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Multiple abiotic and biotic drivers of long-term wood decomposition within and among species in the semi-arid inland dunes: A dual role for stem diameter

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Abstract

1. Litter decomposition in sunny, semi-arid and arid ecosystems is controlled by both biotic factors including litter traits and abiotic factors including UV light, but for wood decomposition it still remains uncertain which of these environmental factors are the predominant controls among different woody species. In these dry ecosystems, it is likely that the stem diameter and spatial position of the dead wood are of particular importance especially where wood can be buried versus exposed due to substrate displacement by wind. Here we focus on the fact that stem diameter can affect decomposition rates both *via* the relative surface exposure to sunlight or soil and *via* higher resource quality of narrower stems to decomposers.
2. In a field manipulation experiment, we investigated the relative importance of litter position (sand burial vs. surface vs. suspended above the surface), UV radiation (block versus pass) and stem diameter class (<2, 2–4, 4–8, 8–13 and 13–20 mm) on the mass loss of woody litters of four shrub species in an inland dune ecosystem in northern China.
3. We found that after 34 months of in situ incubation, the mass loss of buried woody litters was three times faster than those of suspended and surface woody litters ($53.5 \pm 2.7\%$, $17.0 \pm 1.0\%$ and $14.4 \pm 1.2\%$, respectively). In surface and suspended positions, litter decomposition rates were almost equally low and most mass loss was during the first 2 years, when bark was still attached and UV radiation had no significant effect on woody litter mass loss. These findings suggest that sand burial is the main environmental driver of wood decomposition *via* its control on microbial activity. Moreover, wood N and diameter class were the predominant factors driving woody litter decomposition. A key finding was that wider stems had slower litter decomposition rates not only directly (presumably *via* greater relative surface exposure) but also indirectly *via* their higher wood dry matter content or lower wood N; these effects were modulated by litter position.
4. Our findings highlight a dual role of stem diameter on wood decomposition, that is, *via* relative surface exposure and *via* wood traits. The accuracy and confidence

of global carbon cycling models would be improved by incorporating the different effects of stem diameter on woody litter decomposition and below-ground wood decomposition processes in drylands.

KEYWORDS

dryland, functional traits, litter position, sand burial, shrub encroachment, stem diameter, wood litter decomposition

1 | INTRODUCTION

Litter decomposition is a key process in the carbon (C) and nutrient cycles in terrestrial ecosystems (Berg & McClaugherty, 2008; Swift, Heal, & Anderson, 1979). Generally, woody litter decomposition is mainly controlled by substrate quality, climate and decomposing organisms (Cornwell et al., 2009; Harmon et al., 1986; Swift et al., 1979). Wood decomposition within mesic temperate or tropical ecosystems is strongly modulated by biotic factors such as soil fauna and microbes due to their high abundances and activity at suitable environmental moisture regime (Bradford et al., 2014; González, Gould, Hudak, & Hollingsworth, 2008; Liu, Cornwell, Cao, et al., 2015; Torres & González, 2005; Ulyshen, 2016). Microbial wood decomposition is mainly controlled by fungi that are highly specialized in resource requirements (Rayner & Boddy, 1988), although Wu et al. (2018, 2019) found that the decomposition rate of woody debris in subtropical forests was accelerated by an abiotic factor, that is, UV light. By contrast, lower vegetation canopy cover, that is, high irradiance, and lower annual precipitation could constrain decomposer abundances and activity. Therefore, there is accumulating evidence that litter decomposition in semi-arid and arid ecosystems is controlled by both biotic and abiotic factors (Austin & Vivanco, 2006; King, Brandt, & Adair, 2012; Liu et al., 2018). The abiotic conditions are a consequence of the dynamics of these ecosystems, where litter can either be strongly exposed to sunlight or get buried by wind-displaced soil material. This has been recognized in recent research on litter decomposition in sunny drylands, which has highlighted the importance of several abiotic mechanisms related to light exposure and burial, including photodegradation, photo priming effect and litter-soil mixing (Austin & Vivanco, 2006; Hewins & Throop, 2016; Lin & King, 2014; Liu et al., 2018). Austin and Ballaré (2010) suggested that lignin inhibits litter decomposition in mesic ecosystems while it enhances litter decomposition in arid ecosystems due to photochemical processes. Also, photodegradation of plant litter can reduce the structural and chemical bottleneck imposed by lignin in secondary cell walls, thereby increasing microbially driven litter decomposition (Austin, Méndez, & Ballaré, 2016). These are mechanisms that may explain why litter decomposition in drylands is faster than expected from biotic mechanisms alone (Throop & Archer, 2009). Indeed, several studies reported that the rate of decomposition in sunny drylands is accelerated by stronger solar exposure including UV radiation (Austin & Vivanco, 2006; King et al., 2012) and also by burial under displaced soil material (Austin,

Araujo, & Leva, 2009; Liu, Cornwell, Pan, et al., 2015; Liu et al., 2018) as compared to decomposition of surface litter.

Changes in plant species have strong effects on biogeochemical processes via plant-soil feedback (Hobbie, 2015) and this must certainly be true for changes in the relative abundance of herbaceous versus woody plants, which possibly mediate changes in incubation microclimate (Gottschall et al., 2019). Shrub encroachment, a common phenomenon in arid and semi-arid grasslands, affects soil C and N accumulation and turnover (Hibbard, Archer, Schimel, & Valentine, 2001). Moreover, there exist many vegetation types in drylands in which woody plants are common and likely important to biogeochemical cycling, such as desert, inland dunes, semi-desert, woodland, shrubland and savanna. It is therefore surprising that research on woody debris decomposition in arid and semi-arid ecosystems is scarce when compared with non-woody plant materials such as leaves or herbaceous stems. The sparse evidence that has accumulated suggests that, compared to mesic ecosystems, woody debris decomposes slowly in water-limited ecosystems such as in dry woodland, savanna, shrubland, semi-desert or desert, even if and where the decomposition rates are increased substantially due to termite activity (Andersen, Stricker, & Nelson, 2016; Ebert & Zedler, 1984; Milton & Dean, 1996). For example, Milton and Dean (1996) found that dead shrubs lying on the soil in an arid shrubland had woody litter mass half-lives of 9–18 years for different species. Moreover, Lyons and McCarth (2010) found there was no difference in *Juniperus ashei* wood decomposition in open and shaded habitats after 29 months of incubation. These observations seem a contradiction with the findings for herbaceous litter, which showed faster than expected decomposition due to sun exposure or burial, as explained above. Here we argue that the effect of solar radiation on wood decomposition should be weak or significantly decreased due to the lower surface area to volume ratio of wood, that is, its relatively low exposure to solar radiation compared to that of herbaceous litter in arid and semi-arid regions. Moreover, bark could provide a powerful protective layer against photodegradation of the wood beneath. As for leaf litter, there is very scarce knowledge about the effects of burial on wood decomposition, but one desert study showed that soil movement mediated burial provides an optimal microclimate with higher moisture and relatively stable temperature for microbial wood degradation (Moorhead & Reynolds, 1993). In contrast, Moroni et al. (2015) suggested that wood buried by soil, litter or ground vegetation in wide-ranging forest ecosystems was efficiently preserved, that is, slowly decomposed. However, this

review included relatively few dryland sites and our understanding of decomposition processes of buried wood in drylands is still poor.

