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Higher rates of decomposition in standing vs. surface litter in a Mediterranean ecosystem during the dry and the wet seasons

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Abstract

Aims Plant litter decomposition in drylands is not well understood, and even less is known about decay of the abundant standing dead residues. Here, we followed decomposition of standing and surface litter, and assessed the underlying drivers and mechanisms.

Methods In a field experiment during contrasting seasons, litterbags were suspended at 0.05 and 1 m above ground (standing litter) and were placed on the ground (surface litter). We also quantified the moisture content of free-standing litter.

Results During nighttime in the dry, rainless season, minimum temperature was 2–3 °C lower in standing litter, leading to higher litter moisture and a doubling of microbially-driven CO_2 emissions from standing compared with surface litter. Free-standing litter moisture increased linearly with height to almost 2 m above ground. Ultimately, mass loss was higher in standing than in surface litter during the dry season (11–12% vs. 7%) and over both the dry and the wet seasons (27–34% vs. 23%), and was positively related to potentially active microbial biomass.

Conclusions Our results suggest that standing litter decomposed faster than surface litter because of enhanced microbial degradation, and possibly photodegradation, all-year-round. Therefore, carbon turnover in drylands and beyond may be underestimated by only considering surface litter decay.

Abbreviations
RH   relative humidity
SIR   substrate induced respiration
T   temperature

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Introduction

The decay of dead plant material (litter) is a key process in the carbon cycle in terrestrial ecosystems (Berg and McClaugherty 2008). Decomposition studies usually

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focus on plant litter at the soil surface (surface litter), and not much is known about decomposition of standing dead material (standing litter) which is left after the senescence of herbaceous plants (annuals and perennials) and is abundant in many biomes, such as shrublands and grasslands. Since grasslands alone contain about 20% of the global soil carbon stock (Parton et al. 1995), quantifying decay rates of standing litter is crucial for our understanding of the global carbon cycle. Additionally, with landscapes opening and drying in the course of climate and land-use changes (Allen et al. 2010; Davidson et al. 2012), the standing herbaceous litter stocks could increase substantially worldwide.

The decay of standing litter is of special interest in drylands where our understanding of decomposition is partial. Earlier studies found that the litter-climate relationship that is valid in more humid regions, does not hold in drylands (Whitford et al. 1981). An alternative relationship is yet to be found, as model predictions substantially underestimated litter decay rates in drylands (Parton et al. 2007; Adair et al. 2008; Bonan et al. 2013). Accurate quantification of litter decay rates in drylands is required for predictions of the substantial potential of carbon sequestration in these ecosystems (Luo et al. 2007; Wohlfahrt et al. 2008; Ahlström et al. 2015).

To enhance our understanding of litter decay in drylands, it was suggested to consider abiotic decay mechanisms that operate during hot and dry periods (Parton et al. 2007). Among those mechanisms, solar radiation degrades litter photochemically (photodegradation) via mineralization of photo-reactive compounds and photo-oxidation of chemical bonds, thus breaking down litter constituents, such as lignin (Moorhead and Callaghan 1994; Austin and Vivanco 2006; King et al. 2012; Barnes et al. 2015). Thermal degradation is another abiotic decay mechanism, which often functions simultaneously with photodegradation, and leads to cleavage of chemical bonds in organic materials or to their reaction with reactive compounds at high temperatures >30 °C (Lee et al. 2012). In addition to abiotic degradation, it was shown that biotic degradation can also occur during dry periods when water vapor and dew are absorbed by litter or soil to facilitate microbial activity (Dirks et al. 2010; Jacobson et al. 2015; McHugh et al. 2015; Gliksman et al. 2017b). This process occurs above litter moisture contents of about 13% and relative humidity of 75% (Bartholomew and Norman 1947; Nagy and Macauley 1982). Additionally, the infiltration of soil particles into the litter can be an important factor enhancing biotic and reducing abiotic decay by

litter-surface abrasion, inoculation with microorganisms and protecting them from high temperatures, desiccation and UV irradiance (Barnes et al. 2012; Hewins et al. 2013; Lee et al. 2014).

Since most models rely on surface litter decay, it is important to understand the relation between standing and surface litter. However, the studies that compared decomposition of standing and surface litter in arid and semi-arid ecosystems yielded mixed results. Some showed lower decay rates for standing than for surface litter (Douglas et al. 1980; Dukes and Field 2000; Almagro et al. 2017), while others showed higher rates for standing litter (Lin and King 2014; Wang et al. 2017) or did not find differences in decay rates in relation to litter height (Almagro et al. 2015; Liu et al. 2015). This diversity of results may arise not only from the large variability in litter materials and environmental conditions, but might also be attributed to differences among experimental designs, including actual litter height, and how well they capture specific microclimatic conditions in the study site.

Surface litter is typically compared categorically with standing litter placed at a certain height above the ground (ranging between 5 and 60 cm). However, standing litter is not a homogeneous category, and variation in litter heights can create differences in microclimatic conditions. At night, litter cools faster with increasing distance from the ground which may increase dew formation (Baier 1966; Jacobs et al. 1990; Xiao et al. 2009), and thus enhancing microbial activity and litter decay. During daytime, we may find that litter temperature varies with litter height due to differences in radiation transmittance (Amatangelo et al. 2008), thus affecting thermal degradation. Beyond the microclimatic gradients, the measured decay rates can be affected by the starting point of the field incubation, such as the beginning of the dry season vs. the beginning of the wet season when focusing on different periods of the year (Dukes and Field 2000; Almagro et al. 2015), or placing the standing litter in different positions (horizontal or vertical) in relation to the ground level (Douglas et al. 1980; Almagro et al. 2015). Finally, even while quantifying the contribution of specific decay drivers to carbon emissions from standing litter, the measurements were performed without differentiating between litter at different heights (Schade and Crutzen 1999; Rutledge et al. 2010; Gliksman et al. 2017b). Thus, it is important to establish a common methodology that mimics, as closely as possible, the in-situ conditions of standing litter.

