LAND DEGRADATION & DEVELOPMENT
Land Degrad. Develop. **27**: 1424–1431 (2016)
Published online 1 September 2015 in Wiley Online Library (wileyonlinelibrary.com) **DOI**: 10.1002/ldr.2419

RECOVERY OF MEDITERRANEAN VEGETATION AFTER RECURRENT FOREST FIRES: INSIGHT FROM THE 2010 FOREST FIRE ON MOUNT CARMEL, ISRAEL

Naama Tessler[1,2]*, Yuval Sapir[3], Lea Wittenberg[1], Noam Greenbaum[1,4]

[1]*Department of Geography and Environmental Studies, University of Haifa, Haifa 3498838, Israel*
[2]*Department of Biology and Environment, Faculty of Natural Sciences, University of Haifa–Oranim, Tivon, Israel*
[3]*The Botanical Garden, Department of Molecular Biology and Ecology of Plants, Tel Aviv University, Tel Aviv 69978, Israel*
[4]*Department of Natural Resources and Environmental Management, University of Haifa, Haifa 3498838, Israel*

Received: 22 April 2015; Revised: 2 August 2015; Accepted: 2 August 2015

ABSTRACT

The December 2010 forest fire on Mount Carmel – the largest recorded in Israel – burned about 2500 ha of Mediterranean forest. We documented the immediate and short-term changes of the vegetation following this fire. Relative vegetation cover and plant species richness were sampled in five sites in spring 2009 and 2010, prior to the fire, and were re-sampled in 2011 and 2012. The number of recurrent fires (between 0 and 3) and time intervals between fires were documented for each site. We observed a strong decrease in total vegetation cover, associated with reduction of relative cover of woody vegetation. In the second year after the fire, shrubs and dwarf shrubs became dominant at all sites. Time intervals between fires played an important role in determining the extent of regeneration of the vegetation cover and plant species richness. Plant species richness immediately decreased after the fire in sites with a short fire interval, while in sites with a long fire interval, plant species richness increased. Relative plant cover was associated with the time from the last previous fire, and this association differed among different plant groups. These results suggest that vegetation and plant community regeneration after recurrent fires is accelerated when time intervals between fires are longer, whereas high fire frequency may suppress vegetation regeneration. Based on the results, we propose that forest regeneration after recurrent fires depends largely on time from the previous fire, rather than on the number of previous fires. Copyright © 2015 John Wiley & Sons, Ltd.

KEY WORDS: Mediterranean maquis; Mount Carmel; recurrent forest fires; short-term changes; vegetation cover

INTRODUCTION

Wildfires have important impacts on the Earth's ecosystems, including soil properties, runoff and erosion, vegetation composition and biomass. Wildfires often have negative implications on human societies and are a cause of land degradation (Cerdà, 1998 a, b; Martín *et al*., 2012; Guénon *et al*., 2013; Carreiras *et al*., 2014; Keesstra *et al*., 2014; Pereira *et al*., 2014). The impact of fires can damage the soil system, and then the benefits that soils offer can be lost, which will trigger the desertification processes (Keesstra *et al*., 2012; Brevik *et al*., 2015).

Fire is a frequent disturbance and a dominant factor in the evolution and ecology of Mediterranean areas (Ne'eman, 1997; Schaffhauser *et al*., 2012; León *et al*., 2013; Navora *et al*., 2013; Hedo *et al*., 2014). Ash is also an important factor that controls nutrient and erosional response and may change all ecological systems (Pereira *et al*., 2015).

Although most fires in the Mediterranean basin are anthropogenic rather than natural (Keidar, 2001; Espelta *et al*., 2008), fire frequency is expected to increase owing to global warming, resulting in increasing temperature and evapotranspiration (Díaz-Delgado *et al*., 2002; Pausas, 2004; Herman, 2009), changes in precipitation regime and decrease in the length of the rainy season (Wittenberg *et al*., 2007a). Other factors, such as changes in land use, fire suppression and rural abandonment, influence the increase in fire frequency (De Luis *et al*., 2003; Úbeda *et al*., 2006; Pérez-Cabello *et al*., 2010; Carreiras *et al*., 2014). Studies show an increase in the number and area of fires, as well as in fire frequency, resulting in recurrent fires (Pausas *et al*., 2008). Thus, the effect of recurrent fires on vegetation regeneration after fires becomes a relevant question for ecological management of burnt areas.

Mediterranean-type ecosystems are generally resilient to forest fire, mainly owing to the high proportion of plant species adapted to fires (Naveh, 1990). Post-fire plant species composition tends to revert to pre-fire composition through auto-succession or direct regeneration (Hanes, 1971; Buhk *et al*., 2007). However, fire frequency may change the vegetation cover and community structure (Naveh, 1990; Lloret & Montserrat, 2003; Lloret *et al*., 2003). An increase in fire frequency prevents reversion to pre-fire condition of the forest vegetation and homogenizes the vegetation into shrubland or grassland, regardless of the pre-fire species composition (Moreira *et al*., 2011). Recurrent fires reduce vegetation cover and plant density (Lloret *et al*., 2003; Eugenio & Lloret, 2004, 2006; Delitti *et al*., 2005; Eugenio *et al*., 2006; Herman, 2009), but their effect on plant species

*Correspondence to: N. Tessler, Department of Geography and Environmental Studies, University of Haifa, Haifa, 3498838 Israel.
E-mail: naamates@gmail.com

Copyright © 2015 John Wiley & Sons, Ltd.

richness is not clear – increasing (Delitti *et al*., 2005) or decreasing it (Goudelis *et al*., 2007). Species-relative abundance is also affected by recurrent fires; for example, the population of the common shrub *Ceanothus oliganthus* Nutt nearly became extinct in California owing to recurrent fires (Zedler *et al*., 1983). The time interval between successive fires also plays a crucial role in vegetation resilience. Increase in plant biomass after recurrent fires is positively correlated to the time between two successive fires (Díaz-Delgado *et al*., 2002).

Biological traits of the dominant species can also affect the rate and direction of forest post-fire resilience. For example, Díaz-Delgado *et al*. (2002) showed that forests dominated by resprouting *Quercus* spp. were more resilient than *Pinus* spp. forests after the second fire. The transformation of tree-dominated landscape into shrubland or grassland after recurrent fires is mostly due to elimination of species that require a relatively long recovery time, such as *Pinus halepensis* Mill., which requires 15–20 years to fully recover after fire (Eugenio *et al*., 2006; Moreira *et al*., 2011; Tessler *et al*., 2014). Short intervals between recurrent fires reduce the time available for dominant species to re-establish before the next fire (Beckage & Jack, 2000; Delitti *et al*., 2005) and change the regeneration ability of species that regenerate by seeders ('obligate-seeders') and species that regenerate by resprouting (Keeley, 1986; Beckage & Jack, 2000; Delitti *et al*., 2005).