While the above litter positions and related decomposition processes have focused on herbaceous versus woody litter in general terms, there is now much literature showing that species differ greatly in their traits as well as in the 'afterlife effects' these traits have on decomposition. This is the case both for leaf litter (Bakker, Carreño-Rocabado, & Poorter, 2011; Cornwell et al., 2008; Kazakou, Vile, Shipley, Gallet, & Garnier, 2006) and for woody litter (Cornwell et al., 2009; Freschet, Weedon, Aerts, van Hal, & Cornelissen, 2012; Hu et al., 2018; Pietsch et al., 2014; Zuo et al., 2018). For instance, wood nitrogen was the best predictor of the decomposition rates of woody debris across angiosperm clades based on a global meta-analysis (Weedon et al., 2009). Also, thicker stems tend to be decomposed more slowly than thinner ones and this difference has been attributed to the lower surface to volume ratio of the former. Indeed, stem diameter could explain 41% of the variance of wood decomposition rates of 15 Neotropical tree species (van Geffen, Poorter, Sass-Klaassen, van Logtestijn, & Cornelissen, 2010). Recently, Hu et al. (2018) found that wood nitrogen and diameter could explain approximately half of the global variation in wood decomposition rates. Moreover, wood density or wood dry matter content controlled the rate of wood decomposition in diverse forests (Freschet et al., 2012; Liu, Cornwell, Cao, et al., 2015; Pietsch et al., 2014; Zuo et al., 2018). However, these studies have not considered the possibility that stem diameter and stem tissue quality traits (e.g. dry matter content) may be confounded. That is to say, stem diameter might affect decomposition rates not only *via* relative exposure but also because younger, narrower stems might have better resource quality to decomposers. Additionally, as the outermost covering of wood material, bark plays an important role in stem protection against insect or pathogen damage (Rosell, 2016). Moreover, bark may have a moisture-retention function in woody debris and it could increase microbially driven wood decomposition (Dossa, Paudel, Cao, Schaefer, & Harrison, 2016; Ulyshen, Müller, & Seibold, 2016). Recently, Dossa et al. (2018) found that bark can enhance coarser WD decomposition but slows twig decomposition in some species. Bark thickness may affect both microbial invasion and microenvironment (Cornwell et al., 2009). Rosell (2016) showed that bark thickness is strongly positively correlated with stem sizes. Thus, it is likely that bark thickness affects woody litter decomposition, directly or *via* its relation with diameter, but empirical data are lacking. The same is true for the effect of bark traits on wood decomposition in general (but see Zuo et al., 2018).

It still remains uncertain to which extent litter position versus initial litter traits of different species, or their interactions, predominantly control the decomposition of woody litter in arid and semi-arid environments. Therefore, to fill this research gap, we designed an experimental study to examine the effects of litter position (sand burial, suspended above the surface and in a surface litter layer) on the decomposition of woody litters from four shrub species with different diameters (φ : <2, 2–4, 4–8, 8–13 and 13–20 mm) in an inland dune ecosystem, where the effects of litter position *via*

UV radiation on above-ground wood decomposition were explicitly examined through experimental UV blocking. Thus, the question is how UV radiation and litter positions together influence the decomposition of woody litters across different diameters in a semi-arid dune ecosystem? To answer this question, we hypothesized that (1) buried woody litters would have higher decomposition rates than surface and suspended woody litters due to stable and favourable moisture regime and well-developed microbial community; (2) UV radiation would increase the decomposition rate of woody litters; (3) bark thickness would be negatively correlated with the rate of wood decomposition; (4) woody litters of smaller diameter, with higher relative surface exposure to external microbes and sunlight, and possibly higher resource quality, should be decomposed faster than wider ones.

2 | MATERIALS AND METHODS

2.1 | Study site

The field work was conducted at the Ordos Sandland Ecological Research Station (OSERS) in the *Mu Us* inland sand dune area, Institute of Botany, Chinese Academy of Sciences (Inner Mongolia, China, 39°29'37.6"N, 110°11'29.4"E, 1,290 m a.s.l.). Site details can be found in Erdenebileg et al. (2018). Briefly, in this site, mean annual temperature is 6.2°C and mean annual precipitation is 369 mm, 80% of which falls during the growing season from April to August. Soil texture in this area is aeolian sand. Soil fertility is low with low N concentration. Since strong wind occurs in winter and early spring, both wind erosion and sand burial are common processes in this area. The woody vegetation in this region comprises perennial subshrubs (dominated by *Artemisia ordosica* Krasch and *Hedysarum laeve* Maxim.). In order to combat land desertification, two shrubs, that is, *Salix psammophila* C. Wang et Ch. Y. Yang and *Caragana korshinskii* Kom., have been planted by local governments for over 20 years in some areas in order to stabilize the dunes, but large areas with strong sand dune dynamics remain in this region, so burial of dead wood of all four shrubs mentioned is a widespread phenomenon.