The dynamics of microbial and thermal degradation during rainless periods are of special interest for understanding the decay of standing litter in drylands as they are likely to be less limited than photodegradation by the litter surface area (Henry et al. 2008; Brandt et al. 2009; Pan et al. 2015). In contrast, thermal degradation and water vapor-related microbial degradation can affect the entire standing litter mass because those decay mechanisms are not limited by the surface area of litter exposed to solar radiation. On the other hand, both of these mechanisms might be affected to some degree by the distance from the ground, as described above.

Here we addressed the importance of height and position for litter decomposition and assessed the underlying decay mechanisms by studying the microclimate, litter mass loss, and CO_2 emissions from standing and surface litter in a semi-arid dryland during dry and wet seasons. We attempted to mimic, as much as possible, the naturally occurring conditions of litter by vertically deploying litterbags at different heights and by placing litterbags horizontally on the ground. We hypothesized that (i) microbial degradation at night increases with litter height above ground because of higher water vapor availability, and (ii) during daytime, thermal degradation is more pronounced in a horizontal position on the ground than in a vertical position above ground because of higher solar heating.

Materials and methods

This study consists of the following parts: (i) a litterbag experiment conducted in the dry and subsequent wet seasons of 2012–2013 to investigate the impact of litter position and height on mass loss, litter CO_2 emission, potentially active microbial biomass, litter moisture content, and litter temperature; (ii) an experiment conducted in the dry season of 2010 to investigate the dynamics of litter moisture content along the entire vertical axis of natural standing litter. Both parts of the study took place in the same study area of 0.2 ha.

Field site

The field site was located in the dry sub-humid Mediterranean climatic zone of Israel, on the southern end of Carmel Ridge in Ramat Hanadiv Nature Park (32°30'N, 34°550'E), ~4 km from the Mediterranean coast at 120 m above sea level. The climate is characterized by

mild and moist winters, and hot and dry summers, with a rainless period from May till October. Mean annual precipitation is 530 mm (20-year average). The UV irradiance ranged from 9.9 MJ m^{-2} d^{-1} in January to 29.3 MJ m^{-2} d^{-1} in June (11-year average, measured 26 km north of the site, Israel Meteorological Service). The substrate is hard limestone covered by red brown Terra rossa soil (Chromic Luvisol or Rhodustalf). Vegetation is a maquis-type shrubland dominated by evergreen shrubs and winter annuals. The herbaceous litter between shrubs was composed of 44% standing and 56% surface litter on average [3-year mass-based means, with a range of 36–51% standing litter; each year, litter was sampled from 10 quadrats (25 × 50 cm) in the study area immediately after senescence of the herbaceous vegetation]. Litter typically remained standing throughout the dry season and started to bend and break only during the subsequent wet season (DG, personal observation). By March–April litter was mostly lying on the ground.

Litter decay at different heights: Litterbag experiment during 2012–2013

We assessed the effect of position and height above ground on litter microclimate and decay dynamics by performing a litterbag experiment from early June 2012 till mid-January 2013 (225 days). One month prior to the start of the experiment, freshly senesced straw (wheat, *Triticum aestivum* L.; litter quality: N% = 0.41 ± 0.02, C% = 43.4 ± 0.27, C:N = 105.9) was collected from an agriculture field. The straw was dried at 55 °C, and 2.5 g were placed and evenly distributed within each litterbag (12 X 12 cm). The lower part (or northern part, for standing litterbags) of the litterbag was made of grey fiberglass (1 mm mesh opening), the upper or southern part was made of transparent polyethylene [1 mm mesh opening (Nayer Ltd., Elkana, Israel), 87.0–90.4% transmittance (Fig. S1 in Supplemental material) over the photochemically active wavelengths of 280–550 nm (Brandt et al. 2009; Austin and Ballaré 2010)]. Five litterbags were placed on the ground in each of five 1-m^2 field plots (25 bags in total) that were randomly distributed in the study area (termed "surface litter"). Thirty litterbags were suspended vertically ("standing litter") at each of the two following heights: 0.05 m and 1 m above the ground on six separate constructions (5 bags per height and construction; we used six constructions instead of five as a precaution against potential

damage by large native mammals). Each construction was built by inserting bamboo poles (3 cm in diameter) into the ground at east-west orientation. The six constructions were randomly distributed among the plots with the surface litter (see above), while avoiding shading of litterbags at any height. Two pairs of nylon strings (4 mm diameter) connected the poles at each of the two heights. Each pair of strings was separated vertically by 10 cm to fasten litterbags between them, with the transparent mesh of the litterbag facing south. The strings were firmly tightened and were re-tightened as required throughout the experiment, thus preventing movement of the litterbags. We removed natural standing litter (height range: 20–160 cm) inside or near the plots of the standing and the surface litter, to avoid shading and to ensure homogeneous exposure to solar radiation on the plot level. Naturally occurring surface litter that covered most of the soil surface was left untouched.

