

Litter decomposition in Mediterranean pine forests is enhanced by reduced canopy cover

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Abstract

Aims This study investigated the impact of canopy cover and seasonality on litter decay in Mediterranean pine forests to enhance climate predictions.

Methods We conducted litterbag experiments in plots of different tree densities in two Mediterranean pine forests differing in precipitation amounts. In each plot, local litter was placed in forest gaps and under tree canopies for 613 days, starting in the dry season.

Results Litter mass loss was greater in forest gaps than under tree canopies across forests and tree densities.

Similarly, a reduction in tree density tended to increase mass loss. Additionally, while the decay rate slowed down from the first to the second wet season, the decay rate remained constant during the first and the second dry season, and the dry seasons contributed 30% to the overall mass loss.

Conclusions Reduction in canopy cover enhances litter decay, and the stability and magnitude of the dry season contribution to annual mass loss have the potential to control litter mass loss when accounting also for the dry periods in the wet season. Combined, the ongoing tree mortality and the predicted prolongation of dry periods due to climate change may enhance litter decay, possibly reducing ecosystem carbon stocks in drylands.

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Keywords Canopy cover · Litter decomposition · Photodegradation · Solar radiation · Thermal degradation · Tree density

Abbreviations

C Carbon
DBH Stem diameter at breast height
LAI Leaf area index
MAP Mean annual precipitation
N Nitrogen
RH Relative humidity

Introduction

Semi-arid ecosystems regulate the long-term trend and the interannual variability in the terrestrial carbon (C) cycle

(Poulter et al. 2014; Ahlström et al. 2015). The relevance of drylands for the global C cycle arises from their vast spatial extent (~41% of Earth's land area), the fraction of the global soil organic C stored in drylands (~27%; Safriel et al. 2005), and their large C sequestration potential (Luo et al. 2007; Wohlfahrt et al. 2008; Ahlström et al. 2015). Furthermore, drylands are predicted to increase in range due to desertification processes (D'Odorico et al. 2013), thus their global importance is likely to rise in the future. However, the decomposition of organic plant material in dryland ecosystems is not well understood (Throop and Archer 2009; Poulter et al. 2014; Carvalhais et al. 2014). In particular, the decomposition of above-ground plant litter in biogeochemical models tends to be greatly underestimated (Parton et al. 2007; Adair et al. 2008; Bonan et al. 2013), and thus poses a source for uncertainty in our predictions of the terrestrial C cycle.

It was suggested that this underestimation of litter decay in drylands stems from the fact that models do not include abiotic and biotic “non-rainfall decay mechanisms” operating in dry periods (Barnes et al. 2015; Glikzman et al. 2017). Among the abiotic daytime decay drivers, (i) solar radiation causes photodegradation of litter through mineralization of photo-reactive compounds and photo-oxidation of chemical bonds (Moorhead and Callaghan 1994; King et al. 2012; Barnes et al. 2015), and (ii) high temperatures (>30 °C) lead to thermal degradation of litter (Lee et al. 2012; Van Asperen et al. 2015). These drivers can contribute up to 60% of the annual litter mass loss and the dry-season ecosystem CO₂ flux (Austin and Vivanco 2006; Rutledge et al. 2010). Additionally, biotic degradation occurs in rainless periods when high levels of water vapor and dew are absorbed by litter at night, thus facilitating microbial degradation (Dirks et al. 2010; Day et al. 2015; Jacobson et al. 2015), which can control the dry-season mass loss (Glikzman et al. 2017). In addition to their direct contribution to decomposition, these abiotic and biotic decay mechanisms can facilitate each other on a daily scale (Glikzman et al. 2017), and solar radiation can also determine the annual mass loss by facilitating or inhibiting decay (“photopriming”) in subsequent wet periods (Pancotto et al. 2003; Henry et al. 2008; Gallo et al. 2009; Smith et al. 2010; Baker and Allison 2015; Austin et al. 2016). Studies in which photodegradation was simulated showed the great potential of these mechanisms to improve litter decay models in drylands (Foereid et al. 2011; Chen et al. 2016).

The contribution of decay drivers operating in rainless periods can be strongly affected by changes in the tree or shrub canopy cover. Forest ecosystems in drylands are especially vulnerable to changes in climate, land use and fire, which lead to the opening of landscapes due to tree mortality (Allen et al. 2010; Davidson et al. 2012). Reduced canopy cover increases the amount of solar radiation that reaches the litter layer, thus enhancing photochemical and thermal degradation (Mlambo and Mwenje 2010; Araujo and Austin 2015). Similarly, lower canopy cover is likely to increase dew formation through enhanced nighttime heat loss (Baier 1966; Jacobs et al. 1990; Xiao et al. 2009; Pan et al. 2010), thus increasing the microbial degradation of litter (Glikzman et al. 2017). For this reason, there is a need to assess how litter decay will be influenced not only by changes in climate, but also by changes in the vegetation structure.

Beyond the effects of canopy cover on decay, we also have little knowledge concerning the dynamics and magnitude of litter decay in forests when differentiating between dry and wet periods. Dynamics of litter decay are commonly described as a decay function with a fast initial decay which decreases over time (Swift et al. 1979; Cornwell and Weedon 2014). However, such functions may not be accurate if we examine the decay occurring in dry and wet seasons separately. In hot and dry periods without precipitation, abiotic and biotic degradation can alternate on a daily basis in their consumption of ‘recalcitrant’ and ‘labile’ compounds, thus potentially reducing bottle necks for each degradation type (Glikzman et al. 2017), and allowing the decay rate to remain constant over time. Such decay dynamics coupled with long rainless periods can lead to a substantial contribution of the non-rainfall decay mechanisms to the annual mass loss.