2.2 | Litter collection and functional trait measurements

The four shrub species used in this study are *A. ordosica*, *C. korshinskii*, *H. laeve* and *S. psammophila*. For each species, recently senesced finer woody litters were collected from 30 to 50 individual plants from the beginning of October through the middle of November 2015. For each species, we collected stem, branches and twigs from each of five diameter classes (φ : <2, 2–4, 4–8, 8–13 and 13–20 mm), where the total length collected per class was inversely related to diameter in order to obtain broadly equal total mass across the diameter classes (Figure S1). For measurements of initial undecomposed or decomposed woody litter density that may correlate to

woody litter decomposition rates, initial and decomposed woody litter subsamples (collected at subsequent harvests; see below) were immersed in water in plastic containers for 4 days to be fully saturated and to ensure homogeneous filling of air spaces (Freschet et al., 2012; also see wood water absorption curve based on the largest wood size, Figure S2). Initial and decomposed litter volumes were measured using the Archimedes' principle of water displacement (details in Williamson & Wiemann, 2010). The saturated samples were then gently blotted dry with filter paper and weighed to obtain saturated mass, subsequently oven-dried at 65°C for 72 hr to obtain dry mass. Wood dry matter content (Wood DMC, g/g) was calculated as dry mass divided by its saturated mass and initial or decomposed wood density (g/cm³) was calculated as litter dry mass divided by saturated litter volume. Because bark could affect wood decomposition by providing a protective barrier around the wood (Cornwell et al., 2009; Dossa et al., 2018), bark thickness (mm) and bark dry matter content (Bark DMC, g/g) were also determined. Bark thickness was measured using digital calipers. Bark was separated from the initial wood subsamples and then was immersed into water to be saturated for 1 day. The saturated bark samples were gently blotted dry with filter paper and weighed to obtain saturated bark mass, subsequently oven-dried at 65°C for 24 hr to obtain its dry mass.

2.3 | Experimental design

In order to assess the influences of UV radiation and litter position (i.e. suspended above the surface to represent the position of the litter still attached to the shrub; on the soil surface; buried below the sand) on woody litter decomposition, we used five subplots (two UV treatments × two above-ground positions and one sand burial) to examine responses of woody litter decomposition to litter position or UV radiation. We adopted a UV screen treatment design based on the method reported by Brandt, King, Hobbie, Milchunas, and Sinsabaugh (2010). The detailed description can be seen in Erdenebileg et al. (2018). Briefly, we experimentally manipulated UV radiation received by the above-ground litter by utilizing two pairs of steel frames (l × w × h: 440 × 240 × 50 cm) carrying plastics with removable louver sheets that either block or pass UV radiation. Considering the distinct optical properties, two types of plastic materials were used: UV-transparent acrylic (UV pass, which transmits approximately 90% of UV-A and UV-B radiation, Zhongshan Good Life Sun Sheet Co., Ltd.) and UV-absorbing polycarbonate (UV block, which blocks approximately 95% of UV radiation, Zhongshan Good Life Sun Sheet Co., Ltd.). Screens were custom-designed and constructed in a louvered design to allow for penetration of rainfall to the litter layer, to allow free air movement and avoid heating. A logger (iButton) was laid in each incubation site to automatically record temperature and relative humidity at intervals of 2 hr (DS1923, Maxim). We acknowledge that the readers on relative humidity obtained from loggers could not represent gravimetric moisture content, but they could still be a valid proxy of gravimetric moisture

content based on a microcosm-based experiment conducted by Wang, Throop, and Gill (2015).

We used the litterbag approach to capture the mass loss of woody litter of the four species for five diameter classes at different harvests, that is, 6, 12, 18, 24 and 34 months (from December 2015 through September 2018) by sealing more than 5 g of pre-weighed air-dried woody litter into each litterbag. This amount depends on the actual situation because woody litters are quite distinct from leaf litters. That is to say, we cut shrub wood into fixed 10-cm long segments before sealing litters into bags. Three subsamples for each species were used to correct air-dried litter mass *via* initial air-dried and oven-dried mass (at 65°C for 48 hr). The size of the litterbags was 15 cm × 20 cm with a mesh size of 2 mm for the top side exposed to the sun, and a 0.5-mm mesh for the bottom side in order to prevent loss of small woody litter fragments (Baker & Allison, 2015). We acknowledge that the commonly used litter bag method might cause small change in microenvironment, which could affect wood decomposition to a small extent. The number of replicates was 5. Therefore, the number of litterbags used was 2,500 (4 species × 5 diameter classes × 5 treatments × 5 harvest times × 5 replicates). The top 10-cm layer of soil had first been cleared of plant material and removed before the litterbags were laid out, after which the soil layer was mixed and put back on (see Figure S3a,b). The 500 litterbags were placed in each of the five subplots either in suspended position supported by a fishing net at 10 cm distance below the UV screen (see Figure S3c), on the soil surface (see Figure S3d) or buried in the sandy soil at 10 cm depth. We retrieved litterbags after five periods of incubation (see above), cleaned the samples in the laboratory by brushing, oven-dried them at 65°C for 72 hr to obtain dry masses.

2.4 | Data analysis

All statistical tests, except for the structural equation modeling (SEM), were carried out in R (v3.3.1, R Core Team, 2016). Bark thickness, N concentration and C:N ratio of initial wood litter and *k* values for litter decomposition were Log10-transformed to satisfy the assumptions of normal distribution. A three-way repeated-measures ANOVA with incubation period as a repeated factor was used to examine the effects of species, diameter class, treatment (sand burial and combinations of UV radiation and litter position) and all their interactions on the woody litter mass loss. In order to disentangle the influence of UV radiation on wood decomposition, a four-way repeated-measures ANOVA was used to examine the effects of species, diameter class, UV radiation, litter position (suspended and soil surface) and all their interactions on wood mass loss; the sand burial treatment was excluded from this analysis. For each of the five harvests, Tukey HSD tests with Bonferroni correction were used to examine the differences in wood mass loss between the three positions, the differences between UV treatments for each of surface and suspended positions and the differences between surface and suspended positions for each of the UV treatments. Tukey HSD tests with Bonferroni correction were also used