Samplings were performed three times during the dry season and twice in mid-winter during rainless periods (at least one week after a rain event). On each sampling day, we collected a single litterbag from each replication, i.e. six bags in total at each height for standing litter and five bags in total from the soil surface. At predawn of each sampling day (starting 2 h before sunrise), we measured CO_2 emissions from litter of each sampled bag in the field using a custom-built respiration system (for Methods, see below), and then litterbags (mesh + litter) were weighed using a small scale (Scalz, Petah Tikva, Israel) to determine litter moisture content. Prior to CO_2 measurements and weighing, foreign materials were removed from bags, and dew, if present, was carefully soaked up by a dry cloth from the mesh of bag, but not from litter itself. Following these measurements, litterbags were immediately returned to their previous field location and were weighed again during midday to assess the change in litter moisture content from predawn to midday. After the midday weighing, litterbags were collected, stored in zip locked plastic bags, placed in a cooler, and brought back to the lab (bags collected at the end of a sampling day were not returned to the field). In the lab, litter was removed from bags, and wet and dry weights of litter (2 days, 55 °C) were determined (XB 620 M-FR, Precisa Gravimetrics, Dietikon, Switzerland; used for all lab weighing) to assess litter moisture content (calculated as the mass of water divided by litter dry mass and multiplied by 100% to account for the decrease in litter weight over the study period). Potentially active microbial biomass was assessed by the substrate induced respiration technique (see below).

We assessed in-situ microbial activity by performing field measurements of litter CO_2 emissions using a closed-path, custom-made respiration system. The system consisted of a commercially available container used as measuring chamber (HPL822, 600 ml, transparent polypropylene, Lock&Lock, Chatswood NSW, Australia) fitted with a UV-transparent lid [Solacryl™ SUVT, PolyOne (formerly Spartech Polycast), Stamford, CT, USA] and connected to an infrared gas analyzer (IRGA, LI-7500, LI-COR Inc., Lincoln, NE, USA, with the calibration tube installed), with a small pump (WP1000, 700 ml/min flow rate, Welco Co., Tokyo, Japan) circulating the air between the chamber and the IRGA. The overall volume of the system was 650 ml. A thermistor (9975–019#, LI-COR) was placed inside the chamber. The power supply was provided by a 12 V battery. For an emission measurement, a litterbag was placed in the chamber for a short time (70–100 s), with the measurement starting at ambient CO_2. Blanks were taken frequently. Emissions were calculated according to Jasoni et al. (2005). The data processing was performed using MATLAB 2012b (The MathWorks Inc., MA, USA). The first 10 s of each measurement were omitted due to a short pressure instability following the chamber closure and a mixing delay (Rutledge et al. 2010).

In the lab, we estimated potentially active microbial biomass by substrate induced respiration (SIR; Beare et al. 1990) to assess the influence of litter height on the microbial activity. This measurement was performed for all samplings except for the first dry season sampling. Litterbags were collected from the field at the end of the sampling day (see above) and were stored at 4 °C until processing on the following day. Subsamples of 0.5 g at field moisture were chopped lightly (approximately 1–2 cm long and 0.5 cm wide) to homogenize the litter segments and were then placed in a 40-ml glass vial fitted with a septum. The air inside the vial was flushed through two syringe needles by 400 ml of synthetic air containing 400 ppm CO_2 to obtain a near-ambient CO_2 concentration. The incubation started with the injection of 2.5 ml glucose solution (8 g glucose/l, G-5000, Sigma Aldrich Chemical, St. Louis, MO, USA) through the septum. After an incubation of 1–2 h at 25 °C, 0.5 ml of air was sampled from the vial headspace and injected to a gas chromatograph (Hewlett Packard 5890 gas chromatograph Series II, Santa Clara, CA, USA). Potentially active microbial biomass was expressed as the amount of carbon emitted as CO_2 for a gram of litter per hour. Litter mass loss was determined on ash-free (550 °C, 4 h) dry-weight

basis, after removal of foreign objects from the litter. Ash percentage was also used as an index to monitor soil infiltration or removal to and from the litter (Throop and Archer 2007). Mass loss was calculated as the difference in litter mass between initial placement in the field and retrieval on sampling day, divided by the mass on the day of placement (before litter was incubated in the field), and multiplied by 100%.

To assess site-level microclimate near the ground, a temperature/RH data logger (HOBO, Pro v2 U23–001, Onset, Bourne, MA, USA) protected by a radiation shield (RS1, Onset, Bourne, MA, USA) was placed 0.2 m above ground in one of the surface litter plots (no shading by natural standing litter). In order to assess litter temperature, two small temperature loggers per litter height (iButton DS1922L-F5# - Thermochron, Embedded Data Systems, Lawrenceburg, KY, USA) were placed as follows: under the litterbags for surface litter and inside the litterbags for standing litter; all sensors were shielded from direct solar radiation by the litter material in the bags. All loggers performed one measurement every hour.

Litter moisture content along the vertical axis of natural standing litter during the dry season of 2010

We monitored the moisture content of local standing litter at various heights above ground to examine the effect of height on litter moisture content in a natural setting of standing litter (natural standing litter was left in place; mean total litter density was 149 g m^{-2}). During five predawn samplings, evenly distributed from the end of June till the end of September 2010, we collected a total of 30 standing and senesced individuals (two individuals per species per sampling day; some individuals were later excluded for not having fully senesced). Each individual was cut to 12-cm segments, and each segment was inserted to a capped 15-ml plastic tube and brought to the lab in a cooler. Litter moisture content (dry-weight basis) of each segment was assessed in the lab by weighing it before and after drying in an oven (2 days, 55 °C). We sampled standing individuals from four species of different taxonomic families: *Carthamus tenuis* (Boiss. et Blanche) Bornm (*Asteraceae, n* = 10 individuals, ranging 55–134 cm in height), *Cephalaria joppensis* (Rchb) Coult. exDC. (*Dipsacaceae, n* = 8, 116–185 cm), *Daucus broteroi* Ten. (*Apiaceae, n* = 7, 59–85 cm), *Piptatherum blancheanum* Desv. exBoiss. (*Poaceae, n* = 5, 73–97 cm). As in the litterbag

experiment in 2012–2013, we assessed the site-level microclimate using a shielded temperature/RH data logger (HOBO) placed 0.2 m above ground.