Here, we investigated the effects of variations in canopy cover on litter decay in Mediterranean pine forests by using experimental plots of different tree densities and by selecting exposed and shaded microsites within plots. We also compared the impact of the extreme Mediterranean seasonality by following litter decay over two consecutive dry season-wet season cycles. We hypothesized that (1) litter decay in Mediterranean forests increases with the reduction in canopy cover due to a higher contribution of non-rainfall decay mechanisms; (2) the contribution of consecutive dry and wet seasons to litter decomposition decreases as a consequence of increasingly decomposed litter; and (3) the dry periods have a significant contribution to the annual decay due to the long rainless periods in the studied forests.

Materials and methods

Study sites

The study was performed in two Aleppo pine (*Pinus halepensis*) forests in Israel that are part of the long-term ecological research network of the national forest service (JNF-KKL). The first study site was in the Kdoshim forest, located in the dry sub-humid Mediterranean climatic zone, on the lower western slopes of the Jerusalem mountains (400–500 a.s.l.), with topographic aspect ranging from south- to north-western and average slope of 25% (31°78'N, 35°02'E). The long-term (40 yr) mean annual precipitation (MAP) is 550 mm (during the last 10 years, MAP was 15% lower), all of which falls between October and April; minimum and maximum mean monthly air temperatures are 16 and 25°C in the daytime, and 16 and 19°C in the nighttime. The forest canopy is composed of Aleppo pine trees planted in 1968, the understory by broad-leaf trees and shrubs dominated by *Quercus calliprinos* WEBB (tree), *Pistacia lentiscus* L. (shrub) and *Rhamnus lycioides* L. (shrub) and a variety of ephemeral herbaceous species. Average pine tree height, stem diameter at breast height (DBH) and leaf area are 12.6 ± 0.5 m, 18.9 ± 0.6 cm and 71.6 ± 9.2 m², respectively. During the years of this study (2011–12), the forest has suffered 15% tree mortality as a result of consecutive drought years. The soil is a shallow Terra rossa, bedrock is mostly dolomite and lime. More detailed information about this site is provided in Calev et al. (2016).

The second site was in Yatir forest, located in the Mediterranean semi-arid zone on a plateau of the northern Negev (650 a.s.l.; 31°20'N, 35°20'E). The climate is drier, with 280 mm MAP, most of which falls between November and April. Minimum and maximum mean monthly air temperatures are 11 and 28°C in the daytime,

and 8 and 21°C in the nighttime. The canopy is composed of Aleppo pine trees planted mostly during 1964–1967, the understory is sparse and dominated by dwarf shrubs, mainly *Sarcopoterium spinosum* L. and *Phagnalon rupestre* (L.) DC. and a variety of ephemeral herbaceous species. Before this study began, the forest suffered 5–10% tree mortality (2010–2011) as a result of consecutive drought years (Klein et al. 2014). The substrate is light colored Rendzina above chalk and limestone. Trees are ~12 m high, stand density of ~300 trees ha⁻¹ and DBH of ~21 cm.

Plots of different tree densities were created by thinning in both forests in 2009, as follows: 0, 100 and 300 trees ha⁻¹ in the dry sub-humid forest, 100, 200 and 300 trees ha⁻¹ in the semi-arid forest. Subsequently, monitoring plots were set up, with each plot extending over 3000 m² (of which the center 1500 m² were used for measurements) in the dry sub-humid forest and 800 m² in the semi-arid forest.

Litter collection and litterbag preparation

During June 2011, nets were placed on the ground in both forests to collect freshly shed pine needles (termed as “pine litter”) at the annual peak of needle fall. Additionally, fresh standing-dead material of the dominant annual grass *Avena sterilis* L. (dry sub-humid forest) and a mixture of *Poaceae* (semi-arid forest) was harvested and chopped to 4-cm segments (termed “grass litter”, see Table 1 for initial litter quality). Litter was dried at 55 °C for two days, after which 2 g of litter were placed in 10 cm × 10 cm litterbags made of grey fiberglass (facing the ground, 0.5 mm mesh) and transparent polyethylene [facing up, 1 mm mesh, 90% transmittance over the photochemically active wavelengths of 280–550 nm (Austin and Ballaré 2010)].

Table 1 Initial litter quality

Forest	Litter type	C%	N%	C:N ratio
Dry sub-humid	Pine	51.6 ± 0.1a	0.79 ± 0.02b	65.2 ± 1.2a
	Grass	44.3 ± 0.3b	0.62 ± 0.02b	71.2 ± 2.5a
Semi-arid	Pine	51.3 ± 0.6a	0.67 ± 0.04b	76.7 ± 3.7a
	Grass	44.1 ± 0.4b	1.22 ± 0.07a	36.4 ± 2.5b

Different letters indicate statistically significant differences within a column ($P \leq 0.05$, Tukey-Kramer HSD test). Means ± SE are shown. $n = 2$ –5 litter samples

Local litter experiment: Tree density and canopy cover effect on litter decomposition