to examine the differences in bark and wood traits among diameter classes for each species and among species for each diameter class. We fitted six litter decomposition trajectories reported by Cornwell and Weedon (2014) via the LITTERFITTER package (<https://github.com/cornwell-lab-unsu/litterfitter>) on our wood litter decomposition data, most of which obeyed a negative exponential model of fractional mass loss through time. Thus, we carried out nonlinear regressions using the 'nls' function to calculate the k values (yr^{-1}) based on Olson's (1963) negative exponential model ($Y_t = Y_0 e^{-kt}$, where t is the incubation time and Y_0 and Y_t represent mass remaining at incubation times 0 and t , respectively) across all incubation times and replicates for each combination of diameter class, species and treatment. Pearson correlation analysis was used to test the relationships between the respective bark and wood traits and between these traits and k values of woody litter decomposition. We used multi-model inference to determine how changes in rates of wood decomposition were related to influential bark and wood traits. We quantified the effects of all possible combinations of predictors on k values using the Dredge function of MUMIN package (Bartoń, 2009). Prior to running full models, we standardized the predictor variables using the standardize function in the ARM package, which is essential for interpreting parameter estimates (Grueber, Nakagawa, Laws, & Jamieson, 2011). We excluded models with highly correlated predictor variables ($|r| > 0.5$) to reduce any collinearity problem among explanatory variables so that the candidate models only contained one of a pair of highly correlated variables (Dormann et al., 2013). The best candidate models were ordered based on AICc and we used the model averaging procedure on top order models with $\Delta\text{AICc} \leq 4$ criteria (Anderson & Burnham, 2002). In the multi-model inference, we transformed the five diameter classes into a continuous predictor variable using the simple mean of each range (also see Abbott & Crossley, 1982). There were strong correlations on the k values for wood decomposition between UV block and UV pass on surface or suspended location ($r = 0.93, 0.96$, both $P < 0.001$, respectively). Therefore, the k values were averaged across surface or suspended location in SEM. Using the SEM, we tested how wood decomposition rates among three positions were affected by diameter directly and indirectly, that is, via changing wood N, DMC and bark thickness, which we considered to be plausible based on possible causal relationships. The SEM was fitted using IBM SPSS Amos 21 (Amos Development Corporation). The significance level was set at $p < 0.05$ except for the Chi-square test of model fit in the SEM at $p > 0.05$.

3 | RESULTS

3.1 | Initial wood litter traits

The morphological and chemical traits of initial wood litter differed among the four species and among five diameter classes (Figure 1). Overall, there was remarkable covariation of several wood and bark traits with diameter class. The initial bark thickness and wood DMC increased with increasing diameter class especially for *A. ordosica*;

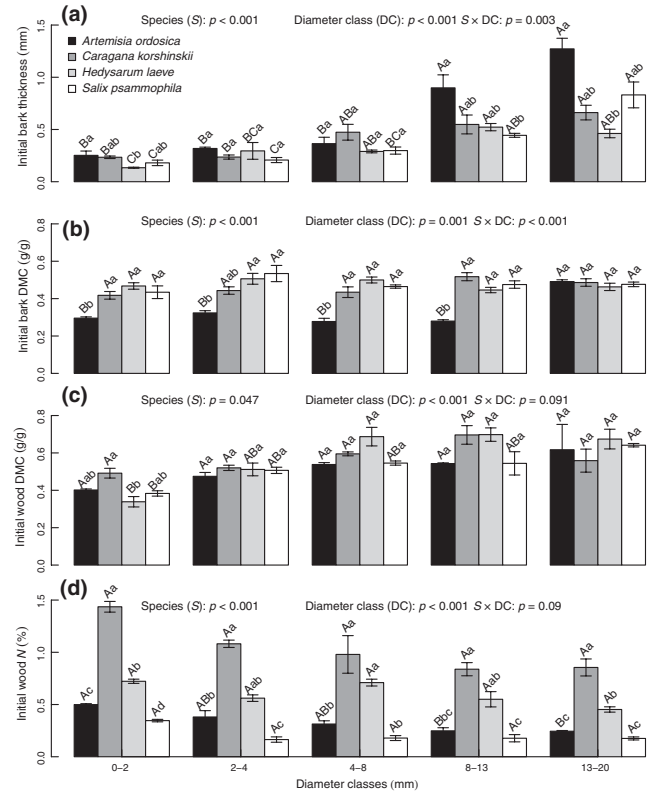


FIGURE 1 Differences in initial bark and wood traits among species and diameters in the semi-arid dune ecosystem. Bark DMC: bark dry matter content, Wood DMC: saturated wood dry matter content. The bars represent means \pm SE ($n = 5$ for bark traits or $n = 3$ for other traits). The same lowercase denotes no significant difference in bark or wood traits among species within each of the diameter classes, while the same uppercase denotes no significant difference among diameter classes within each species at $p < 0.05$

initial wood DMC was significantly positively correlated to bark thickness or wood density (Figure 1a,c; Table S1). *A. ordosica* had lower bark DMC than the other species for most of the diameter classes (Figure 1b). Initial wood N decreased with increasing diameter class for most species (Figure 1d). The woody litter of *C. korshinskii* and *H. laeve* had higher N concentration of initial litter than the two other species for each of the five diameter classes (Figure 1d). Initial wood C:N ratio was a proxy for initial wood N concentration due to the stable C concentration ($r = -1.00$, $p < 0.001$; Table S1).

3.2 | Rates of wood litter decomposition

The three-way repeated-measures ANOVA showed that position/UV treatment ($F_{4,400} = 2,503$, $p < 0.001$), diameter class ($F_{4,400} = 549$, $p < 0.001$), species ($F_{3,400} = 87.6$, $p < 0.001$) and all their interactions had significant effects on woody litter mass loss (Table 1). However, when only above-ground positions (surface and suspended) were considered in the four-way repeated-measures ANOVA, UV radiation did not have a main effect on woody litter mass loss and the interaction between UV and position was marginally significant

(Table S2). UV radiation significantly affected mass loss of surface woody litters, but it did not change mass loss of suspended woody litters (Table S3). As we expected, after 12, 24 and 34 months of incubation, the mass losses of buried woody litters were higher than

TABLE 1 Results from the three-way repeated measures ANOVA of predictive variables on wood mass losses in the semi-arid dune ecosystem

	Variation	Dfn, Dfd	F	p Value
Between-subjects effects	Species (S)	3, 400	87.63	<0.001
	Diameter class (DC)	4, 400	548.51	<0.001
	Litter treatment (LT)	4, 400	2,503.19	<0.001
	S × DC	12, 400	13.32	<0.001
	S × LT	12, 400	4.26	<0.001
	DC × LT	16, 400	33.32	<0.001
	S × DC × LT	48, 400	2.80	<0.001
Within-subjects effects	Time (T)	4, 1587	1,324.03	<0.001
	T × S	12, 1587	5.19	<0.001
	T × DC	16, 1587	21.36	<0.001
	T × LT	16, 1587	100.99	<0.001
	T × S × DC	48, 1587	0.87	0.717
	T × S × LT	48, 1587	1.09	0.319
	T × DC × LT	64, 1587	2.38	<0.001
	T × S × DC × LT	192, 1587	1.18	0.056