Statistical analysis

In the litterbag experiment in 2012–2013, we compared litter heights for differences in litter moisture content, SIR, CO_2 emissions and mass loss using the Tukey–Kramer HSD post-hoc test. We describe the relation between SIR and mass loss using a linear correlation. The relation between moisture content and litter CO_2 emission was described using a full-factorial general linear model containing litter moisture content and sampling day as independent variables; the variable sampling day had two levels, (*i*) the first sampling day and (*ii*) the following sampling days in the experiment (two samplings in the dry season and two samplings in the wet season). A similar analysis was performed using ash content and the season (dry or wet season) to predict the level of mass loss. For analyzing litter moisture content along the vertical axis of natural standing litter (2010), we divided the heights into 12-cm bins. We averaged the moisture values from all individuals at each height for each species separately. Then, we applied a full factorial general linear model containing the factors height above ground (binned) and species. Where heterogeneity of variance occurred, data were log transformed. Data were analyzed using JMP 10 software (SAS Institute, Cary, NC, USA).

Results

Litterbag experiment during 2012–2013

During the dry season of 2012, nighttime minimum temperatures (daily minimum, T_{min}, relevant for dew formation) were lower by approximately 2 °C and 3 °C for standing litter at 1 m and 0.05 m height as compared with surface litter (Table 1, Fig. S2a). Site-level nighttime maximum RH (RH_{max}) measured by the microclimate logger at 0.2 m above ground was high at most nights throughout the dry season and averaged 95.5% (Table 2, Fig. S2a). Maximum daily temperature (T_{max}, relevant for thermal degradation; Table 1, Fig. S2b) of standing litter at 1 m height was about 6 °C lower than T_{max} of standing litter at 0.05 m height, and about 19 °C lower than T_{max} at ground level (surface litter). Site-level mean daily minimum RH was low (43.0%).

Table 1 Mean daily minimum and maximum temperature (min. and max. T) of the litter during dry and wet seasons in the litterbag experiment

Season	Litter position	Height (m)	Mean daily min. T (°C)	Mean daily max. T (°C)
Dry season	Surface	0	$23.4 \pm 0.1a$	$53.3 \pm 0.2a$
2012	Standing	0.05	$20.2 \pm 0.2c$	$40.8 \pm 0.2b$
	Standing	1.0	$21.4 \pm 0.1b$	$34.7 \pm 0.1c$
Wet season	Surface	0	$14.1 \pm 0.3a$	$29.6 \pm 0.8a$
2012–2013	Standing	0.05	$12.1 \pm 0.3b$	$29.4 \pm 0.5a$
	Standing	1.0	$13.6 \pm 0.3a$	$26.0 \pm 0.4b$

Values are shown for the dry season of 2012 (June–October 2012) and the subsequent wet season of 2012–2013 (October 2012–March 2013) at different heights unshaded by neighboring standing litter. Sensors were placed under litterbags for surface litter and inside litterbags for standing litter; all sensors were shielded from direct solar radiation by the litter material. Means followed by different letters within a column and a season are significantly different ($P < 0.05$). Mean ± SE, $n = 107$ and 106 days for the 2012–2013 dry and wet seasons, respectively

In the dry season of 2012, litter moisture content measured during predawn hours was considerably higher in standing litter (both heights) than in surface litter, especially at the first and third sampling dates (Fig. 1a). When averaging across samplings, the moisture content in standing litter at 1 m and 0.05 m was 1.7 and 1.5 times higher, respectively, than moisture in surface litter. There was a trend of higher moisture content in the standing litter at 1 m height compared with moisture in standing litter at 0.05 m, but this trend was statistically significant only in the last sampling of the dry season. At midday, litter moisture content was low (below 8% at all heights, Fig. S3).

In all the dry season samplings, the CO_2 emissions measured at predawn were approximately twice as high in the standing litter (both heights) as in the surface litter (Fig. 1b). At the end of the dry season, the standing litter at 1 m height had the highest levels of potentially active microbial biomass, with 1.5 and 1.8 times more potentially active microbial biomass than standing litter at 0.05 m

height and surface litter, respectively (Fig. 2). Ash content at the end of the dry season decreased gradually from litter at 1 m height to litter at 0.05 m and surface litter (Table S1). By the end of the dry season (after 107 days), decomposition of standing litter at both heights was significantly higher by a factor of 1.6–1.7 compared to decomposition of surface litter (Fig. 3).