Four plots of each of the following tree densities were selected for the experiment (24 plots in total in both forests): 0, 100 and 300 trees ha⁻¹ (leaf area index, LAI = 0, 1.0 and 1.7, respectively, based on Caley et al. 2016; see Fig. S1 for the radiation distribution under the different tree densities) in the dry sub-humid forest and 100, 200 and 300 trees ha⁻¹ in the semi-arid forest (with LAI in 2011 of about 0.8, 1.3 and 1.8, respectively, unpublished data, for methods see Supporting Information; see Fig. S2 for radiation distribution). In early July 2011, at solar noon time, we selected two microsites in each plot for placing the litterbags: one in the center of the largest gap in the forest canopy (“forest gap”) and the other one in the middle of the largest shade patch under the canopy of pine trees (“canopy cover”). The diameter of the gaps ranged between 5 and 10 m in the high tree-density plots to 10–30 m in the low density plots. In the clear-cut plots (0 trees ha⁻¹) of the dry sub-humid forest, the microsites for litterbags placement were either close to or far from pine stumps. A total of 384 litterbags were placed on the ground in both forests in mid-July 2011, with 4 litterbags (one litterbag for each of four retrieval dates) for each combination of litter type (2), microsite (2), plot (12), and forest (2). The litter in all bags was local, i.e. collected and incubated in the same forest. The deployment of litterbags took place as early as possible following the shedding of needles in late-June. The experiment lasted 613 days, and the four litterbag retrievals were performed at the end of the dry season of 2011 and of 2012 (both retrievals at the end of September) and at the end of the wet season of 2012 and 2013 (both in mid-March). Here, we define the dry season as the rainless period from mid-March till end of September. The dry seasons were without rain except for a single rainy day at the beginning of the second dry season in the dry sub-humid forest (Fig. 1; 9 mm rain, late-March 2012).

Common garden experiment

To separate the effect of litter quality from that of the environment, we conducted a common-garden litter decomposition experiment under two contrasting conditions. We chose two microsites in the dry sub-humid forest, one with full exposure to solar radiation (in a clear-cut plot, termed as forest gap) and a second one

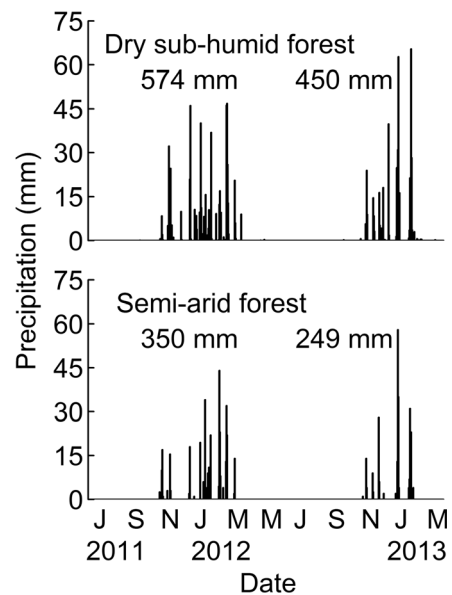


Fig. 1 Daily precipitation over the experimental period in the dry sub-humid and semi-arid forests. Values above the rain distribution represent the total annual rain amount

under dense canopy cover in a 600 trees ha⁻¹ plot. Twenty replicated bags of each of the two types of litter collected from each forest (four litter types overall) were placed for decomposition at each microsite (160 litterbags in total). On each of the four retrieval dates, five litterbags were collected from each litter type and microsite. The placement and retrieval of litterbags was performed simultaneously with the ones in the local litter experiment.

Chemical analyses of litter

Initial litter and litter retrieved from the field were analyzed in the lab for dry weight (55 °C, 48 h) and ash content (550 °C, 4 h) to assess ash-free litter dry mass for calculating the litter mass loss. The C and nitrogen (N) concentration of the initial litter were measured on finely ground powder (Pulverisette 7 Planetary Micro Mill; Fritsch, Idar-Oberstein, Germany) in an elemental analyzer (FlashEA 1112; Thermo, Waltham MA, USA), and was expressed on ash-free base.

Climate monitoring

We placed small data loggers (DS1922L-F5#, iButtons, Embedded Data Systems, Lawrenceburg, KY, USA) between the litterbags and the soil in both forests to monitor litter temperature during the experimental period. In the

dry sub-humid forest, the loggers were placed in the two microsites of the common garden experiment (a clear-cut plot and under a dense canopy cover), both under pine and grass litter collected from the dry sub-humid forest (one logger per litter type and microsite, four loggers overall). In the semi-arid forest, loggers were placed under pine and grass litterbags in a forest gap of a 100 trees ha⁻¹ plot and under litterbags below canopy cover in a 300 trees ha⁻¹ plot (overall four loggers). The locations of logger placement in both forests represent the extremes within the range of the canopy cover. Rainfall was collected in meteorological stations positioned in the both forests (for the semi-arid site see Tatarinov et al. 2016). The same station in the dry sub-humid forest measured also relative humidity (RH) at 2.5 m above-ground.