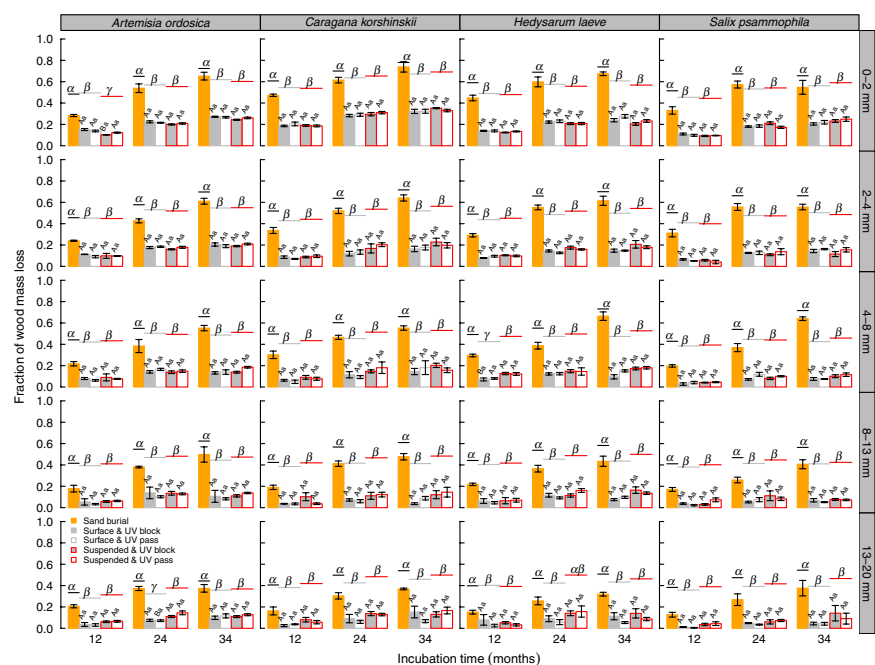
Note: The predictive variables include species, diameter class, litter treatment (i.e. environment in terms of position and UV exposure; see Table 2) and all their interactions. Dfn and Dfd denote numerator and denominator degrees of freedom, respectively. The p values in bold denote significant terms.

those in the above-ground treatments; they ranged 12.7%–47.3%, 25.7%–61.5% and 31.9%–73.9% with averages of $25.7 \pm 2.1\%$, $43.0 \pm 2.6\%$ and $53.5 \pm 2.7\%$, respectively (Figure 2). By contrast, after 12, 24 and 34 months of incubation, the mass losses under surface and suspended conditions were 2%–15%, 6%–23%, 7%–27% and 5%–13%, 11%–23%, 12%–27%, respectively (Figure 2; Table S4). During the whole incubation, litter mass loss of suspended woody litter was significantly higher than that on the surface ($17.0 \pm 1.0\%$ vs. $14.4 \pm 1.2\%$, respectively; Table S2). Overall, the mass loss of buried woody litters was three times faster than those of suspended and surface woody litters (Figure 2).

3.3 | Correlations between bark and wood traits and decomposition rates

The *k* value for woody litter decomposition was higher towards smaller diameter classes, particularly in the sand burial treatment (Figure 3). Pearson's correlation analyses indicated that *k* values were strongly negatively correlated with initial bark thickness, wood dry matter content (wood DMC), wood C:N ratio and diameter class in all treatments; the *k* values were significantly negatively correlated with initial wood density on the surface and in the sand burial treatment but not in the suspended treatment (all $p < 0.05$; Table S5). The *k* values were significantly positively correlated with initial N concentration in all treatments (all $p < 0.05$; Table S5). The bark DMC did not exhibit significant correlation with decomposition rate for any of the treatments (Table S5). The structural equation modelling showed that diameter, initial wood DMC and N had direct effects on *k* values, among which diameter had the stronger influence on decomposition rates of buried wood (Figure 4). Diameter also had a strong indirect effect on *k* values by

FIGURE 2 Effects of treatment, species and diameter on wood mass losses over 34 months in the semi-arid dune ecosystem. The bars represent mean \pm SE ($n = 5$). The same Greek symbol denotes no significant difference among three positions including sand burial, soil surface and suspended locations at $p < 0.05$. The same lowercase denotes no significant difference between UV treatments for soil surface and suspended position, respectively, and the same uppercase denotes no significant difference between the surface and suspended positions for each of the UV treatments at $p < 0.05$



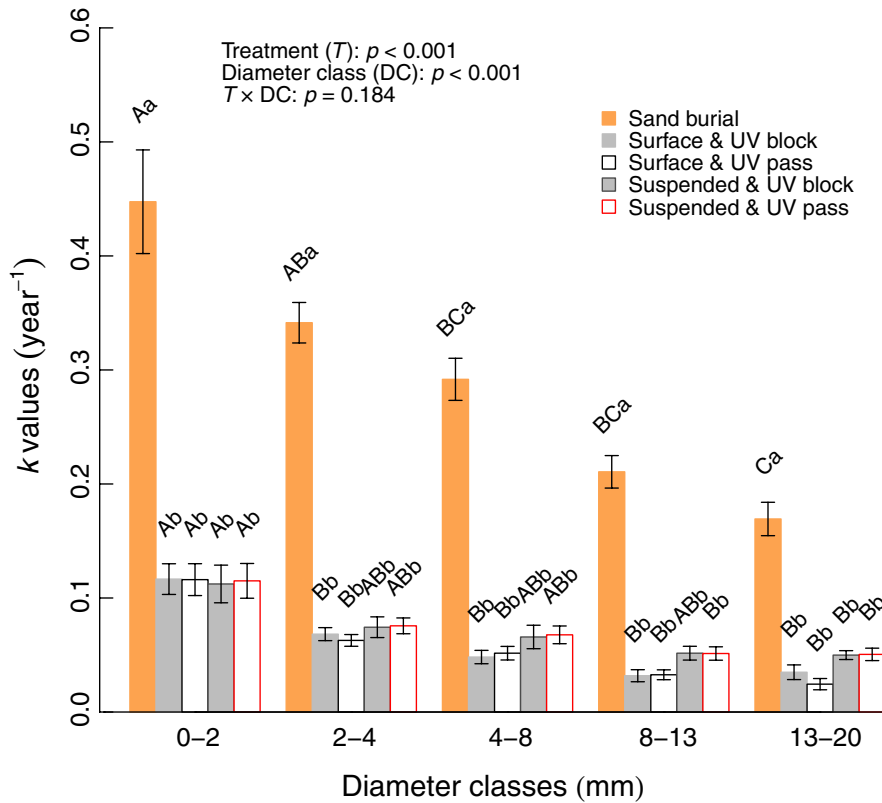


FIGURE 3 Effects of treatment and diameter on k values for wood decomposition in the semi-arid dune ecosystem. The bars represent means \pm SE ($n = 4$ species). The same lowercase denotes no significant difference in k values among species within each of the diameter classes and the same uppercase denotes no significant difference in k values among diameter classes within each of the litter treatments at $p < 0.05$