The present study examined the patterns of vegetation resilience after recurrent fires in Mediterranean forest and maquis, following the December 2010 fire on Mount Carmel. This fire, in an area susceptible to recurrent fires (Tessler *et al*., 2012), provided a unique opportunity to study the effect of recurrent fires on vegetation properties and rehabilitation. The objectives of this study were as follows: (i) to assess the effect of recurrent fires on species richness and community structure during the dynamics of vegetation recovery; (ii) to test the effect of different intervals between recurrent fires on vegetation recovery; (iii) to estimate the synergistic effect between number and time intervals between recurrent fires on vegetation recovery; and (iv) to quantify the short-term dynamic of vegetation recovery.

Although there is a considerable amount of knowledge on post-fire forest regeneration, there is still a gap in understanding the short-term processes shortly after fire. In addition, most studies on the effect of recurrent fires on vegetation cover used remote sensing analyses (Wittenberg *et al*., 2007b; Malkinson *et al*., 2011), but their ability to detect regeneration of the vegetation community or to identify the structure of the vegetation communities is limited. Our study provides a unique high-resolution short-term documentation of the dynamics of the vegetative recovery process. Specifically, we (i) partitioned the vegetation into functional plant groups, (ii) introduced the effect of time interval between recurrent fires and (iii) documented the immediate effect of fires. Introducing these three components into the study of post-fire vegetation recovery provides a detailed view into the dynamics and enables us to identify processes otherwise masked.

Incidentally, shortly before the 2010 fire, we performed vegetation sampling in Mount Carmel (Tessler, 2013). This offered an opportunity to document the initial recovery by re-sampling these sites immediately after the 2010 fire and during the following year, and to compare the results with the pre-fire situation. Here, we present the results of this sampling and test the hypotheses of different pathways by which recurrent fires and the intervals between them affect vegetation resilience in a Mediterranean forest.

A recent study of Mount Carmel, which compared the effect of recurrent fires on the vegetation cover using remote sensing, suggested that recurrent fires reduce the cover of woody vegetation (trees, shrubs and dwarf shrubs) at a regional scale (Malkinson *et al*., 2011). While the interaction between the number of fires and the time between them is important, there is also evidence that the negative effect of recurrent fires on woody plant cover is independent of the time interval between successive fires (Delitti *et al*., 2005). This supports the expectation that species composition change in Mount Carmel will be accompanied by a change in vegetation cover during the recovery after the 2010 fire.

MATERIALS AND METHODS

The December 2010 fire was the largest forest fire ever recorded in Israel. The fire burned about 2500 ha of natural and planted forest. The fire spread rapidly owing to the large amount of dry biomass (fuel) that had accumulated on the surface over many years, and specifically after the extremely dry 8 months since the end of the rainy season prior to the fire (Kutiel, 2012). Low humidity (20%) and strong easterly winds (above $40\,\mathrm{km\,h^{-1}}$; Paz *et al*., 2011) facilitated the spread of the fire over a large area. The fire burned about a third of the area of Mount Carmel National Park ($>3\times10^6$ trees) and caused 44 fatalities and extensive damage to settlements and to the Nature Reserve (Perevolotsky *et al*., 2011; Tessler, 2012; Ne'eman *et al*., 2013).

Mount Carmel is a mountain range rising from the northern Mediterranean coast of Israel to an elevation of 546 m above sea level, isolated by a belt of surrounding lowlands (Figure 1). The climate in Mount Carmel is typical Mediterranean: hot dry summers and rainy winters, with average annual precipitation of up to $750\,\mathrm{mm\,y^{-1}}$ at the highest parts and about $550\,\mathrm{mm\,y^{-1}}$ along the coast (Kutiel, 2012). The mean annual temperature is 11·2 °C in January and 24·7 °C in August (Ashbel, 1970). Mean annual potential evaporation exceeds $1500\,\mathrm{mm\,y^{-1}}$.

The bedrock is composed of Upper Cretaceous carbonate rocks, including limestone, chalk, dolomite, marls and some intrusions of volcanic tuff, which create a heterogenic landscape (Karcz, 1959; Kashai, 1966; Zilberman *et al*., 2006; Segev & Sass, 2009). The typical soils in the region are Brown Rendzina (Haploxerolls, Xerochrepts) and Terra Rossa (Xerochrepts, Rhodoxeralfs) (Soil Survey Staff, 2006). Both soil types are reddish-brown in colour, with a silty-clay loam texture, and contain considerable amounts of rock clasts. Some Grey Rendzina rich in lime covering soft

Copyright © 2015 John Wiley & Sons, Ltd.

