



The structural and nutrient chemistry during early-stage decomposition and desiccation of cacti in the Sonoran Desert

Anna H. Bilderback, Alexander J. Torres, Miranda Vega, Becky A. Ball^{*}

School of Mathematical and Natural Sciences, Arizona State University at the West Campus, Glendale, AZ, USA

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ABSTRACT

Despite the abundance of cacti in the Sonoran Desert, most research focuses on population dynamics and physiology. Relatively little is known about their decomposition dynamics. A better understanding of cactus decomposition is important, considering the number of threatened and endangered cactus species. We measured mass, water, nutrient, and structural chemistry over one year of decomposition of two common cactus species, *Opuntia chlorotica* and *Cylindropuntia acanthocarpa*, in the Sonoran Desert of Arizona, U.S.A. Our results demonstrate the contribution of cactus decomposition to carbon and nutrient recycling, with comparable dynamics to woody and herbaceous leaf litter for most elements. We enumerate, however, the particularly important role in calcium dynamics. Despite initial differences, both cacti released nutrients at a statistically equivalent rate, though with altered timing due to temporary mass gain in cholla. The resources released from decaying cacti have a modest influence on underlying soil CO₂ flux, secondary to a dominant influence of soil microclimate. Our data provide a baseline for understanding the decay dynamics of two common cactus species and suggest that, while there is still a lack of information pertaining to cactus decomposition, the similarities with leaf litter will aid our predictions of the consequences of future cactus population changes.

1. Introduction

The Sonoran Desert is the most biodiverse desert in the United States, housing over 3000 species of plants uniquely adapted to the arid environment, including >300 species of cactus alongside other succulents, woody shrubs and herbaceous plants (Shreve, 1951; Turner et al., 1995; Chester, 2012). Cacti, in particular, are ubiquitous in deserts throughout the Americas, including various widespread species that are capable of withstanding the extreme temperatures and aridity. Among the cacti, the saguaro cactus (*Carnegiea gigantea*) is one of the most studied plants in the world, with much understood about their establishment, abundance, and realized niche (sensu Winkler et al., 2018). Significantly less ecological research has focused on other cactus species in natural settings, such as those in the prickly pear (*Opuntia* spp.) or cholla (*Cylindropuntia* spp.) genera, despite their widespread occurrence in the Sonoran Desert and importance as a food source for indigenous communities (Shreve, 1951; Turner et al., 1995; Bowers, 2005; Shupe, 2005). Further, ecological research on cacti has largely focused on understanding population dynamics, physiology, and growth and

reproduction (e.g., Godínez-Álvarez et al., 2003; Bowers, 2005; Drezner and Lazarus, 2008; Winkler et al., 2018). Across cactus species, there is a dearth of knowledge about their role in ecosystem processes and biogeochemical fluxes, such as their role in nutrient recycling through the process of decomposition. A few studies have described the nutrient content of living cacti in a natural setting, demonstrating that cacti contain higher levels of Ca, Mg, and Mn but lower Na and P than other plant species with varying profiles of complex compounds (Kircher, 1982; Nobel, 1983) that can provide an important nutrient source to desert herbivores (Wolf and Rio, 2003; Orr et al., 2015) and detritivores (Kircher, 1982). While the soils beneath living cacti tend to be low in soil nutrients compared to the “islands of fertility” that develop beneath woody and herbaceous plants in the desert, their impact on soil nutrients is likely greater after death or senescence when their biomass decays (Fabre et al., 2006; Butterfield and Briggs, 2009; Solomon Abera Bariagabre, 2016).

Decomposition studies have been conducted for decades to improve our understanding of how nutrient cycling, energy flow in food webs, and soil formation are linked by the process of decay. Decomposition of

^{*} Corresponding author. School of Mathematical and Natural Sciences Arizona State University at the West Campus 1407 W. Thunderbird Rd. Glendale, AZ, 85306 USA.

E-mail address: becky.ball@asu.edu (B.A. Ball).

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organic material is an essential ecological process, cycling material and energy throughout ecosystems (Swift et al., 1979). Most studies conducted, including those in arid and semi-arid ecosystems, have focused on leaf litter material from trees, shrubs, and grasses (e.g. a recent selection of examples: Day et al., 2018; Predick et al., 2018; Ball et al., 2019; Levi et al., 2020), with only a handful of studies investigating succulent decomposition (e.g., Pérez-Harguindeguy et al., 2000; Arriaga and Maya, 2007; Simões et al., 2011; Canessa et al., 2021). Such decomposition studies have aided scientists in the understanding of nutrient cycling and carbon dynamics across different ecosystems, and how these dynamics are impacted by global change. From these studies we know that leaf litter decomposition is a multi-phase process wherein litter initially loses soluble compounds, followed by a buildup of microbial biomass that rapidly degrades labile compounds, then slower consumption of the remaining recalcitrant compounds (Chapin et al., 2002). Mass loss rates vary across climates and species, but overall are often predictable from initial litter chemistry parameters (Aber et al., 1990; Aerts, 1997). While carbon dynamics are an essential component of decomposition, the recycling of other nutrients such as nitrogen and phosphorus are also of great interest. Nutrient dynamics during mass loss also relate to the initial chemical content of the leaves, with often a phase of nutrient immobilization during the early stages of decomposition, followed by mineralization (e.g., Parton et al., 2007). Much of this knowledge, however, is from mesic ecosystems, and patterns differ in arid locations.

