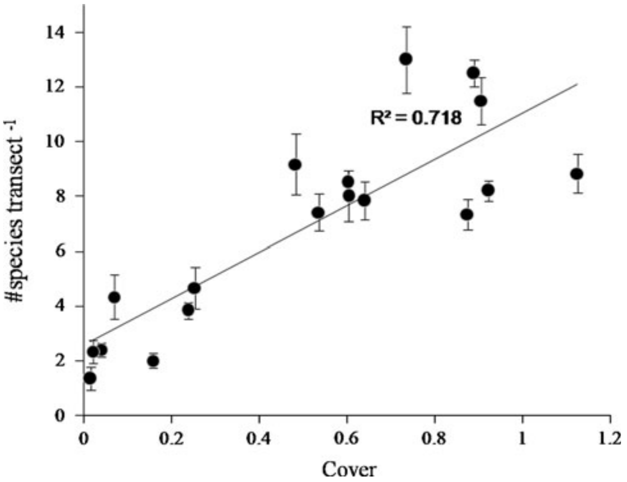

Fig. 4 The relationship between species richness and vegetation cover of the forest understory woody vegetation

clear statement regarding a shift from a positive productivity–diversity relationship to none or a negative one (i.e., unimodal). We hypothesize that in the current successional stage, i.e., about 40 year since site preparation and planting, UWV diversity is limited by water availability throughout most of the studied climatic range. However, at the upper end of the rainfall gradient, a limitation resulting from interspecific competition within the understory is becoming apparent. This finding is supported by our observation that UWV diversity increased sharply with increasing vegetation abundance up to nearly 100% cover and 1-m height, i.e., specific volume about 1 $m^3 \times m^{-2}$), whereas further increase in understory abundance, i.e., in specific volume, was not associated with further increase in diversity. We hypothesize that competitive interactions within the understory vegetation might become increasingly important and more evident in dryer zones also, as the succession progresses and the understory vegetation approaches full surface cover in additional forest areas.

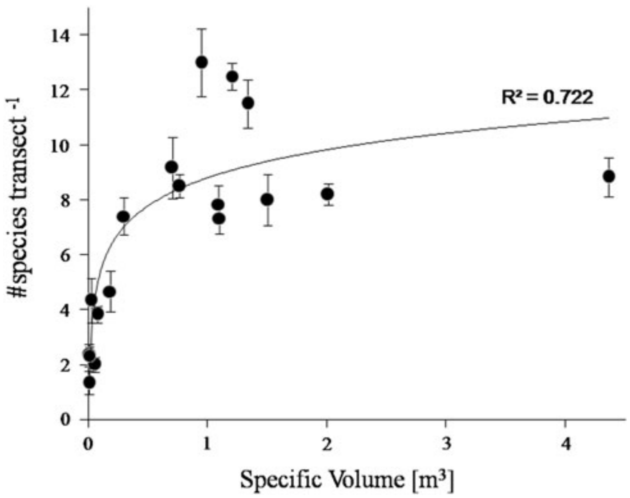

Fig. 5 The relationship between species richness and specific volume of the forest understory woody vegetation

General conclusion

The spontaneous development of a diverse native woody vegetation layer in the understory of *P. halepensis* plantations is a process of major importance with regard to the structure and function of these manmade systems. We found this process to be strongly determined by rainfall amount throughout the studied climatic range, i.e., annual rainfall ranging from 280 to 900 mm × year^{-1}. The importance of water availability as a predominant limiting factor, also at the wetter end of the rainfall gradient, may be attributed, to some extent, to negative effects of the planted pines on the water balance, which cause the forest understory to be exposed to more stressful conditions than those in unforested habitats. Another explanation for the observed strong relationships between rainfall amount and UWV structure may lie in the fact that the studied systems

Table 6 Ordination of the common understory woody species along the rainfall gradient

Semiarid dry Mediterranean	Mediterranean	Mesic Mediterranean
Asparagus horridus Mediterranean, semiarid, arid (Vine)	*Clematis cirrhosa* Mesic Mediterranean (Vine) *Lonicera etrusca* Mesic, Mediterranean, semiarid (Vine) *Asparagus aphyllus* Mediterranean, semi arid (Vine)	*Pistacia palaestina* Mediterranean, semiarid (Tree)
Phagnalon rupestre Mediterranean, semiarid, arid (Dwarf shrub)	*Ceratonia silliqua* Mesic, Mediterranean, semiarid (Tree)	*Arbutus andrachne* Mesic, Mediterranean (Tree)
Teucrium capitatum Mediterranean, semiarid, arid (Dwarf shrub)	*Rhamnus alaternus* Mediterranean (Tree)	*Cistus creticus* Mesic, Mediterranean, semiarid (Dwarf shrub)
Ephedra foeminea Mediterranean, semiarid (Vine)	*Rhamnus lycioides* Mesic, Mediterranean, semiarid (Shrub)	*Smilax aspera* Mesic, Mediterranean (Vine)
Ballota undulate, Mediterranean, semiarid, arid (Dwarf shrub)	*Phlomis viscose* Mesic, Mediterranean (Dwarf shrub)	*Quercus calliprinos* Mesic, Mediterranean, semiarid (Tree)
Prasium majus Mediterranean, semiarid (Vine) (Dwarf shrub)	*Phillyrea latifolia* Mediterranean (Tree)	*Styrax officinalis* Mesic, Mediterranean, semiarid (Tree)
Sarcopoterium spinosum Mediterranean, semiarid, arid (Dwarf shrub)	*Pistacia lentiscus* Mediterranean (Shrub)	*Cistus salviifolius* Mesic, Mediterranean, semiarid (Dwarf shrub)
Amygdalus communis Mediterranean (Tree)	*Rubia tenuifolia* Mesic, Mediterranean, semiarid (Vine) .	*Crataegus aronia* Mesic, Mediterranean, semiarid (Tree)
Majorana syriaca, Mediterranean, semiarid (Dwarf shrub)	*Calicotome villosa* Mesic, Mediterranean, semiarid (Shrub)	*Laurus nobilis* Mesic, Mediterranean (Tree)
Micromeria fruticosa Mediterranean (Dwarf shrub)	*Salvia fruticosa* Mediterranean (Dwarf shrub)	*Quercus boissieri* Mesic, Mediterranean (Tree)

The species are ordered according to their distribution along the rainfall axes, i.e., starting from the top of the left column the species that was associated with the driest sites (read down the column and then right) and ending at the bottom of the right column the one that was associated with the most humid sites were still relatively young, so that the role of competitive interactions had not yet reached its full potential. Our findings should not exclude light availability as an important limiting factor in the forest understory; water and light are complementary factors in limiting growth, and their relative importance depends mainly on temporal and spatial variations in soil moisture. We suggest that the design and management of Mediterranean forests should be more strongly focused on allocation of the water resource among the various forest components. The following practical implications may be offered: (a) forest thinnings should be prescribed according to habitat water condition and related carrying capacity, (b) understory control by thinning and/or grazing may be implemented to increase water availability for the overstory and (3) silvicultural strategies regarding forest regeneration and diversity should focus on optimizing water availability to the understory. Accordingly, considerations of water consumption and competition should be taken in mind along with considerations of microclimate and facilitation.

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