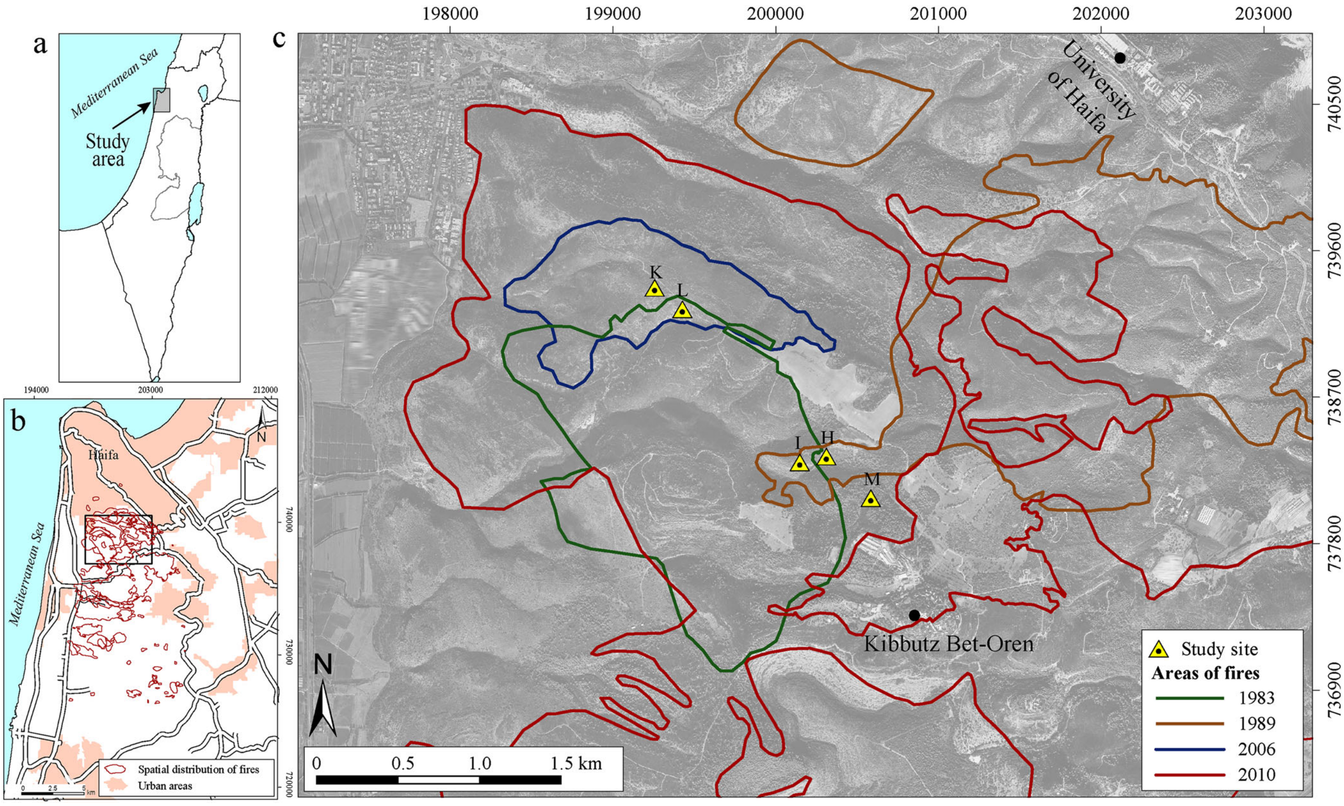

Figure 1. Map of the 2010 fire in the Mt. Carmel (solid outline), fires before 2010 (dashed line) and location of study sites (triangles). This figure is available in colour online at wileyonlinelibrary.com/journal/ldr.

chalk is located in the north-facing slopes (Komyumdjisky *et al*., 1966; Dan *et al*., 1972; Dan & Komyumdjisky 1979; Yaalon, 1995).

The vegetation on Mount Carmel is a typical Mediterranean forest and maquis, consisting of both natural and planted *P. halepensis* Mill. (Ne'eman *et al*., 1995; Schiller *et al*., 1997; Tessler *et al*., 2014). *Quercus calliprinos* Webb. occurs in a more open and patchy mosaic of maquis and open shrubland. The open patches are dominated by either shrubs (dominated by *Cistus salviifolius* Webb. and *Cistus creticus* L.), or herbaceous vegetation, which occur among the *Pinus* spp. trees (Zohary, 1962; Izhaki *et al*., 2000). Pre-fire vegetation in all study sites was composed of natural, long-standing (80–100 years), mixed forest of *P. halepensis* Mill., *Q. calliprinos* Webb. and a dense understorey of shrubs and dwarf shrubs (Lorentzen *et al*., 2009). Early auto-succession vegetation after fires consists of seedlings of *P. halepensis* Mill., which compete with seedlings of both *Cistus* spp. and thorny shrubs such as *Calicotome villosa* Poir. and *Genista fasselata* Decne. (Ne'eman *et al*., 1992; Ne'eman, 1997; Eshel *et al*., 2000).

All study sites were located in the higher part of Mount Carmel, about 350 m above sea level, on south-facing slopes in five areas that were re-burnt (Figure 1 and Table I). Each fire area is represented by a site of 0·1–0·3 ha, selected in a previous study by Tessler (2013) to represent different numbers of fires. The study area is a National Park, and the study sites remained with no management practices and gave a good opportunity to follow the natural vegetation recovery with no human action.

The study examined the effect of recurrent fires on vegetation cover, plant species richness and species composition in five sites, differing by the following: (i) number of previous fires and (ii) time elapsed since the last fire. The study sites were burnt during the 1983, 1989, 2006 and 2010 fires. Three categories were analysed: single-fire sites, two-fire sites and three-fire sites. Sampling was performed at three time periods. Pre-fire sampling was performed in spring 2009 (Sites H and I in Table I) and in spring 2010 (Sites M, K and L in Figure 1), prior to the 2010 fire. These samplings were performed as a part of a research project aimed at testing the effect of recurrent forest fires on soil and vegetation (Tessler *et al*., 2012; Tessler, 2013). The second sampling took place at all sites in spring 2011, 4 months after the fire. The third sampling was performed in spring 2012, 16 months after the fire.

Vegetation cover and species richness were measured along randomly placed linear transects (Stohlgren, 2007).

Table I. Study plots and their fire history

Single fire	Two fires	Three fires
M (2010)	H (1989; 2010) K (2006; 2010)	I (1983; 1989; 2010) L (1983; 2006; 2010)

Years of fires of each site are in parentheses.

Copyright © 2015 John Wiley & Sons, Ltd.

Each plant on the line was recorded, as well as its cover along the transect. The total sampling length of transects before the 2010 fire was 240 m in each site. Preliminary analyses showed that optimal sampling must be 100 m in order to obtain satisfactory plant species richness, where 240 m sampling is too long and does not provide significant increase in the information (data not shown). Hence, the total length of the sampling transects in 2011 and 2012 seasons was reduced to 100 m.

Plants recorded along the transects were divided into three main groups: (i) 'herbaceous', including geophytes and annuals; (ii) 'trees', including mature trees (unless died in the fire), sprouting trees (such as *Q. calliprinos* Webb.) and seedlings of trees (mostly of *P. halepensis* Mill.); and (iii) 'shrubs', including shrubs and dwarf shrubs such as *Pistacia lentiscus* L., *C. salviifolius* Webb. and *Micromeria nervosa* Desf. We also sampled exposures of bare soil and rock. The relative vegetation cover of each group was calculated as the length of the transect segment covered by vegetation, divided by the total transect length.

All plants were identified to the species level. Species were recorded as either 'present' or 'absent' in each site and in each sampling period. Plant species richness was defined as the number of species recorded along the transect.