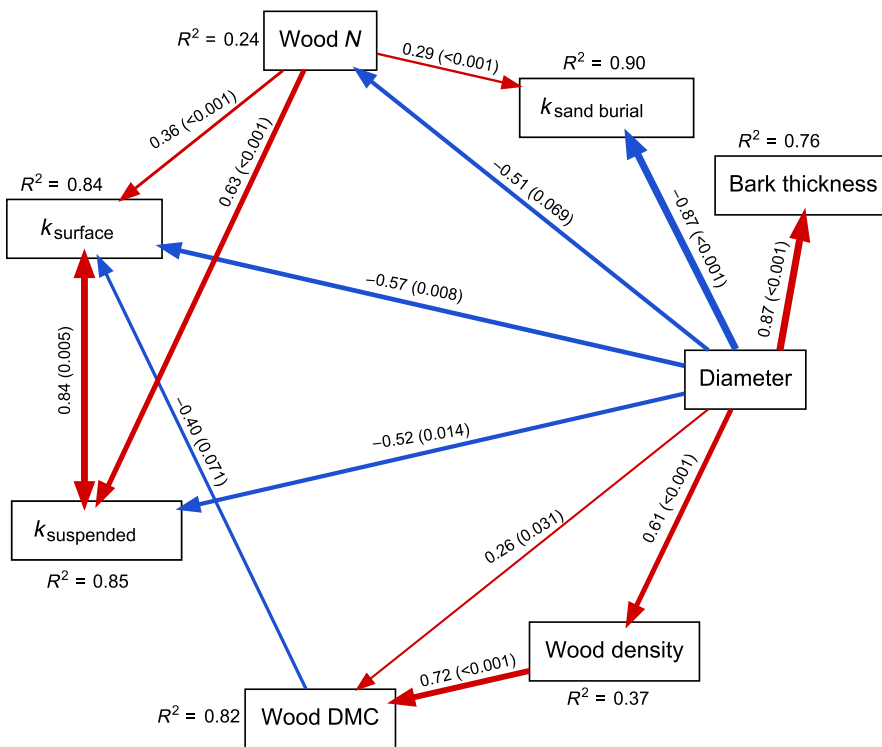


FIGURE 4 The structural equation model (SEM) depicting pathways by which wood traits may influence k values in the semi-arid dune ecosystem. The model parameters in the SEM were $\chi^2_{df=3} = 1.013$, $p = 0.798$, GFI = 0.987, RMSEA < 0.001. The red and blue arrows represent positive and negative relationships, respectively. The widths of the arrows are proportional to the strengths of the path coefficients. The double headed arrows between $k_{suspended}$ and $k_{surface}$ indicate there were no causal relationships of wood decomposition rates between these two positions; just a correlation because both were driven by the same traits. The value in parentheses denotes the p value

affecting initial wood DMC directly or indirectly via wood density in the surface treatment. There was a marginally significant positive trend of diameter on k values via wood N in all the treatments ($p = 0.069$; Figure 4). The full model analyses showed higher importance of initial N concentration (or C:N ratio) and diameter class in explaining variation in the k values for most treatments; for the

surface litter under UV blocking, the higher importance was owed to initial wood DMC and N concentration (or C:N ratio; Table 2). Generally, the density of decomposed wood litter was negatively correlated with wood mass loss, in which the stronger relationships were observed in sand burial than in the other two positions (Figure S4).

TABLE 2 Effects of initial traits on wood decomposition rates *via* model averaging in the semi-arid dune ecosystem

Treatment	Source	Estimate	SE	z Value	p Value	RVI
Suspended and UV block	Intercept	-1.181	0.017	66.11	<0.001	-
	Diameter	-0.170	0.035	4.48	<0.001	1.00
	Initial wood C:N ratio	-0.110	0.108	1.01	0.311	0.52
	Initial wood N	0.100	0.107	0.93	0.355	0.48
Suspended and UV pass	Intercept	-1.172	0.018	59.64	<0.001	-
	Diameter	-0.159	0.081	1.95	0.052	0.83
	Initial wood C:N ratio	-0.097	0.095	1.01	0.314	0.54
	Initial wood N	0.084	0.095	0.88	0.379	0.46
	Initial wood dry matter content (DMC)	-0.030	0.068	0.44	0.659	0.17
Surface and UV block	Intercept	-1.288	0.029	41.45	<0.001	-
	Initial wood DMC	-0.366	0.059	5.74	<0.001	1.00
	Initial wood N	0.119	0.122	0.97	0.334	0.52
	Initial wood C:N ratio	-0.109	0.121	0.90	0.371	0.48
Surface and UV pass	Intercept	-1.317	0.027	44.65	<0.001	-
	Diameter	-0.441	0.059	6.95	<0.001	1.00
	Initial wood C:N ratio	-0.062	0.078	0.77	0.440	0.45
	Initial wood N	0.058	0.077	0.74	0.459	0.43
Sand burial	Intercept	-0.564	0.013	40.43	<0.001	-
	Diameter	-0.281	0.028	9.47	<0.001	1.00
	Initial wood C:N ratio	-0.041	0.043	0.92	0.356	0.53
	Initial wood N	0.036	0.043	0.84	0.403	0.47

Note: Model-averaged coefficients and important values for explanatory variables predicting wood decomposition rates (*k* values) are shown for models based on all treatments in terms of litter position and UV exposure. RVI denotes relative variable importance. Diameter classes were transformed into a continuous predictive variable. The *p* values in bold denote significant terms.

4 | DISCUSSION

Here, we assessed the interactive effects of woody litter diameter, position (sand burial vs. surface vs. suspended) and UV exposure on decomposition rate in a semi-arid inland dune ecosystem across four shrub species over almost 3 years. Among the various abiotic and biotic drivers addressed here, we found that woody litter position (suspended, surface and buried), stem diameter and wood traits and the interactions between these factors, all had substantial effects on decomposition rates, while differences in exposure to UV radiation did not affect decomposition rates significantly. A key finding was that stem diameter not only had direct effects on decomposition rate, presumably *via* surface area to volume ratio, but also indirect effects *via* differences in wood traits, especially wood dry matter content and wood N. Below we will discuss these findings in more detail in the context of previous literature.