During the wet season of 2012–2013, T_{min} was lower at 0.05 m height than at ground level or at 1 m height (Table 1, Fig. S2a). Site-level RH_{max} remained high ($95.3 \pm 0.9\%$, mean ± SE, $n = 109$ days). The trend of litter moisture content and CO_2 emissions in relation to litter height contrasted with the respective trend found in the dry season of 2012 (two samplings in rainless periods during January 2013). At predawn, litter moisture content tended to decrease with litter height, which was especially evident in the first wet season sampling when dew was abundant and moisture content reached peak levels of 120% in surface litter (Fig. 1a). The CO_2 emissions measured at predawn followed the trend in litter moisture content, with the standing litter at 1 m height emitting the lowest amount of CO_2 followed by the standing litter at 0.05 m and the surface litter (Fig. 1b). In the second wet-season sampling, the overall rates of CO_2 emissions were much lower than in the previous sampling, due to the low litter moisture content, yet a pattern similar to the first sampling was observed, with highest CO_2 emissions emitted from surface litter. During daytime, T_{max} in the wet season was below 30 °C, and standing litter at 1 m had the lowest T_{max} (Table 1).

Potentially active microbial biomass and litter mass loss increased with height in the wet season of 2012–2013, similar to the findings of the preceding dry season (Figs. 2, and 3), but in contrast to the wet-season litter moisture and CO_2 emission patterns (Fig. 1). The potentially active microbial biomass levels of standing litter at 1 m height were 1.4 and 2.6 times those of standing litter at 0.05 m and surface litter, respectively. Similarly, mass loss at the end of the experiment reached 34% for standing litter at 1 m height, which was 1.3 and

Table 2 Site-level daily maximum and minimum relative humidity (RH) and temperature (T) measured at 0.2 m above ground during the 2010 and 2012 dry seasons

Year	Daily max. RH (%)	Daily min. T (°C)	Daily min. RH (%)	Daily max. T (°C)
2010	91.3 ± 0.5	21.9 ± 0.2	47.5 ± 0.7	35.1 ± 0.2
2012	95.5 ± 0.4	20.4 ± 0.2	43.0 ± 0.6	37.5 ± 0.3

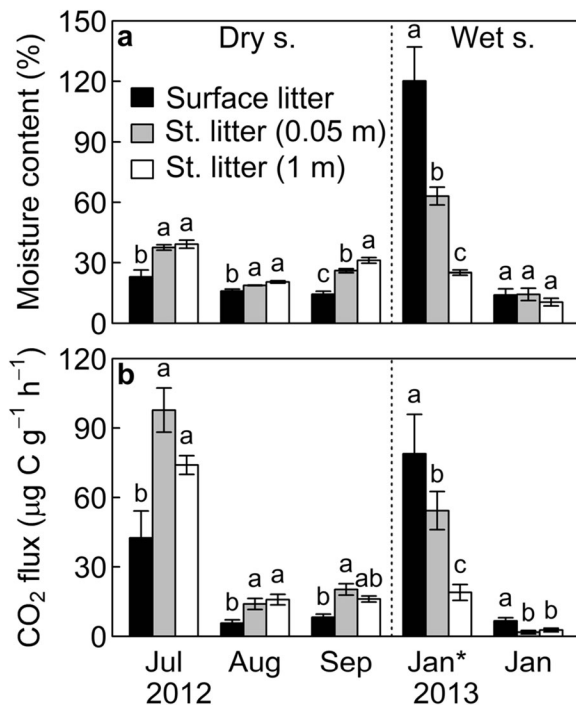Sensors were installed in radiation shields. Mean ± SE, $n = 104–112$ days

Fig. 1 Litter moisture content as percentage of dry weight (**a**) and CO_2 emission (**b**) during predawn measurements of surface and standing litter ("St. litter") at different heights (litterbag experiment). Measurements were performed during the dry season ("Dry s.", July to September 2012) and the subsequent wet season ("Wet s.", January 2013). "Jan*" is the first of the two samplings performed in January 2013, a day with abundant dew; no dew was observed on the second sampling day during this month ("Jan"). Different letters indicate significant differences between means within a sampling date at $P \leq 0.05$ (Tukey–Kramer HSD test). $n = 4$–6 litterbags per category, mean ± SE
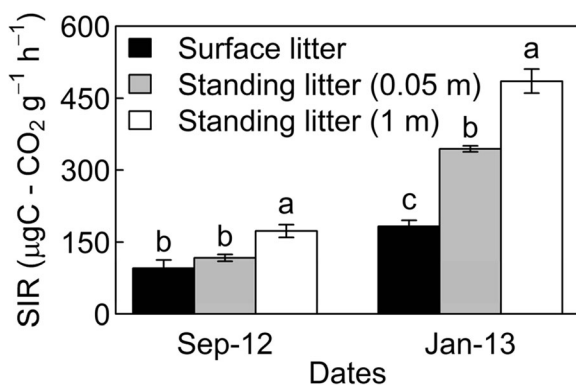
Fig. 2 Levels of potentially active microbial biomass (as estimated by substrate induced respiration, SIR) at the end of the dry season (September 2012) and at the last sampling of the litterbag experiment during the wet season (January 2013). Different letters indicate significant differences between means within a sampling date at $P \leq 0.05$ (Tukey–Kramer HSD test). $n = 5$–6 litterbags per category, mean ± SE
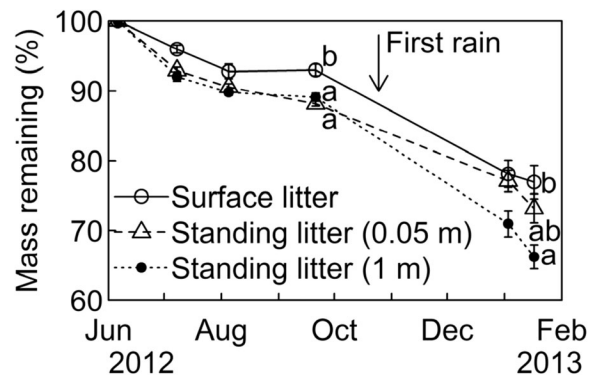