All statistical analyses were performed in R software (R Development Core Team, 2011). We used generalized linear model (GLM) to analyse the vegetation cover of each vegetation type (in %) as a function of sampling period (before the 2010 fire, and one and two seasons after the fire), time interval between the 2010 fire and the previous fire (either 4 or 21 years) and the number of fires before the 2010 fire (zero, one or two). It is important to note that all sites were burnt in 2010; hence, the total number of fires in the sites was one, two or three, respectively. Initially, we performed GLM with all the factors and their interactions and compared this full model with nested ones using the Akaike information criterion to test for the contribution of each factor.

To test for possible changes in species composition, we recorded for each species whether it was present or absent in each site and each sampling period. For each plot separately, we produced a list of all the species that were recorded in at least one sampling. A species was scored as '1' if present in a sampling and '0' if absent. Hence, the number of species present in a certain year is taken from a specific (observed) species pool, and thus, the presence of a species in a plot was assumed to be taken from a binomial distribution. We performed GLM with binomial distribution to test for the effect of site and sampling period on species richness.

RESULTS

The relative cover before the 2010 fire was the highest (192%) in the area that was not burnt before 2010 (Site M) and was reduced in all plots after the fire (Table II). Total cover at all sites decreased from between 112% and 192% before the 2010 fire to less than 100% (up to 70%) after the fire. Although an increase in the relative cover was documented at all sites between the first and second sampling seasons after the fire, only in Site M, which was not burnt before 2010, did the relative cover increase to slightly over 100% in the second year (Figure 2).

Tree species composition after the fire was dominated by *P. halepensis* Mill., *Q. calliprinos* Webb., *Rhamnus alaternus* L., *Pistacia palaestina* Boiss. and *P. halepensis* Mill., similar to that prior to the fire.

In Site M, which was not burnt before 2010, the relative cover of trees decreased from 93·4% before the fire to less than 6·5% in the first sampling after the fire, and to less than 3·2% in the following year (Table III). This was mostly due to delayed death of mature *P. halepensis* Mill. trees that survived the fire (also Tessler *et al*., 2014).

The relative vegetation cover of the various vegetation types changed significantly through time after the 2010 fire (Table IV). The relative cover of trees in both sites that were burned in 1989 and 2006 was initially low (average of 27% and 8%, respectively) and decreased to an average of less than 2% in both sites after the 2010 fire (Table III). The recovery of trees in the second year was low in these sites (5·2% and 2·9%, respectively; Table III). In the sites that were previously burnt in 2006 (Sites K and L), the relative cover of shrubs and dwarf shrubs was similar before 2010 (average of 88%). Immediately after the 2010 fire, the relative shrub and dwarf shrub cover decreased to 1·4–17% at all sites and increased to 20–59% in the following year. In the site that was not burnt before 2010 (Site M), the relative cover of shrubs and dwarf shrubs was 50·7% before the 2010 fire and reached 40·8% in the second year after the fire

Table II. Number of plant species and total vegetation relative cover in five plots in Mount Carmel before the 2010 fire and in the following years

			Before 2010 fire		2011		2012	
Plot	Fires	Interval	Spp.	Tot.co.	Spp.	Tot.co.	Spp.	Tot.co.
H	2	21	39	124	41	70	79	94
I	3	21	49	142	57	82	61	92
K	2	4	91	127	41	96	53	91
L	3	4	91	112	68	78	81	86
M	1	0	52	192	36	100	43	103

Fires, number of fires that occurred in the sample area (2010 fire included); Interval, years between the 2010 fire and the previous fire (0 denotes no previous fires); Spp., number of species; Tot.co., total vegetation cover (%).

Copyright © 2015 John Wiley & Sons, Ltd.

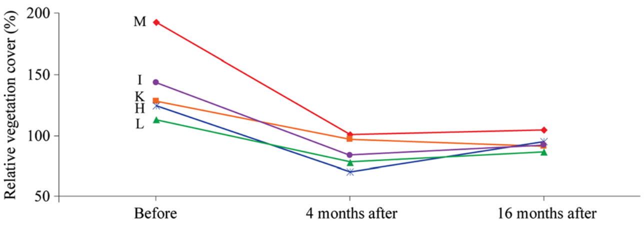

Figure 2. Relative vegetation cover (%) before the 2010 fire and in the first and second years after the fire. M – control site, not burnt before 2010; K and H – one fire before 2010; L and I – two fires before 2010; K and L – last fire in 2006; H and I – last fire in 1989. This figure is available in colour online at wileyonlinelibrary.com/journal/ldr.

(Table III). The relative cover of herbaceous species increased at all sites immediately after the 2010 fire and decreased in the following year almost to the same level as before the fire at all sites (Table III).

The differential change in time of the relative cover of the various vegetation types was also affected by the number of fires before the 2010 fire (Tables IV and V). On the contrary, the time interval between the 2010 fire and the previous fire did not affect this change in relative cover (Table IV).

A total of 278 species were recorded in this study in all sampling sites and years. Prior to the 2010 fire, the number of species varied between plots according to the time since the previous fire (Table II). Species composition was significantly different between sampling periods, nested within sites (analysis of variance with binomial distribution: $F_{10,\,1638} = 10{\cdot}60$, $p < 0{\cdot}001$). In all sites, species composition before the 2010 fire was significantly different from that after the 2010 fire (contrast analyses, $p < 0{\cdot}05$; Figure 3).

Table IV. Results of analysis of variance for the differences of plant groups, year of sampling and time from the last fire on relative vegetation cover

Source	DF	SS	*F* value	Significance
Cover type	4	15,605	71·53	$p < 0{\cdot}001$
Year	2	3,923	35·97	$p < 0{\cdot}001$
Number of previous fires	2	202	1·85	$p = 0{\cdot}191$
Time from last fire	1	10	0·18	$p = 0{\cdot}675$
Cover type × year	8	14,225	32·6	$p < 0{\cdot}001$
Cover type × number of previous fires	8	5,656	12·96	$p < 0{\cdot}001$
Cover type time from × last fire	4	3,827	17·54	$p < 0{\cdot}001$
Cover type × year × number of previous fires	20	5,725	5·25	$p < 0{\cdot}001$
Cover type × year × time from last fire	10	874	1·6	$p < 0{\cdot}05$
Residuals	15	818		

Significant effects are marked in bold.

DISCUSSION

Our results indicate clear differences between short-term and long-term dynamics. We found that differential long-term dynamics among sites were associated with differences in the number of previous fires and time intervals between them (Tessler, 2013; Tessler *et al.*, 2014).