4.1 | Environmental rivers of woody litter decomposition

In terrestrial ecosystems, differences in litter decomposition during different periods of incubation are associated with the seasonal changes in solar radiation, temperature and moisture (Lin, Scarlett, & King, 2015; Wang, Liu, Wang, & Chen, 2015). We found that relatively fast rates of wood decomposition occurred in the subsequent summers (Figure 2; Table S4), when environments conditions benefitted wood decomposition (Figure S5). As hypothesized (1), buried woody litter decomposition was faster in the entire decomposition period due to relatively stable and higher moisture as compared with those above-ground (Figure 2; Table S4). As expected, we found that the mass losses of buried woody litters during 34 months of incubation were three times faster than those of suspended and surface woody litters (Figure 2). This supports the reported pattern that the difference between the rate of buried and surface wood decomposition

increased with decreasing precipitation (Smyth et al., 2016). The accelerating effect of sand burial on wood decomposition is even stronger compared with previous studies in similar dry habitats, in which litter burial less than doubled the rate of litter decomposition compared to that on the soil surface (Austin et al., 2009; Liu, Cornwell, Pan, et al., 2015; Santos, Elkins, Steinberger, & Whitford, 1984; Vivanco & Austin, 2006). Also, this finding contrasts with the fact that buried wood had slower decomposition rate than that on the soil surface in diverse forest ecosystems (Fasht, Harmon, Sexton, & White, 2011; Romero, Smith, & Fourqurean, 2005). The likely reason is that the sand burial exposes dead wood to an abundant microbial community and to relatively beneficial humidity to microbially driven decomposition. The previous work on soil enzymatic activity in the *Mu Us* inland dunes showed larger values for polyphenoloxidase, peroxidase and polyphenol oxidase at 0–5 cm of soil depth than those at 5–10 cm of soil depth in the *S. psammophila* community (45.00 ± 3.07 vs. $24.24 \pm 0.68 \mu\text{g g}^{-1} \text{hr}^{-1}$, 730.85 ± 24.95 vs. $354.42 \pm 69.35 \mu\text{g g}^{-1} \text{hr}^{-1}$, 318.14 ± 35.2 vs. $153.01 \pm 11.3 \mu\text{g g}^{-1} \text{hr}^{-1}$, respectively; Wang, 2018). Indeed, the fungal/bacterial biomass ratios based on the phospholipid fatty acid (PLFA) technique nearby the incubation site were 0.378 ± 0.015 , 0.381 ± 0.018 , 0.398 ± 0.019 and 0.382 ± 0.018 at 0–5, 5–10, 10–15 and 15–20 cm of soil depth, respectively (G. F. Liu, unpubl. data), which indicates that this dry region hosts relatively high fungal abundance (Chen et al., 2015). According to High Throughput DNA Sequencing methodology, the dominant fungal species in the top soil (0–10 cm) of *Artemisia ordosia* vegetation on Ordos plateau were *Ascomycota* (64.6%), *Mortierellomycota* (12.3%) and *Basidiomycota* (8.4%), accounting for 85.3% of total number of OTUs (G. F. Liu, unpubl. data). Since especially *Ascomycota* are predominantly saprophytic, these complementary observations imply that relatively faster buried wood decomposition could be owed to fungal activity. There was no visible evidence of termites in our study (observations inside and outside litterbags by the authors), contrasting to strong termite effects on wood decomposition in hot drylands (Buxton, 1981). In forests, slow decomposition of dead wood burial has been associated with exposure to low temperatures in peat or after being overgrown by mosses. These differences emphasize the different driving mechanisms of litter decomposition in different biomes.

In contrast with the fast rate of buried wood decomposition, above-ground decomposition rates were very low in the soil surface and suspended position with exposure to solar radiation; most mass loss in these treatments occurred during the first 2 years (Table S4). This relatively slow decomposition is consistent with previous studies (Abbott & Crossley, 1982; Buxton, 1981; Milton & Dean, 1996) and can explain why almost 20% of organic carbon is owed to standing and surface litters in inland dune ecosystems (Li, 2006). We acknowledge that the litter bags could intercept a small portion of solar radiation, so in our experiment we may have slightly underestimated the effect of photodegradation on wood mass loss. Longer-term studies are needed to investigate the trajectory of above-ground wood decomposition more comprehensively (Cornelissen et al., 2012; Prescott, 2005). Many studies have shown that woody plant encroachment increases fluxes of soil C and N

(Hibbard et al., 2001; McCulley, Archer, Boutton, Hons, & Zuberer, 2004). This present study highlights that relatively fast decomposition of buried woody litter may be an important contributor to this phenomenon.

Within the above-ground positions, woody litter decomposition rates were somewhat faster in suspended litter than in surface litter (Figure 2; Table S4), consistent with previous studies (Erdenebileg et al., 2018; Lin & King, 2014). In dryland, decomposition of suspended litters is likely strongly determined by abiotic factors, such as photodegradation and wind abrasion, but also by a favourable combination of temperature or moisture at night promoting microbial decomposition (Wang et al., 2017). However, this conflicts with the finding that termite-mediated decomposition rate of ground-placed wood debris was over four times greater than that in suspended condition in tropical rainforest (Law, Eggleton, Griffiths, Ashton, & Parr, 2019). These findings imply that contrasting influential factors determined the carbon turnover between ecosystems varying in water limitation and soil fauna abundance. As revealed by our UV blocking treatments, UV radiation alone had no significant effect on woody litter decomposition (Table S2), which is inconsistent with our hypothesis (2); this hypothesis had been informed by the findings of Erdenebileg et al. (2018), who found that UV radiation had a significant effect on leaf litter decomposition. The discrepancy between leaf litter and woody litter in response to UV light may be due to the contrasting architecture between leaf and wood tissues. UV radiation did not affect suspended wood decomposition but it decreased surface wood decomposition, suggesting that UV radiation possibly decreases the activity of colonizing microbes (Wang, Liu, et al., 2015). This study reinforces how different plant tissues decay in very different ways and how these differences also depend on their vertical position.