Statistical analysis

In both forests and experiments, we analyzed the decay rates after the first dry season and at the end of the experiments. In the local litter experiment, mass loss in the two microsites of the clear-cut plots in the dry sub-humid forest did not differ over all samplings and litter types ($P > 0.31$; next to tree stumps or between stumps). Therefore, we combined both microsites to be a “forest gap” microsite, and divided the analysis of litter decay for each litter type in the dry sub-humid forest into two parts. For each litter type, we performed a full factorial ANOVA using the variables microsite (forest gap/canopy cover) and tree density, with two tree densities of 100 and 300 trees ha⁻¹ (excluding the 0 trees ha⁻¹). Then, we used a one-way ANOVA for comparing the three densities in the non-shaded microsite (forest gaps in plots of 0, 100 and 300 trees ha⁻¹). In the semi-arid forest, we used a full factorial ANOVA for each litter type, using the variables microsite and tree density (all levels). We analyzed the common garden experiment in the dry sub-humid forest using a one-way ANOVA for each litter type to find differences between the microsites. Interactions are mentioned when significant. The forests were analyzed separately because of differences in experimental design (densities) and the difference in litter quality of the grass litter collected from each forest.

We calculated the mass loss per month for each of the four seasons to allow comparisons of decay rates between different seasons, while eliminating differences in the length of the season. In the local litter experiment, the rate of decay per month for each litter type is the average of means of mass loss per month from the six

combinations of microsite and tree density (five in the dry sub-humid forest). This averaging represents the decay rate for a litter type under the different conditions within a forest with the purpose of receiving uniform results across all litter types to transcend the differences between forests which originate from the different tree densities in each forest. For each litter type we compared the means of two dry seasons or two wet seasons using Student's t-test. In addition, we performed two full-factorial analyses to examine if the change in monthly decay rates between two consecutive seasons (either dry or wet seasons) was affected by the microsites and litter types, across all densities. In the common garden experiment the rate of decay per month is the average of the mean mass loss per month of the eight combinations of canopy cover and litter type. The Tukey-Kramer HSD test was used for post hoc comparisons of multiple means. When several specific contrasts between means were tested at $\alpha = 0.05$, Holm's correction was applied (Rice 1989). When heterogeneity of variance occurred, data were log-transformed prior to statistical analyses. Data were analyzed using JMP 11 software (SAS Institute, Cary, NC, USA).

Results

Over both dry seasons, forests and litter types, the mean daytime maximum temperatures measured under the litterbags (i.e., protected from direct solar radiation) were about 19 °C higher in forest gaps than under canopy cover (Table 2, $P < 0.001$; t test). Nighttime minimum temperature in the dry seasons was lower by 2 °C in forest gaps than under canopy cover in the dry sub-humid forest, while in the semi-arid forest the trend reversed and the minimum temperature was higher by 1.7 °C in forest gaps than under canopy cover ($P < 0.001$; t test for both forests). During the wet seasons, no clear trend was obtained for daytime maximum temperature, but minimum temperature at night was lower by 1.7 °C in forest gaps than under canopy cover ($P < 0.001$; t test across litter types, forests and both wet seasons). The wet seasons differed in rainfall amounts (Fig. 1; 574 vs. 450 mm and 350 vs. 249 mm in the first vs. the second wet season in the dry sub-humid and semi-arid forests, respectively). Nights were with high RH (77.1 ± 0.6 , $n = 639$ days) in the dry sub-humid forest, with small fluctuations between the different seasons (Fig. S3).

Table 2 Temperature (°C) measured under the litterbags at two microsites in the dry sub-humid and semi-arid forests during consecutive dry and wet seasons

Season	Variable	Order of seasons	Dry sub-humid forest				Semi-arid forest				
			Pine litter		Grass litter		Pine litter		Grass litter		
			Gap	Canopy	Gap	Canopy	Gap	Canopy	Gap	Canopy	
Dry	Max. T	1st						62.0 ± 1.4	39.6 ± 0.8	54.9 ± 1.0	40.8 ± 0.9
		2nd	65.1 ± 0.7	42.2 ± 0.5	63.2 ± 0.7	43.4 ± 0.6	68.1 ± 0.7	51.6 ± 1.0	63.6 ± 0.5	47.7 ± 0.9	
	Min. T	1st					19.6 ± 0.4	19.9 ± 0.3	21.7 ± 0.3	18.8 ± 0.4	
		2nd	20.8 ± 0.2	23.2 ± 0.2	17.6 ± 0.3	19.3 ± 0.3	17.1 ± 0.3	16.3 ± 0.3	18.8 ± 0.3	15.6 ± 0.4	
Wet	Max. T	1st		21.2 ± 0.6	25.5 ± 0.8	20.8 ± 0.5	30.9 ± 1.0	29.4 ± 0.8	26.7 ± 0.9	35.8 ± 1.2	
		2nd	22.7 ± 0.8	25.6 ± 0.8	27.7 ± 0.9	23.5 ± 0.6	39.3 ± 1.1	35.6 ± 1.0	36.7 ± 1.0	37.3 ± 1.1	
	Min. T	1st		11.5 ± 0.3	9.1 ± 0.3	10.6 ± 0.3	6.7 ± 0.3	8.8 ± 0.4	8.0 ± 0.4	8.4 ± 0.3	
		2nd	8.5 ± 0.3	11.2 ± 0.3	11.7 ± 0.3	13.3 ± 0.4	9.0 ± 0.4	11.1 ± 0.3	9.4 ± 0.4	10.7 ± 0.3	

The data for the first dry season in the dry sub-humid forest and the first wet season data for pine litter in a forest gap in the dry sub-humid forest was not available. Max. T and Min. T stand for maximum and minimum temperatures averaged over the season. $n = 76$ days for the first dry season in the semi-arid forest, 170 and 176 days for the first wet season in the dry sub-humid and semi-arid forests, 55–189 days for the second dry season and the second wet season in both forests. Means ± SE