Dramatic changes in vegetation cover and plant species richness immediately after the December 2010 fire, in comparison with those of the next season, were found at all sites (Table III and Figure 3). A decrease in vegetation cover was expected to occur after a fire, where even low fire severity changes the vegetation (Lavorel, 1999; Brown & Smith, 2000). Similar to our results, a general increase in vegetation cover was documented in Mount Carmel 3 years after recurrent fires using remote sensing techniques by Malkinson *et al.* (2011).

Although Mediterranean species are resilient to fire, short intervals between recurrent fires affect the persistence of some species. However, different plant functional types differ in their persistence, a difference that also depends on the history of the burnt area (Morrison *et al.*, 1995; Lavorel, 1999; Lloret & Vila, 2003; Delitti *et al.*, 2005; Syphard *et al.*, 2006; Tessler, 2013).

Plant functional types showed differential recovery rates in our sampling sites (Table III). Tree cover before the fire was higher in the plot that was not burnt than in plots that experienced recurrent fires (Figure 2). Nevertheless, immediately after the fire, herbaceous plants were the dominant group at all burnt plots, as previously shown by Trabaud & Lepart (1981). In the second year after the fire, shrubs dominated the burnt areas, but this dominance varied among sites with different time intervals between fires (Table III). Similarly to our findings, other studies also showed a lower recovery rate of some woody species as a result of recurrent fires (Espelta *et al.*, 2008; Herman, 2009). Recurrent fires have different effects on seeders and resprouters. Seeders, such as *P. halepensis*, require a relatively long period before renewing the canopy-stored seeds (Ne'eman *et al.*, 2004; Tessler *et al.*, 2014), whereas resprouters, such as

Table III. Relative cover (%) of three plant groups before the 2010 fire and in the first and second seasons after the fire

	Control sites			2006–last fire before 2010			1989–last fire before 2010		
	Before	4 months	16 months	Before	2011	2012	Before	2011	2012
Herbaceous	41·3	20·9	53·0	55·8	70·9	61·9	16·8	45·3	30·3
Trees	93·4	6·5	3·2	8·1	0·0	2·9	27·0	1·5	5·2
shrubs and dwarf shrubs	50·7	1·4	40·8	88·1	5·8	25·8	88·4	13·6	55·8

Results were averaged for sites that experienced the last fire before 2010 in the same year (K, L and H, I).

Copyright © 2015 John Wiley & Sons, Ltd.

Table V. Mean relative cover (%) before and after the 2010 fire

	A – before 2010 fire				B – 4 months after the fire				C – 16 months after the fire			
Sites	Tot.co.	Tre.	Shr.	Her.	Tot.co.	Tre.	Shr.	Her.	Tot.co.	Tre.	Shr.	Her.
M	192·1	93·3	50·6	41·3	100·4	6·5	1·4	20·8	103·8	3·2	40·8	53·0
H + K	125·9	22·8	78·3	36·5	83·2	0·4	6·5	55·5	92·8	5·7	36·5	51·5
I + L	127·9	12·2	98·1	36·1	80·5	1·0	12·8	60·7	89·3	2·3	45·0	40·6

Sites, sampling site divided to groups of fire numbers; Tot.co., total vegetation cover (%); Tre., trees; Shr., shrubs and dwarf shrubs; Her., herbaceous.

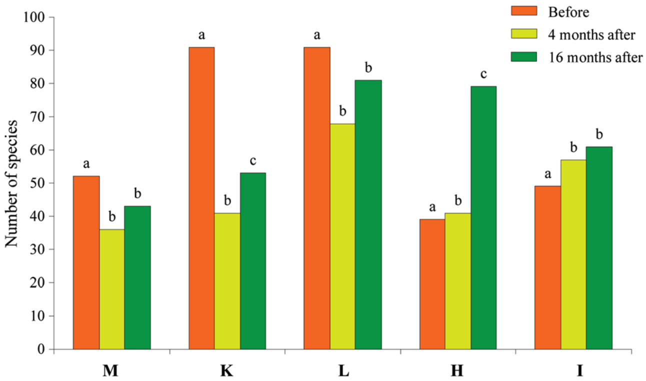

Figure 3. Number of species in the study sites before 2010 fire, and in the following 2 years. Site M – control, not burnt before 2010; K and H – one fire before 2010; L and I – two fires before 2010; K and L – last fire in 2006; H and I – last fire in 1989. Different letters above bars within site denote significant differences in species composition in years (analysis of variance with binomial distribution, contrast analysis, $p < 0.05$, see text). This figure is available in colour online at wileyonlinelibrary.com/journal/ldr.

Q. calliprinos Webb., suffer from short intervals between fires as well, because of the exhaustion of stumps and roots (Trabaud & Lepart, 1981) and because of the lower nutrient availability in areas experiencing recurrent fires (Pausas *et al*., 2003; Eugenio *et al*., 2006).

Shrub cover in the second year after the fire was higher in sites with longer periods between recurrent fires (21 years; Table III) and increased by an average of 55%, compared with an average of 25% for sites with a shorter period between recurrent fires (4 years). This is in contrast to the findings of Delitti *et al*. (2005), where herbaceous and dwarf shrub species cover was shown to be higher in sites with fire intervals of more than 3 years than in sites that were burnt more frequently. As of now, we are not aware of any hypothesis that can test for the reason for such differences.

Although plants in Mediterranean environments show high post-fire regeneration ability (Trabaud *et al*., 1985; Naveh, 1990), our results suggest that the extent of vegetation recovery is related to the time elapsed since the last fire. We found that post-fire plant species richness varied according to the history of the fires, specifically owing to the time since the previous fire (Table V). While plant species richness decreased in sites that were burnt a short time (4 years) before the 2010 fire, it increased in sites with longer periods (20 years) since the previous fire. As previous studies have suggested, an increase of fire frequency in Mediterranean-type ecosystems reduces ecosystem resilience (Keeley *et al*., 1999; Lavorel, 1999; Díaz-Delgado *et al*., 2002; Pausas *et al*., 2008; Nijhuis, 2012). Other studies documented an increase in plant species richness (Watson & Wardell-Johnson, 2004; Delitti *et al*., 2005). For example, Delitti *et al*. (2005) indicated that the most recurrently burnt areas with short fire intervals showed higher species richness, mainly the herbaceous and subshrub species group, and of these, the hemicryptophytes.

Reduced species richness and lower relative plant cover in areas with 3-year recurrent fires were documented by Goudelis *et al*. (2007). While the difference between species richness before and after the fire was correlated to the time since the last fire, species composition was affected mainly by the number of recurrent fires. Species composition in the site where the 2010 fire was the first documented fire was not significantly different from the first and second seasons after the fire in sites that experienced recurrent fires before 2010 (Figure 3).