Fig. 3 Mass remaining in litterbags at different heights above ground (litterbag experiment in 2012–2013). The rainless dry season lasted from May to October 2012. Different letters indicate significant differences between means within a sampling date at $P \leq 0.05$ (Tukey–Kramer HSD test). $n = 5$–6 litterbags per category, mean ± SE

1.5 higher than mass loss of standing litter at 0.05 m and surface litter. Additionally, the difference in mass loss between the standing litter at 1 m height and surface litter increased from 4% at the end of the dry season to 11% during the wet season, due to the higher mass loss occurring in the wet season ($P < 0.05$). The difference in mass loss between the standing litter at 0.05 m height and the surface litter did not increase over the wet season. Ash content decreased over the wet season in standing litter at 1 m, but increased considerably in standing litter at 0.05 m and in surface litter (Table S1).

Over both the dry and the wet seasons of 2012–2013, mass loss values were positively correlated with levels of potentially active microbial biomass across all heights and samplings ($P < 0.001$; Fig. 4). In addition, we found
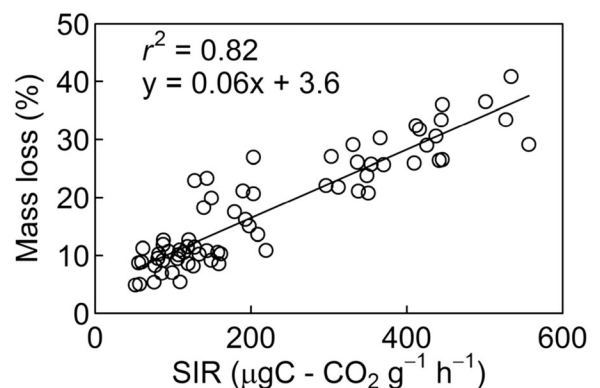

Fig. 4 Relationship between mass loss and potentially active microbial biomass as estimated by substrate induced respiration measurements (SIR) over all heights and samplings (litterbag experiment 2012–2013). SIR was not assessed for the first dry season sampling. $n = 67$

a positive linear relation between litter moisture content and CO_2 emissions (entire model $r^2 = 0.82$, Table S2, Fig. 5), but the slope of the first sampling in the dry season differed from the slope of all the other samplings of the dry and wet seasons combined (interaction $P < 0.001$). While both slopes were significant and positive ($P < 0.001$), the slope of the first sampling was three times steeper than the slope of the other samplings. Mass loss was also related to ash content, but while in the dry season mass loss increased with ash content, the trend reversed during the wet season (Fig. 6, Table S3).

Litter moisture content during the 2010 dry season

Similar to the trend found in the 2012 dry season, the predawn samplings of natural standing litter during the dry season of 2010 showed increasing litter moisture content with increasing height across the different plant species (Table S4, Fig. 7, $r^2 = 0.84$, $P < 0.001$). Litter moisture content increased linearly with height at a rate of 16.2% per meter (averaged over all species). Site-level T_{min} was slightly higher and RH_{max} slightly lower during the 2010 than during the 2012 dry season (Table 2, Figs. S2a and S4).

Discussion

The majority of decomposition studies conducted so far have focused on surface litter as the representative location for assessing decay, and the few studies on standing litter referred to litter position in a categorical way,
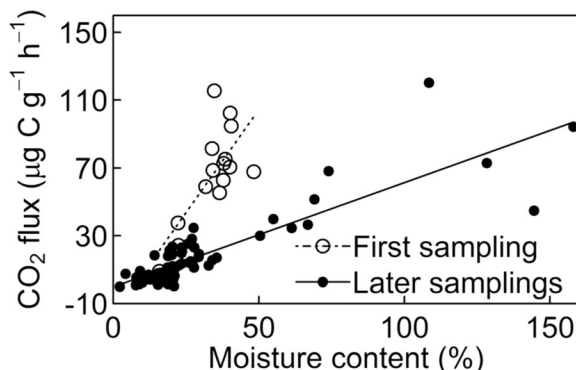

Fig. 6 Relationships between ash-free mass loss and ash content over the dry season (○) and the wet season (△) in the 2012–2013 litterbag experiment (see Table S3 for model details). $n = 63$ and 47 for the dry and wet seasons, respectively

without ascribing importance to litter height. Here we show that a change in litter position and height can significantly affect the decay rate as a consequence of diverging microclimatic conditions and the associated decay mechanisms. Litter decomposition and potentially active microbial biomass increased with litter height over both the dry and the wet seasons. Furthermore, the changes in decomposition with litter height, and the associated differences in minimum temperature, litter moisture, litter CO_2 emissions and potentially active microbial biomass indicate that microbial degradation is the underlying dominant mechanism of decay during the dry season.