In the local litter experiment, mass loss in the dry sub-humid forest at the end of the first dry season was greater in forest gaps than under canopy cover by a

factor of 1.5 for pine and 1.6 for grass litter (Table 3a, Fig. 2, $P = 0.002$ and 0.018 , respectively; full factorial models without clear-cut plots). Moreover, pine litter

Table 3 Analysis of variance models for each litter type in the local litter experiment in the dry sub-humid forest (a) and in the semi-arid forest (b)

a. Dry sub-humid forest						
Period	Litter		Microsite ¹	Density ¹	M x D ¹	Density ²
1st dry Season	Pine	P	0.002	0.037	0.617	0.207
		F	17.3 _{1,11}	5.6 _{1,11}	0.3 _{1,11}	1.8 _{2,13}
	Grass	P	0.018	0.366	0.101	0.8
		F	7.6 _{1,11}	0.9 _{1,11}	3.2 _{1,11}	0.2 _{2,13}
Entire Study Period	Pine	P	0.429	0.32	0.998	0.001
		F	0.7 _{1,10}	1.1 _{1,10}	0.0 _{1,10}	19.2 _{2,11}
	Grass	P	0.475	0.545	0.068	0.95
		F	0.6 _{1,9}	0.4 _{1,9}	4.3 _{1,9}	0.0 _{2,11}
b. Semi-arid forest						
Period	Litter		Microsite	Density	M x D	
1st dry season	Pine	P	0.001	0.079	0.661	
		F	19.0 _{1,17}	3.0 _{2,17}	0.4 _{2,17}	
	Grass	P	0.362	0.886	0.242	
		F	0.9 _{1,15}	0.1 _{2,15}	1.6 _{2,15}	
Entire Study Period	Pine	P	< 0.001	0.057	0.874	
		F	29.3 _{1,16}	3.5 _{2,16}	0.1 _{2,16}	
	Grass	P	0.002	0.854	0.749	
		F	14.8 _{1,14}	0.2 _{2,14}	0.3 _{2,14}	

The periods refer to the decay occurring during the 1st dry season and over the entire experimental period. M x D refers to the interaction between the explanatory variables microsite (forest gap and under canopy cover) and tree density. For all models, first the P values and then the corresponding F value (degrees of freedom in subscript) are presented. In the dry sub-humid forest, for each litter type the analysis was split in two. First a full factorial model is presented in which clear-cut plots are not included (¹). Second, in the rightmost column (²) there is a complementary model where only the effect of density on litter decay in forest gaps was analyzed (with clear-cut plots). In the semi-arid forest, such separation was not needed and all microsites and densities were analyzed in one model

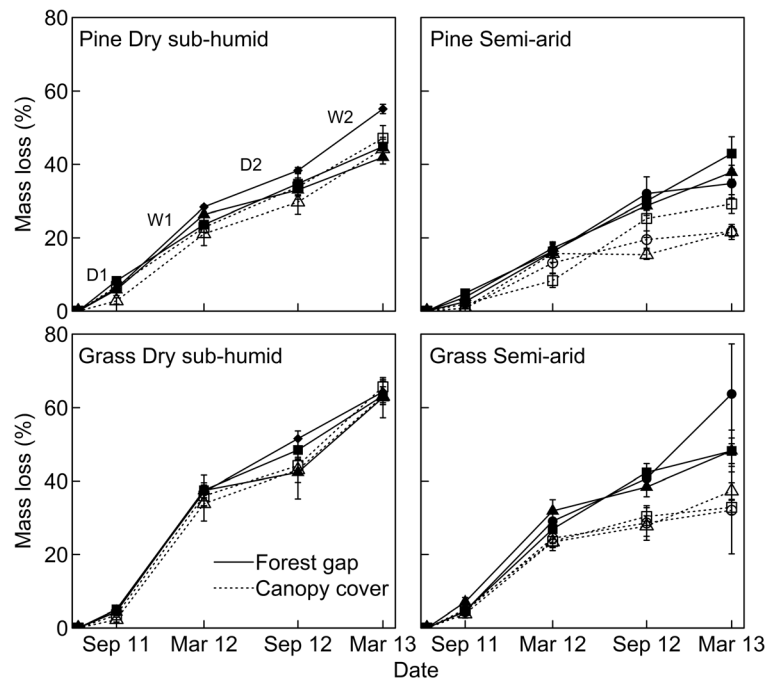


Fig. 2 Dynamics of pine and grass litter decay in the two forests and under three tree densities in the local litter experiment. “D1” and “D2” stand for the two dry seasons that lasted from July 2011 till September 2011 and from March 2012 till September 2012, and “W1” and “W2” stand for the two wet seasons that lasted from September 2011 till March 2012 and from September 2012 till March 2013. The solid symbols (and full lines) represent different

tree densities in the forest gap microsites of the dry sub-humid forest (\diamond , \blacksquare and \blacktriangle for 0, 100 and 300 trees ha^{-1}) and the semi-arid forest (\blacksquare , \bullet and \blacktriangle for 100, 200 and 300 trees ha^{-1}). The open symbols (and the dashed lines) represent the above densities for the canopy cover microsites. Mean \pm SE; $n = 2\text{--}8$ litterbags per category