Overall, the present study showed that the areas that, prior to the 2010 fire, had reached the stage of 'young forest' because of the longer time interval between the fires recovered better after the 2010 fire, while sites previously dominated by shrubs, owing to a shorter time interval between the fires, had not recovered well. We conclude that the time interval between fires plays a crucial role in vegetation resilience following forest fire, such as the Carmel 2010 fire. We argue that this study contributes to the knowledge on post-fire vegetation recovery because it concentrates on the effect of both the number of fires and the time between recurrent fires on vegetation recovery and plant species richness. This study elucidates both long-term and short-term recovery dynamics and thus sheds light on the expected regeneration processes in the coming years.

CONCLUSIONS

Our conclusions are drawn in a few levels. First, we conclude that the particular combination of vegetation and intervals between fires, namely, shrub-dominated vegetation that underwent longer intervals between fires, recovered better than sites with shorter intervals between the fires. Second, we conclude that vegetation response to fire in the short term is affected by the time elapsed from the previous fire. Third, we conclude that species composition and community structure are influenced by the number of recurrent fires. Finally, these conclusions were revealed mainly owing to the sampling performed immediately after the fire. We argue that sampling vegetation recovery immediately after the fire is

Copyright © 2015 John Wiley & Sons, Ltd.

crucial for partitioning accurately the combined effect of number of recurrent fires and time intervals between them on vegetation and species richness recovery. Unless measured immediately after the 2010 fire, such partitioning would have been obscured.

ACKNOWLEDGEMENTS

This research was supported by a grant from the Israeli Nature and Parks Authority and by a grant from the Mount Carmel Research Institute. We would like to thank Tal Porat, Ella Provizor, Amit Kliner, Lior Negreen, Inbar Hashmonay, Tzlil Didner and Eyal Cohen for their help in the fieldwork. Natan Elbaz and Naftali Gdalyahu of the Carmel Park of the Israel Nature Parks Authority provided logistic support. Aerial photographs and other valuable data were kindly provided by the Jewish National Fund. Noga Yoselevich helped with the cartography and graphics illustrations.

REFERENCES

Ashbel D. 1970. The climate of Haifa. The Hebrew University of Jerusalem (Hebrew): Jerusalem.

Beckage B, Jack I. 2000. Effects of repeated burning on species richness in a Florida pine savanna: a test of the intermediate disturbance hypothesis. *Journal of Vegetation Science* **11**: 113–122.

Brevik EC, Cerdà A, Mataix-Solera J, Pereg L, Quinton JN, Six J, Van Oost K. 2015. The interdisciplinary nature of soil. *SOIL* **1**: 117–129. DOI:10.5194/soil-1-117-2015.

Brown JK, Smith JK. (eds). 2000. Wildland fire in ecosystems: effects of fire on flora. United States Department of Agriculture, Forest Service, Rocky Mountain Research Station [General Technical Report RMRS-GTR-42-vol. 2]

Buhk C, Meyn A, Jentsch A. 2007. The challenge of plant regeneration after fire in the Mediterranean Basin: scientific gaps in our knowledge on plant strategies and evolution of traits. *Plant Ecology* **192**: 1–19.

Carreiras M, Ferreira AJD, Valente S, Fleskens L, Gonzales-Pelayo Ó, Rubio JL, Stoof CR, Coelho COA, Ferreira CSS, Ritsema CJ. 2014. Comparative analysis of policies to deal with the wildfire risk. *Land Degradation & Development* **25**: 92–103. DOI: 10.1002/ldr.2274.

Cerdà A. 1998a. Post-fire dynamics of erosional processes under Mediterranean climatic conditions. *Zeitschrift für Geomorphologie* **42**: 373–398.

Cerdà A. 1998b. Changes in overland flow and infiltration after a rangeland fire in a Mediterranean scrubland. *Hydrological Processes* **12**: 1031–1042.

Dan J, Komyumdjisky H. (eds.). 1979. The classification of Israel soils, Committee on Soil Classification in Israel. Special Publication No. 137, Institute of Soils and Water, Agricultural Research Organization, Bet Dagan, Israel [Hebrew with English abstract].

Dan J, Yaalon D, Komyumdjisky H. 1972. Catenary soil relationships in Israel: II. The Beit Guvrin catena on chalk and nari limestone crust in the Shefela. *Israel Journal of Earth Sciences* **21**: 99–114.

De Luis M, González-Hidalgo JC, Raventós J. 2003. Effects of fire and torrential rainfall on erosion in a Mediterranean gorse community. *Land Degradation & Development* **14**: 203–213. DOI:10.1002/ldr.547.

Delitti WA, Ferran L, Trabud L, Vallejo VR. 2005. Effects of fire recurrence in *Quercus coccifera* L. shrublands of the Valencia region (Spain): I. Plant composition and productivity. *Plant Ecology* **177**: 50–70.

Díaz-Delgado R, Lloret F, Pons X, Terradas J. 2002. Satellite evidence of decreasing resilience in Mediterranean plant communities after recurrent wildfires. *Ecology* **83**: 2293–2303.

Eshel A, Henig-Sever N, Ne'eman G. 2000. Spatial variation of seedling distribution in an east Mediterranean pine woodland at the beginning of post-fire succession. *Plant Ecology* **148**: 175–182.

Espelta JM, Verkaik I, Eugenio M, Lloret F. 2008. Recurrent wildfires constrain long-term reproduction ability in *Pinus halepensis* Mill. *International Journal of Wildland Fire* **17**: 579–585.

Eugenio M, Lloret F. 2004. Fire recurrence effects on the structure and composition of Mediterranean *Pinus halepensis* communities in Catalonia (northeast Iberian Peninsula). *Ecoscience* **11**: 446–454.

Eugenio M, Lloret F. 2006. Effects of repeated burning on Mediterranean communities of the northeastern Iberian Peninsula. *Journal of Vegetation Science* **17**: 755–764.

Eugenio M, Verkaik I, Lloret F, Espelta JM. 2006. Recruitment and growth decline in *Pinus halepensis* populations after recurrent wildfires in Catalonia (NE Iberian Peninsula). *Forest Ecology and Management* **231**: 47–54.

Goudelis G, Ganatsas PP, Spanos I, Karpi A. 2007. Effect of repeated fire on plant community recovery in Penteli, central Greece. *Eco-and Ground Bio-engineering: The Use of Vegetation to Improve Slope Stability* **103**: 337–343.