Soil-litter mixing and photodegradation are mechanisms that may explain why higher than expected non-woody litter decomposition occurred in drylands (Austin & Vivanco, 2006; Hewins & Throop, 2016; Liu et al., 2018). In addition, Liu et al. (2018) found that relative exposure of the leaf surface to sunlight per unit leaf mass (i.e. specific leaf area) could be a predominant factor in explaining variation in leaf litter decomposition. As noted above, together these suggest that sand burial is a main environmental factor in driving woody litter decomposition in shrub-dominated drylands.

4.2 | Controls of initial litter quality on woody litter decomposition

Litter decomposition rates depend on both incubation environment and the afterlife legacy of functional traits of different species through litter substrate quality (Cornwell et al., 2009; Harmon et al., 1986; Swift et al., 1979). We found that the rates of woody litter decomposition increased with increasing initial wood N concentration or decreasing initial C:N ratio in all treatments; initial wood N concentration and C:N ratio were highly correlated due

to their log-transformation and to the stable C concentration. Our observations confirm previous reports that litter with higher nutritional quality (e.g. higher N concentration and lower C:N ratio) can decompose relatively fast (Liu, Cornwell, Cao, et al., 2015; van Geffen et al., 2010; Weedon et al., 2009). Wood dry matter content (wood DMC), as a key trait representing internal litter structure, is known to be a negative predictor of wood decomposition rate (Freschet et al., 2012; Liu, Cornwell, Pan, et al., 2015) and our findings add to this body of evidence. However, a novel finding of our work, revealed by structural equation modelling, was that variation in wood DMC was one of the two different mechanisms by which stem diameter strongly controlled wood decomposition, with thinner stems having lower initial DMC or higher N and faster decomposition. The other mechanism in our study, consistent with our hypothesis (4) based on previous literature, was that the lower wood surface area to volume ratio for larger diameter stems likely lowered the rate of colonization by microbial decomposer communities (Cornwell et al., 2009), thereby reducing their decomposition rate (Hu et al., 2018; van Geffen et al., 2010). We acknowledge that fungal colonization can be facilitated through cuts and wounds. In wider stems, the possibility of colonizing the stem through the cut ends may be relatively higher than in thinner stems. Thus, the effects of stem diameter on wood decomposition would be expected to be stronger if the cut surfaces would be sealed in order to prevent fungal colonization. However, this is inconsistent with the finding that half-buried stems decomposed relatively faster than buried stems in temperate deciduous forest with 1,030 mm of annual precipitation (Oberle et al., 2018), emphasizing that burial effects on woody litter decomposition are dependent on the precipitation and associated soil moisture of different ecosystems. The relationships between wood density and the rate of decomposition are contrasting between different studies. For instance, Liu, Cornwell, Cao, et al. (2015) showed a negative relationship in a rainforest ecosystem. By contrast, wood density could not explain variation in rates of decomposition at local or global scales in some other studies (van Geffen et al., 2010; Weedon et al., 2009). Probably the negative relationship only features in those cases where wood density is strongly correlated with DMC, as the volume basis at which mass is expressed in wood density can at best only be indirectly involved in dry matter decomposition. The model averaging procedure and structural equation modelling demonstrated that initial wood N (or wood C:N ratio) and diameter class were predominant and mostly independent controls on wood decomposition rates. This result at a local scale is consistent with the finding at global scale reported by Hu et al. (2018). These findings together confirm the importance of initial wood N (or wood C:N ratio) and diameter as key wood traits in predicting wood decomposition rates. Different from previous literature, however, we revealed a strong indirect effect of stem diameter on wood decomposition *via* wood DMC and N, an effect that strongly depended on litter position. Indeed, the dual role of stem diameter on decomposition of woody litter was particularly strong under buried condition and incorporating this role may help

to improve the accuracy and confidence of modelling global carbon cycling in drylands.

The bark is of considerable importance as an environment filter for community assembly through habitat access and provision during the early stage of wood decomposition (Zuo et al., 2016). Previous studies showed mixed effects of bark thickness on the abundance of decomposers, for instance negative effects on bark beetles in spruce (Wainhouse, Cross, & Howell, 1990) and positive effects, probably *via* bark fissuredness on wide-ranging macro-invertebrate populations across 11 temperate tree species (Zuo et al., 2016). In our study, with very small stem diameters, invertebrates did not play any significant role in decomposition. In SEM, bark thickness did not regulate woody litter decomposition although it was significantly negatively correlated with rates of wood decomposition due to its tight relationship with diameter (Table S5; Figure 4). By contrast, any direct effect of bark on wood decomposition above-ground was not apparent. Together our findings, which were inconsistent with our hypothesis (3), suggest that the effects of bark on wood decomposition rates are distinct between mesic and dry ecosystems due to contrasting moisture regimes. Additionally, the recalcitrant outer bark might shelter the softer inner bark and wood below from mainly abiotic UV degradation in drylands. Future studies on the effects of bark on wood organic turnover should therefore focus on how such effects vary in importance and mechanisms across diverse terrestrial ecosystems with contrasting precipitation and irradiance regimes. For instance, bark removal experiments are needed to disentangle the effects of bark protection on wood decomposition on the soil surface or suspended above it.

5 | CONCLUSIONS

Over 34 months of incubation, the decomposition rates of buried woody litters were three times faster than those of above-ground woody litters of the same four shrub species in an inland dune ecosystem. UV had no significant influence on the rates of wood decomposition, suggesting that the importance of UV radiation for wood decomposition is negligible compared to that for leaf litters. Among several litter traits previously linked to litter quality, initial wood N concentration (or C:N ratio) and diameter class were predominant factors driving wood decomposition. A key finding (see hypothesis 4) was that stem diameter played a dual role in determining wood decomposition: directly *via* surface area to volume ratio and indirectly *via* its link with wood dry matter content and wood N. This dual role of diameter on wood decomposition and, thereby, as a promotor of below-ground organic fluxes, may be of particular importance in grasslands subject to shrub encroachment and other shrub-dominated semi-arid and arid ecosystems. The accuracy and confidence of global carbon cycling model would be improved by incorporating the different effects of stem diameter on woody litter decomposition and below-ground wood decomposition processes in drylands.

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AUTHORS' CONTRIBUTIONS

G.L., X.Y. and Z.H. conceived the study; E.E., G.L., Q.C. and J.D. collected the field data; E.E., G.L. and J.H.C.C. analysed the data and wrote the first draft of the paper; all authors contributed to revisions.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.3tx95x6c2> (Erdenebileg et al., 2020).

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SUPPORTING INFORMATION

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