decayed more in the 100 trees ha^{-1} plots than in the 300 trees ha^{-1} plots by a factor of 1.7 ($P = 0.037$). When including the clear-cut plots and comparing litter mass loss only in forest gaps, tree density did not have a significant effect on litter decay for pine and grass litter ($P = 0.207$ and 0.8, one-way ANOVA). By the end of the incubation period (after the second wet season), microsite and tree density (without the clear-cut plots) did not significantly affect decomposition of pine ($P = 0.429$ and 0.366) and grass litter ($P = 0.475$ and 0.545). When including the clear-cut plots and analyzing forest gaps only, pine litter decomposed more by a factor of 1.2 and 1.3 ($P = 0.001$, one-way ANOVA) in the clear-cut plots than in the forest gaps at 100 and 300 trees ha^{-1} , respectively, while tree density did not have a significant effect on grass litter mass loss ($P = 0.95$).

In the semi-arid forest, pine litter decay was greater by a factor of 3.1 in forest gaps than under canopy cover by the end of the first dry season (Table 3b, Fig. 2, $P = 0.001$; marginally significant effect for density $P = 0.079$ with the highest mass loss at the lowest tree density). Neither microsite nor tree density significantly

affected grass litter decomposition in this forest ($P = 0.362$ and 0.887). By the end of the incubation period, mass loss for both pine and grass litter was 1.6 times greater in forest gaps than under canopy cover ($P \leq 0.001$ and $P = 0.002$, for pine and grass litter types, respectively). There was a marginally significant effect of tree density on pine litter decay ($P = 0.057$; with highest mass loss at the lowest tree density) and no significant effect on grass litter decay ($P = 0.854$).

In the common garden experiment, decomposition of pine and grass litter from the dry sub-humid forest and grass from the semi-arid forest was greater by a factor of 1.6, 2.7 and 1.5 in forest gaps than under canopy cover by the end of the first dry season (Table 4, Fig. 3, $P = 0.043$, 0.001 and 0.021), while pine litter from the semi-arid forest decayed similarly in both microsites ($P = 0.812$). By the end of the incubation period, the decay was greater in forest gaps than under canopy cover for all litter types by a factor of 1.1–1.3 ($P = 0.03$ and 0.029 for pine and grass litter from the dry sub-humid forest; $P = 0.008$ and 0.006 for pine and grass litter from the semi-arid forest).

Table 4 Analysis of variance models for the common garden experiment in the dry sub-humid forest

Period	Litter	<i>P</i>	<i>F</i>
1st dry season	Pine M	0.043	5.8 _{1,8}
	Grass M	0.001	27.1 _{1,8}
	Pine SA	0.812	0.1 _{1,8}
	Grass SA	0.021	8.3 _{1,8}
Entire Study Period	Pine M	0.03	7.0 _{1,8}
	Grass M	0.029	7.5 _{1,7}
	Pine SA	0.008	12.4 _{1,8}
	Grass SA	0.006	13.5 _{1,8}

Each model compares the mass loss in a forest gap with that under canopy cover. The periods refer to the decay occurring during the 1st dry season and over the entire experimental period. In the category “litter”, M and SA stands for litter origin, either from the dry sub-humid or semi-arid forest, respectively

We compared the monthly rate of litter decay separately between the two dry seasons and the two wet seasons in the local litter experiment. While there was a trend for higher decay rates in the first compared with the second dry season (by a factor of 1.13 on average), this trend was not statistically significant across all litter types and forests ($P = 0.20–0.81$, t-test on means of monthly rates of mass loss; Fig. 4). In contrast, the rate of mass loss per month in the first wet season was significantly greater by a factor of 1.79 on average across all litter types and forests ($P < 0.05$, except for pine from the dry sub-humid forest, $P = 0.053$) compared to the second wet season. Thus, the monthly mass loss rate of the dry season in relation to that of the subsequent wet season increased from the first year to the second year from 45%

to 56% in the dry sub-humid forest and from 50% to 112% in the semi-arid forest (averages of both litter types in each forest). Additionally, we did not detect any effect of the microsite on the difference in monthly decay between the two dry seasons or the two wet seasons (Table S1). In the common garden experiment, there was no difference in rate of mass loss per month between the dry seasons ($P = 0.27$, pooling of litter types; Fig. 4), while the rate was significantly higher in the first wet season than in the second wet season by a factor of 2.5 ($P = 0.004$). Thus, the monthly mass loss rate of the dry season in relation to that of the subsequent wet season increased from the first year to the second year from 46% to 90% (over all litter types).

Discussion

Our results show the importance of decay in rainless periods in determining the turnover of litter. First, following our hypothesis reductions in canopy cover led to enhanced litter decay. The higher decay rate at the end of the first dry season in forest gaps than under canopy cover (greater by 1.77 times on average over all litter types and experiments) can only be attributed to non-rainfall decay mechanisms. Litter located in forest gaps was exposed to considerably higher daytime temperatures than litter under canopy cover, which likely resulted in higher rates of thermal degradation (Lee et al. 2012). Those higher temperatures in forest gaps were most probably caused by higher irradiance. Thus, we can assume that litter in gaps experienced more photodegradation than litter under canopy cover. Our