Guénon R, Vennetier M, Dupuy N, Roussos S, Pailler A, Gros R. 2013. Trends in recovery of Mediterranean soil chemical properties and microbial activities after infrequent and frequent wildfires. *Land Degradation & Development* **24**: 115–128. DOI:10.1002/ldr.1109.

Hanes TL. 1971. Succession after fire in the chaparral of southern California. *Ecological Monographs* **41**: 27–52.

Hedo J, Lucas-Borja ME, Wic C, Andres Abellan M, de Las Heras J. 2014. Soil microbiological properties and enzymatic activities of long-term post-fire recovery in dry and semiarid Aleppo pine (*Pinus halepensis* M.) forest stands. *Solid Earth Discussions* **6**: 3025–3050. DOI:10.5194/sed-6-3025-2014.

Herman J. 2009. Fire recurrence effects on aboveground plant and soil carbon in Mediterranean shrublands with Aleppo pine (*Pinus halepensis*). MSc thesis, forest ecology and forest management group. Final report.

Izhaki I, Henig-Sever N, Ne'eman G. 2000. Soil seed banks in Mediterranean Aleppo pine forests: the effect of heat, cover and ash on seedling emergence. *Journal of Ecology* **88**: 667–675.

Karcz Y. 1959. The structure of the northern Carmel. *Bulletin of the Research Council of Israel, Section G: Geo-Sciences* **8**: 119–130.

Kashai E. 1966. The geology of the eastern and the south-western Carmel. PhD Thesis, The Hebrew University of Jerusalem [Hebrew with English abstract].

Keeley JE. 1986. Resilience of Mediterranean shrub communities to fires. In: Dell B,

Keeley JE, Ne'eman G, Fotheringham CJ. 1999. Immaturity risk in a fire-dependent pine. *Journal of Mediterranean Ecology* **1**: 41–48.

Keesstra SD, Geissen V, Mosse K, Piiranen S, Scudiero E, Leistra M, van Schaik L. 2012. Soil as a filter for groundwater quality. *Current Opinion in Environmental Sustainability* **40**: 507–516. DOI:10.1016/j.cosust.2012.10.007.

Keesstra SD, Maroulis J, Argaman E, Voogt A, Wittenberg L. 2014. Effects of controlled fire on hydrology and erosion under simulated rainfall. *Cuadernos de Investigación Geográfica* **40**: 269–293.

Keidar G. 2001. Causes and factors in forest fires in Israel. MA thesis, Department of Geography, University of Haifa, Haifa, Israel [Hebrew with English abstract], 219 p.

Komyumdjisky H, Yaalon DH, Dan J. 1966. Red and reddish brown Terra Rossa in Israel. *Transaction Conference on Mediterranean Soils*, Madrid 1966.

Kutiel H. 2012. Weather conditions and forest fire propagation: the case of the Carmel Fire, December 2010. *Israel Journal of Ecology and Evolution* **58**: 113–122.

Lavorel S. 1999. Ecological diversity and resilience of Mediterranean vegetation to disturbance. *Diversity and Distribution* **5**: 3–13.

León J, Bodi BM, Cerdà A, Badia D. 2013. The contrasted response of ash to wetting: the effects of ash type, thickness and rainfall events. *Geoderma* **209–210**: 143–152.

Lloret F, Montserrat V. 2003. Diversity patterns of plant functional types in relation to fire regime and previous land use in Mediterranean woodlands. *Journal of Vegetation Science* **14**: 387–398.

Lloret F, Vila M. 2003. Diversity patterns of plant functional types in relation to fire regime and previous land use in Mediterranean woodlands. *Journal of Vegetation Science* **14**: 387–398.

Lloret F, Pausas GJ, Vilà M. 2003. Responses of Mediterranean plant species to different fire frequencies in Garraf Natural Park (Catalonia, Spain): field observations and modeling predictions. *Plant Ecology* **167**: 223–235.

Lorentzen B, Manning SW, Griggs CB, Wazny T, Riklin A, Brand D. 2009. Final report on dendrochronological research in Israel, July 2008–2009, [Report for the Israel Nature and Parks Authority]. 22 pp.

Malkinson D, Wittenberg L, Beeri O, Barzilai R. 2011. Effects of repeated fires on the structure, composition, and dynamics of Mediterranean maquis: short- and long-term perspectives. *Ecosystems* **14**: 478–488.

Copyright © 2015 John Wiley & Sons, Ltd.

Martín A, Díaz-Raviña M, Carballas T. 2012. Short- and medium-term evolution of soil properties in Atlantic forest ecosystems affected by wildfires. *Land Degradation & Development* **23**: 427–439. DOI:10.1002/ldr.1078.

Moreira F, Viedma O, Arianoutsou M, Curt T, Koutsias N, Rigolot E, Barbati A, Corona P, Vaz P, Xanthopoulos G, Mouillot F. 2011. Landscape–wildfire interactions in southern Europe: implications for landscape management. *Journal of Environmental Management* **92**: 2389–2402.

Morrison DA, Gary GJ, Pengelly SM, Ross DG, Mullins BJ, Thomas CR, Anderson TS. 1995. Effects of fire frequency on plant species composition of sandstone communities in the Sydney region: inter-fire interval and time-since-fire. *Australian Journal of Ecology* **20**: 239–247.

Naveh Z. 1990. Fire in the Mediterranean – a landscape ecological perspective. In: Goldammer JG, Jenkins MJ (eds.). Fire in ecosystems dynamics: Mediterranean and Northern perspective, 1–20. SPB Academic Publication: The Hague.

Ne'eman G, Izhaki I, Keeley JE. 2013. Fire in the Mediterranean – from genes to ecosystems. *Israel Journal of Ecology & Evolution* **58**: 2–3. DOI:10.1560/IJEE.58.2-3.103.

Ne'eman G. 1997. Regeneration of natural pine forest – review of work done after the 1989 fire in Mount Carmel, Israel. *International Journal of Wildland Fire* **7**: 295–306.

Ne'eman G, Lahav H, Izhaki I. 1992. Spatial pattern of seedling one year after fire in a Mediterranean Pine Forest. *Oecologia* **91**: 365–370.

Ne'eman G, Lahav H, Izhaki I. 1995. Recovery of vegetation in natural east Mediterranean pine forest on Mount Carmel, Israel as affected by management strategies. *Forest Ecology and Management* **75**: 17–26.

Ne'eman G, Goubitz S, Nathan R. 2004. Reproductive traits of *Pinus halepensis* in the light of fire: a critical review. *Plant Ecology* **171**: 69–79.