Fig. 5 Relationship between CO_2 emissions and litter moisture content as percentage of dry weight (predawn measurements during the litterbag experiment in 2012–2013). The first dry season sampling (July 2012) (○) was separated from the additional dry season and the wet season samplings (•). $n = 15$ and 65 for the first sampling and the additional samplings, respectively
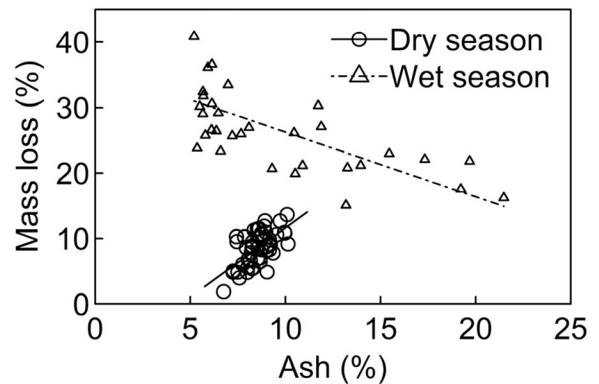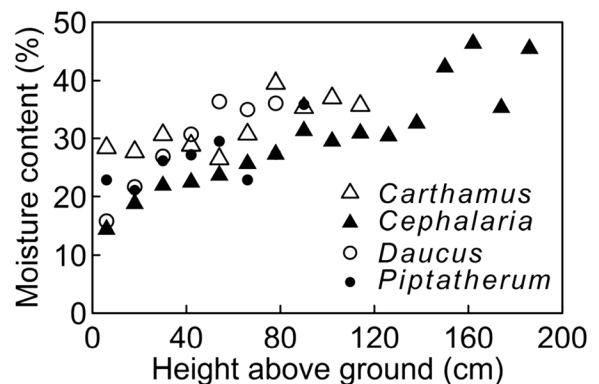

Fig. 7 Litter moisture content as percentage of dry weight in natural standing litter sampled at predawn during the dry season of 2010 (June till late September). Samples from four different species were collected, and litter moisture content was averaged over all individuals of each species in 12-cm bins. The slope of moisture content with height was steeper for the species *Daucus broteroi* than for the other species ($P < 0.018$; Table S4). $n = 7–16$ bins per species

Litter decomposition during dry season nights was caused by microbial degradation, as indicated by litter CO_2 emissions at predawn that must originate almost exclusively from microbial activity because solar radiation was absent (no photodegradation) and the relatively low nighttime temperatures cannot facilitate thermal degradation (Lee et al. 2012; Gliksman et al. 2017b). Microbial activity was higher in standing than in surface litter because litter moisture content increased with height in the litterbag experiment in 2012. The reduction in minimum temperature of standing compared with surface litter most likely increased the frequency and intensity of nighttime dew formation (Baier 1966; McCown and Wall 1981; Xiao et al. 2009), which raised the moisture content of plant litter and led to the increase in potentially active microbial biomass and CO_2 emissions, as we hypothesized. Probably for the same reason, litter moisture increased with height in natural standing litter of four species from different plant families in 2010. The higher CO_2 emissions per unit moisture content early in the dry season, in contrast to later stages of the season, were assumingly the result of the fast microbial degradation of labile litter constituents at the beginning of the decay process. In later stages, the fraction of recalcitrant substances likely increased in the litter, thus slowing down decay rates. In addition, towards the end of the dry season in 2012 and during the following wet season, the gradual decrease in nighttime temperature might also have reduced the microbial activity. We also note the possibility that we underestimated the microbial activity as quantified by CO_2 emission measurements, due to solubilization of CO_2 in water films on and within the litter (Carroll et al. 1991).

The higher mass loss of standing than of surface litter at the end of the dry season in 2012 can be explained at least partly by higher nighttime litter moisture content leading to increased microbial degradation in standing litter. According to the CO_2 emissions measured at predawn, the contribution of microbial degradation was about twice as high in standing litter as in surface litter during the dry season. The substantial increase in mass loss with height (by a factor of 1.6–1.7) and the concomitant increase in SIR, indicates a dominance of microbial degradation during the dry season, at least for standing litter. An additional experiment at the same site showed that surface litter was also mainly degraded by microbial activity (Gliksman et al. 2017b). In contrast to microbial degradation, thermal degradation was probably higher in surface litter than in standing litter over the dry season because daytime temperatures were considerably higher in surface litter. Photodegradation may contribute less to standing litter decay because, at a latitude similar to that of our site, vertical surfaces (such as those of standing litter) were reported to be less exposed to solar irradiance than horizontal surfaces (such as those of litter on the ground) when summing the irradiance over an entire day (Webb et al. 1999). However, it should be taken into account that standing litter has a larger surface area that can be exposed to both direct and reflected solar radiation than surface litter, depending on the sun angle. Therefore, photodegradation could have contributed to the higher decay rate in standing as compared with surface litter, despite the vertical position of standing litter. Finally, soil-litter mixing could also influence our results, as standing litter in both positions tended to have higher ash content than surface litter and ash content was positively correlated to mass loss. Thus, it is possible that increased moisture content with height also increased the infiltration of soil particles into the litter through enhanced adhesiveness. The higher ash content could support microbial degradation by inoculating the litter with microorganisms and protection of the microorganisms from the harsh microclimatic conditions (Lee et al. 2014; Barnes et al. 2015).

The dynamics of microbial degradation as facilitated by water vapor and dew absorption changed in the wet season as compared to the dynamics in the dry season. We observed increased litter moisture content and CO_2 emissions with a decrease in litter height on two sampling days during rainless periods in the wet season. Because soils are a source for water vapor during the wet season (in contrast to the soil conditions in the dry season), water evaporating from the soil could pass through surface litter and moisten it to a higher degree than standing litter. Surface litter was probably not wetted directly by the moist soil, since during daytime litter moisture content reached low levels similar to those measured in the dry season (Fig. S3). Furthermore, during our measurements in the wet season, the litter was not moist from previous rain events as at least one week passed since the last rain event, thus allowing the litter to dry (Raison et al. 1986; Harpole and Haas 1999). Consequently, we showed that water vapor and dew facilitated microbial degradation of litter all year long and that the contribution of precipitation to litter decomposition can be sustained by soil-derived water vapor absorbed by the litter layer.