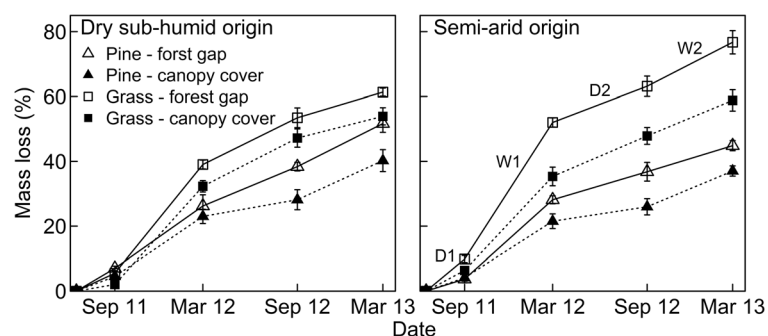


Fig. 3 Dynamics of pine and grass litter decay originating from the dry sub-humid and semi-arid forests in the common garden experiment conducted in the dry sub-humid forest, in two different microsites over the entire experimental period. “D1” and “D2” stand for the two dry seasons that lasted from July 2011 till

September 2011 and from March 2012 till September 2012, and “W1” and “W2” stand for the two wet seasons that lasted from September 2011 till March 2012 and from September 2012 till March 2013. Mean \pm SE; $n = 4–5$ litterbags per combination of litter type, sampling and microsite

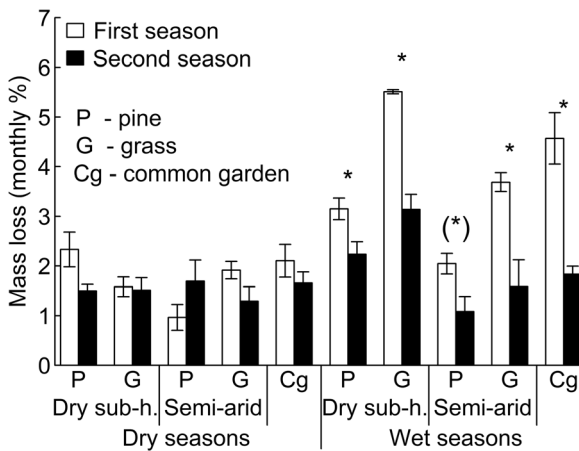


Fig. 4 The monthly decay rate for each of the four seasons in both experiments. “Dry sub-h.” and “Semi-arid” stands for the dry sub-humid and semi-arid forests. The common garden experiment (“Cg”) was conducted in the dry sub-humid forest. In the local litter experiment, $n = 5$ for litter in the dry sub-humid forest and $n = 6$ for litter from the semi-arid forest as averages of the combinations of microsite and tree density. In the common garden experiment, $n = 8$ as averages of litter type and microsite combinations. * indicates significant difference between the microsites at $P < 0.05$, and (*) represent a marginally significant difference $P = 0.053$. Means \pm SE are shown

choice of microsites (forest gaps/canopy cover) were justified by the radiation measurements, which showed that across both forests solar radiation is either mostly blocked or mostly transmitted, with little area exposed to medium levels of radiation (Figs. S1, S2). We expected to find lower minimum temperatures in forest gaps due to greater nighttime heat loss which can lead to higher dew deposition rates and decay (Gliksman et al. 2017). This pattern in temperature was present in the dry sub-humid forest, but the opposite trend was present in the semi-arid forest, which makes the prediction of the extent of nighttime microbial degradation challenging.

At the end of the experiments, the trend of higher decomposition rates in forest gaps than under canopy cover remained (greater by 1.25 times on average over all litter types and experiments after the second wet season), but in this case, multiple processes can lead to higher decay in forest gaps. First, also the wet seasons include long dry periods in which the non-rainfall decay mechanisms can operate and enhance decay in forest gaps. More importantly, enhanced exposure to solar radiation in forest gaps during the dry seasons can lead to photoprimering of decay during wet periods by causing changes in the size and composition of microbial populations, and by altering litter chemistry and structure

through breakdown of recalcitrant materials, such as lignin (Henry et al. 2008; Smith et al. 2010; Austin and Ballaré 2010; Barnes et al. 2015; Austin et al. 2016). Finally, during rain events the canopy reduces the amount of rain reaching the ground and the litter (Llorens and Domingo 2007), thus potentially reducing decay under canopy cover compared to forest gaps. Our results also show that reduced tree density led to increased decay, and while the overall effect was small, it was in agreement with the findings that reduced canopy cover enhances decay. Furthermore, the limited effect of the tree density on decay in relation to the stronger effect of canopy cover indicates that the local microclimate created even by a single tree (commonly occurring in lower tree densities) is more influential than microclimate dictated by the plot density (Bernaschini et al. 2016). Incorporating such a mosaic of microclimatic patterns into spatially explicit models can enhance our predictions for litter decay.

An important difference in the effect of canopy cover on decay was present when comparing the forests and their MAP. The dry sub-humid forest exhibited much less differentiation in decay between microsites than the semi-arid forest. A similar pattern was observed under relatively low annual precipitation (MAP of 249–600 mm) when reduction in canopy cover tended to enhance litter decay following thinning and clear-cut treatments (Bates et al. 2007; Mlambo and Mwenje 2010; but see Lado-Monserrat et al. 2015). However, with the increase in MAP (750–912 mm) this effect was reversed and higher canopy cover was related to greater decay rates (Cortina and Vallejo 1994; Blanco et al. 2011). In our study, both forests in both seasons were below 600 mm MAP and litter decay increased with the decrease in canopy cover, but to a lower degree in the dry sub-humid forest than the semi-arid forest. It appears that there may be a MAP threshold between 600 and 750 mm beyond which the influence of canopy cover on decay is reversed. The cause for such a threshold may be that with the reduction in precipitation there is an overall reduction in decay but an increase in the relative contribution of the non-rainfall decay mechanisms in areas with lower canopy cover.