Nijhuis M. 2012. Burn out. *Nature* News Feature **489**: 352–354.

Novara A, Gristina L, Rühl J, Pasta S, D'Angelo G, La Mantia T, Pereira P. 2013. Grassland fire effect on soil organic carbon reservoirs in a semiarid environment. *Solid Earth* **4**: 381–385. DOI:10.5194/se-4-381-2013.

Pausas JG. 2004. Changes in fire and climate in the eastern Iberian Peninsula (Mediterranean basin). *Climatic Change* **63**: 337–350.

Pausas JG, Ouadah N, Ferran A, Gimeno T, Vallejo R. 2003. Fire severity and seedling establishment in *Pinus halepensis* woodlands, eastern Iberian Peninsula. *Plant Ecology* **169**: 205–213.

Pausas JG, Llovet J, Rodrigo A, Vallejo R. 2008. Are wildfires a disaster in the Mediterranean basin? A review. *International Journal of Wildland Fire* **17**: 713–723.

Paz S, Carmel Y, Jahshan F, Shoshany M. 2011. Post-fire analysis of pre-fire mapping of fire-risk: a recent case study from Mt. Carmel (Israel). *Forest Ecology and Management* **262**: 1184–1188.

Pereira P, Mierauskas P, Novara A. 2014. Stakeholders' perceptions about fire impacts on Lithuanian protected areas. *Land Degradation & Development* . DOI:10.1002/ldr.2290.

Pereira P, Cerdà A, Úbeda X, Mataix-Solera J, Arcenegui V, Zavala LM. 2015. Modelling the impacts of wildfire on ash thickness in a short-term period. *Land Degradation & Development* **26**: 180–192. DOI:10.1002/ldr.2195.

Perevolotsky A, Boneh O, Zalotzky M, Lahav H, Kaplan D, Snir H, Stainer N. 2011. Recommendations of the Committee of Management for the post-December 2010 fire on Mt. Carmel, Israel. Ministry of Environment, Israel [Hebrew].

Pérez-Cabello F, Ibarra P, Echeverría MT, de la Riva J. 2010. Post-fire land degradation of *Pinus sylvestris* L. woodlands after 14 years. *Land Degradation & Development* **21**: 145–160. DOI:10.1002/ldr.925.

R Development Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing: Vienna.

Schaffhauser A, Curt T, Véla E, Tatoni T. 2012. Recurrent fires and environment shape the vegetation in *Quercus suber* L. woodlands and maquis. *Comptes Rendus Biologies* **335**: 424–434.

Schiller G, Ne'eman G, Korol L. 1997. Post-fire vegetation dynamic in a native *Pinus halepensis* Mill. forest on Mt. Carmel, Israel. *Israel Journal of Plant Sciences* **45**: 297–308.

Segev A, Sass E. 2009. The geology of the Carmel region. Ministry of National Infrastructure, Geological Survey of Israel, [Report GSI/7/2009].

Soil Survey Staff. 2006. Keys to soil taxonomy, 10th edn. NRCS: Washington, DC.

Stohlgren TJ. 2007. Measuring plant diversity: lessons from the field. Oxford University Press: Oxford, UK 375 pp.

Syphard AD, Franklin J, Keeley JE. 2006. Simulating the effects of frequent fire on southern California coastal shrublands. *Ecological applications: a publication of the Ecological Society of America* **16**: 1744–1756.

Tessler N. 2012. Documentation and analysis of wildfire regimes on Mount Carmel and the Jerusalem hills. *Themes in Israeli Geography* **79–80**: 184–193.

Tessler N. 2013. Soil and vegetation resilience after recurrent forest fires in Mt. Carmel, Israel. PhD thesis, Department of Geography and Environmental Studies, University of Haifa. 174 pp.

Tessler N, Wittenberg L, Greenbaum N. 2012. Soil water repellency persistence after recurrent forest fires, Mount Carmel, Israel. *International Journal of Wildland Fire* **22**: 515–526.

Tessler N, Wittenberg L, Provizor E, Greenbaum N. 2014. The influence of short-interval recurrent forest fires on the abundance of Aleppo pine (*Pinus halepensis* Mill.) on Mount Carmel, Israel. *Forest Ecology and Management* **324**: 109–116.

Trabaud L, Lepart J. 1981. Changes in the floristic composition of a *Quercus coccifera* L. garrigue in relation to different fire regimes. *Vegetatio* **46**: 105–116.

Trabaud L, Michels C, Grosman J. 1985. Recovery of burnt *Pinus halepensis* Mill. forests II. Pine reconstitution after wildfire. *Forest Ecology and Management* **13**: 167–179.

Úbeda X, Outeiro LR, Sala M. 2006. Vegetation regrowth after a differential intensity forest fire in a Mediterranean environment, northeast Spain. *Land Degradation & Development* **17**: 429–440. DOI:10.1002/ldr.748.

Watson P, Wardell-Johnson G. 2004. Fire frequency and time-since-fire effects on the open-forest and woodland flora of Girraween National Park, south-east Queensland, Australia. *Austral Ecology* **29**: 225–236.

Wittenberg L, Kutiel H, Greenbaum N, Inbar M. 2007a. Short-term changes in the magnitude, frequency and temporal distribution of floods in the Eastern Mediterranean region during the last 45 years – Nahal Oren, Mt. Carmel, Israel. *Geomorphology* **84**: 181–191. DOI:10.1016/j.geomorph.2006.01.046.

Wittenberg L, Malkinson D, Beeri O, Halutzy A, Tessler N. 2007b. Spatial and temporal patterns of vegetation recovery following sequences of forest fire in a Mediterranean landscape Mt. Carmel, Israel. *Catena* **71**: 76–83.

Yaalon D. 1995. Soils in Mediterranean region: what makes them different? *Catena* **28**: 157–169.

Zedler PH, Gautier CR, McMaster GS. 1983. Vegetation change in response to extreme events: the effect of a short interval between fires in California chaparral and coastal scrub. *Ecology* **64**: 809–818.

Zilberman E, Greenbaum N, Nahmias Y, Porat N, Ashqar L. 2006. Middle Pleistocene to Holocene tectonic activity along the Carmel fault – preliminary results of paleoseismic study. Geological Survey of Israel [Report No. GSI/02/2007].

Zohary M. 1962. Plant life of Palestine: Israel and Jordan. Ronald: New York.

Copyright © 2015 John Wiley & Sons, Ltd.