Enhanced mass loss of standing litter at 1 m height compared with mass loss of litter on the ground during the wet season was probably not caused by the water vapor- and dew-driven microbial activity, since litter moisture content and CO_2 emissions were actually higher in surface litter. Yet, the considerable increase with height of potentially active microbial biomass in the wet season indicates that precipitation was the major source of moisture to enable microbial activity. Moreover, the flow of water from the litter during rain events may have been more rapid in standing litter due to lack of contact with the ground, thus enhancing leaching of dissolved organic materials from standing litter. Standing litter may have higher content of dissolved organic carbon than surface litter (Wang et al. 2017), thus further increasing the leaching losses of mass from standing litter. A result supporting this degradation mechanism is the reduced ash content in the wet vs. the dry season in standing litter at 1 m height, which mostly likely resulted from leaching during rain events. Abiotic decay should be strongly reduced in the wet season due to the significant decrease in temperature and solar radiation, making it a less likely source for the substantial difference in mass loss between standing and surface litter. Moreover, the decrease in temperature with height does not support the possibility of greater thermal degradation in standing than surface litter as the cause for the higher mass loss observed in standing litter at 1 m height over the wet season. However, because of the above mentioned larger surface area exposed to radiation of standing litter, it cannot be ruled out that photodegradation enhanced the decay at 1 m height, despite the low levels of solar irradiance in the wet season. Soil-litter mixing was present in standing litter at 0.05 m height and in surface litter as indicated by enhanced litter ash contents, which would have reduced photodegradation in these litter types over the wet season (Barnes et al. 2012). Soil microbial films likely contributed to litter decomposition at low height, but their contribution to overall decay was relatively small considering the inverse relationship between decay and percent ash across all positions and heights.

Facilitation of decomposition during the wet season by processes occurring during the dry season can provide an additional explanation for the higher mass loss in standing than in surface litter during the wet season. In a previous study on surface litter, mass loss during the wet season was positively related to potentially active microbial biomass during the dry season, and likely also by exposure to solar radiation (Gliksman et al. 2017a). The potentially active microbial biomass in the current study increased substantially with height over the dry season and matched the trend in the mass loss over the wet season, thus possibly inducing a form of microbial facilitation by decay during the dry season. The additional facilitation effect could arise from 'photopriming', which is the enhancement of decay in wet periods by photomineralization of structural components in the litter, such as lignin during dry periods (Henry et al. 2008; Gallo et al. 2009; Austin et al. 2016).

The results of this study indicate the activity of different combinations of litter decay mechanisms operating at different heights and in different seasons. Litter at 1 m height is suggested to be decayed by vapor- and dew-driven microbial degradation and possibly photodegradation during both seasons, with rain-driven microbial activity to be added during the wet season. Decomposition of surface litter at our site seems to be advanced by thermal and photochemical degradation and to some extent also vapor- and dew-driven microbial degradation during the dry season, and by microbial degradation enhanced by the different water sources and by soil-litter mixing in the wet season. Furthermore, multiple interactive effects among decay mechanisms most probably contribute to decomposition at all heights and in both seasons. Thus, there is a need in interpreting results to differentiate between sites with high or low water vapor availability and litter height, as determinant of whether studying photodegradation and thermal degradation alone is sufficient in rainless periods (Almagro et al. 2017).

Our results demonstrate the importance of incorporating multiple litter heights and addressing the season of sampling to better understand standing litter decay. Comparing standing litter at 0.05 m with surface litter for mass loss would have yielded no significant difference at the end of both seasons, as also reported in other studies (Almagro et al. 2015; Liu et al. 2015), while standing litter at 1 m height decomposed faster than surface litter. Additional studies in drylands found that litter at 0.05 m height decayed slower (Dukes and Field 2000; Almagro et al. 2017), but litter at 0.1–0.2 m height decayed faster than surface litter (Lin and King 2014; Wang et al. 2017). Because of divergent microclimatic conditions, litter height appears to be crucial in any experimental design with standing litter. The season of measurements must also be taken into account, as shown by the contrasting trends with litter height in litter moisture and CO_2 emissions.

Combining litterbags with free standing natural litter could be the basis for a unified methodological approach to study the decay of standing litter. Such an approach would monitor the dynamics of microclimatic conditions and activity, such as CO_2 emissions in undisturbed standing litter along height gradients, while enabling to quantify changes in mass and nutrients with height and over time. The key decisions concerning litterbag positioning (vertical or horizontal) and height should be derived from the characteristics of the free standing litter in the site which can vary among species (Thurow 1989). Although temperature and dew formation, and thus thermal and microbial degradation, could potentially be affected by the litterbag, this effect on the litter energy budget and its temperature should be small because of the overall low weight of litterbags (only 7–8 g for mesh bag + litter material in our study). Measuring the overall irradiance absorbed by litter with and without a litterbag (from all angles) will be a complex task, and most likely will require either modelling approaches (using parameters such as litter topology, sun positions and irradiance intensity) or using irradiance sensitive substrates that can monitor the accumulative exposure to radiation (Austin and Ballaré 2010).

Our results suggest that standing litter is subjected to different microclimatic conditions than surface litter. These conditions change with height of standing litter and seem to enhance microbial degradation during the dry and probably also the wet season. Therefore, we should not generalize from the decomposition of litter on the ground to the decay of standing dead plant material. Ignoring substantial differences in mass loss of standing litter at different heights compared with surface litter in biogeochemical models will prevent accurate predictions of carbon turnover in the large terrestrial area covered by grassland, savannah, shrubland and additional biomes.

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