Our second key result was that the monthly decay rate occurring in both dry seasons was stable and similar, contrasting with our hypothesis, while rates strongly declined from the first to the second wet season as we predicted. Therefore, the decay during dry seasons did not follow the classic diminishing decay rate over time

(Comwell and Weedon 2014), and its contribution to the annual litter decay increased over the experimental period in relation to the declining contribution of the wet season. Thus, we can support the suggestion that the higher than predicted decay rates in drylands are caused by mechanisms operating during rainless periods (Parton et al. 2007; Adair et al. 2008; Bonan et al. 2013).

The stability of decay during the dry seasons may stem from the co-occurrence of non-rainfall decay drivers. In the dry season, photochemical, thermal and microbial degradation alternate and interact on a daily basis (Gliksman et al. 2017). Photodegradation and thermal degradation operate during daytime and are efficient in degrading litter fractions that are recalcitrant for microorganisms (Austin and Ballaré 2010; Lee et al. 2012). Then, following absorption of water vapor and dew by litter at night, microorganisms can consume the labile fraction (which is likely hydrophilic) with greater ease, exposing recalcitrant tissues for the abiotic decay drivers operating at day. Combined, alternating degradation of different litter constituents can lead to mutual facilitations that maintain the decay during the dry seasons at a similar pace (Gliksman et al. 2017). The decline in decay in the wet seasons on the other hand can be attributed to the observed reduction in precipitation from the first to the second year of the experiment in both forests, and to an increase in the concentration of recalcitrant fractions (Berg and McClaugherty 2008). In both analyses of consecutive dry or wet seasons, we did not find a relation to the microsite, thus it is likely that these dynamics are not influenced by the difference in microclimate between the microsites.

Climate change projections for the Mediterranean Basin include a reduction in precipitation amounts, and an increase in mean air temperature, the frequency of high temperature extremes and drought events, evapotranspiration rates, and the length of the dry season (Diffenbaugh et al. 2007; Giorgi and Lionello 2008; Giannakopoulos et al. 2009; Fischer and Schär 2010; IPCC 2013). According to these projections, we expect that the dry-season contribution to litter decay will increase in relation to that of the wet season. For example, with longer dry periods and higher temperatures the dry season abiotic degradation will likely increase. In our study, the combined decay during the dry seasons contributed 30% to the overall mass loss, confirming our hypothesis of a significant contribution of the rainless period to the annual mass loss. However, this value is likely below the actual contribution of the non-rainfall

decay mechanisms because most days in the wet season are rainless (23% and 12% rainy days during the wet seasons in the dry sub-humid and semi-arid forest, respectively). Since most of the rainy days were clustered, we can assume that during most of the wet season the litter was actually dry. Furthermore, even when we added 3–4 wet days as the expected drying period following each rain event (Raison et al. 1986; Harpole and Haas 1999; applied here for days with >1 mm of rain), there was only a minor change to the percentage of days in which the litter was wet. Finally, while we did not account for possible legacy effects, other studies showed that the dry season can facilitate most of the wet season mass loss through photopriming, as an additional important contribution to the annual mass loss (Henry et al. 2008; Gallo et al. 2009; Baker and Allison 2015). Combined, the dry season is likely to dominate the annual litter mass loss in the Mediterranean climate zone, and possibly in other regions, with low precipitation.

Harsher climate conditions can also affect the canopy cover and litter decomposition through changes in the vegetation composition, and may pose a positive feedback on litter decay during rainless periods. The changing climate is predicted to increase tree mortality in the Mediterranean Basin and in other locations world-wide (Allen et al. 2015), which may enhance litter decay according to our results. However, other factors may attenuate the reduction in canopy cover, such as woody encroachment (Hickler et al. 2012; D'Odorico et al. 2013) and the global increase in CO₂ levels, which can enhance tree growth and canopy cover (Donohue et al. 2013; Zhu et al. 2016). Furthermore, litter production may also vary, with a decrease in tree density which can reduce tree litter production (Caldentey et al. 2001), but can increase the herbaceous biomass production (Bates et al. 2000; Malkinson et al. 2011). Since our results show that grass decomposes faster than pine litter under all conditions (both experiments), there can be a substantial increase in the turnover of litter with the increase of the grass fraction. Furthermore, it should be taken into account that litter quality can also play an important role when the vegetation composition changes. In the common garden experiment, we observed higher mass loss in the forest gap for grass litter from the semi-arid forest than grass litter from the dry sub-humid forest, likely due to lower initial C:N in the grass from the semi-arid forest (Table 1 and Fig. 3).

In conclusion, under climate scenarios that are currently unfolding, the dry season will have a greater role in

controlling litter turnover in drylands. It is important to incorporate not only the non-rainfall decay mechanisms into our prediction efforts, but also shifts in vegetation cover, which may enhance the contribution of these decay mechanisms. Integration of these factors into our modelling efforts can reduce substantially the uncertainty in the predictions of carbon cycling in drylands.

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Compliance with ethical standard

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