Some aspects of aridland decomposition differ from mesic ecosystems. Photodegradation plays a significant role in desert decomposition, with photons breaking chemical bonds, further accelerating the process of decomposition, which can alter nitrogen and phosphorus dynamics (Austin and Vivanco, 2006; Arriaga and Maya, 2007; Martínez-Yrizar et al., 2007; Ball et al., 2019). Cycles of wet and dry weather are also attributed to rates of litter decay in desert ecosystems (Arriaga and Maya, 2007; Martínez-Yrizar et al., 2007). Dry heat that accompanies photodegradation can aide in removing the moisture from decaying litter, allowing decomposition to set in swiftly (Austin and Vivanco, 2006). A lack of water, however, can also adversely impact biological decomposition by limiting microbial activity and slowing the leaching of soluble compounds and nutrients, so rainfall patterns play an important role in desert decomposition (Martínez-Yrizar et al., 2007). Therefore, heavy rain storms in the North American monsoon season, which can deliver up to half of Arizona's annual precipitation just during the summer months (Higgins et al., 1997; Crimmins, 2006), can provide a burst of soil moisture needed to further decomposition (Hewins and Throop, 2016). Additionally, desert plants' unique adaptations for the extreme climate impact their decay, exemplified through the creosote bush, whose leaves contain waxy cuticles for water retention and allelopathic chemicals that can deter decomposer organisms (Woodell et al., 1969; Lei et al., 1998).

Even within deserts, decomposition studies focus on leaf litter of woody and herbaceous plants, which are distinctly different from succulents. Succulents, including cacti are inherently structured differently than plant leaves, allowing for the majority of their bodies to contain water. Their thick-walled structure allows them to retain water to continue with photosynthesis, contributing to their adapted fitness against droughts (Barcikowski and Nobel, 1984), and cacti leaves form typically in the shape of spines or barbed bristles that help cacti to collect and conserve water (sensu Nobel, 1988). Comparatively, the thinner cuticles of herbaceous and woody plant leaves allow for bacteria and organisms to quickly decompose the plant material without having to work through a tough exterior skin to reach the desired nutrients. Thus, the rate of decomposition for non-cacti plants will likely be much quicker, often within just a few years, compared to the decades that may ensue for the cacti (e.g., Pérez-Harguindeguy et al., 2000), but studies of succulent decomposition show slower, faster, and intermediate decay rates compared to woody plant litter (Pérez-Harguindeguy et al., 2000; Arriaga and Maya, 2007; Simões et al., 2011; Canessa et al., 2021).

Fewer studies have investigated decomposition specifically of cacti, but the limited quantity of studies conducted show that decomposition relies on many biotic and abiotic factors, including the organisms that are present, nutrient content, and the environmental factors that influence decay rate. Numerous studies demonstrate the relationship between cacti and insect taxa during decomposition, with Diptera and Coleoptera present in a large abundance to aid in the process of decomposition (Castrezana and Markow, 2012; Martínez-Falcón et al., 2012; Ferro et al., 2013). Cactus species also differ in the bacterial and yeast communities that are associated within their necromass (Starmer et al., 1982; Starmer and Phaff, 1983; Foster and Fogleman, 1993; Ganter and Quarles, 1997). Because cactus fresh mass can be comprised of up to 70–90% water (e.g., Garvie, 2003), desiccation is prominent in early stages of decay. Decaying cacti, such as saguaro, contribute to soil inorganic carbon as calcite, slowly converted from the calcium oxalate within the cacti over decades of decay (Garvie, 2006). Calcium oxalates are common and abundant in cacti, comprising even 50% or more of the cactus dry weight, and their release during decay constitutes the majority of what is known about the chemical dynamics of cactus decay (Garvie, 2003). Cacti tend to be very high in Ca and Mg compared to woody species, and can store large amounts of C in the oxalates, giving cacti a potentially significant role in C, Ca, and Mg cycling in deserts (Garvie, 2003, 2006) that is not yet enumerated.

This limited portion of information creates a gap in understanding of nutrient cycling in desert ecosystems. Cacti are an important functional group in deserts, represented by their abundance and diversity. The nutrients they release, including both macro- and micronutrients, feed decomposer communities in desert soil. However, the only studies to date concerning nutrient dynamics of decaying cacti only go so far as to note the high mineral N levels beneath dead saguaros but not dead cholla (Butterfield and Briggs, 2009), with only one study measuring N content during decay (Martínez-Falcón et al., 2012). The limited understanding of their biogeochemical role in nutrient recycling is a concern, given the high number of threatened or endangered species in this group (Goettsch et al., 2019). Thus, gaining an understanding of the biogeochemistry of decomposition of this functional group is vital to fill in the gaps of knowledge on desert ecosystems.

Therefore, the purpose of this study is to understand the process of cactus decomposition in the Sonoran Desert and create a baseline study for future decomposition projects focused on cacti. We compared two common species of cacti that differ in initial structural and nutrient chemistry, *Cylindropuntia acanthocarpa* (buckhorn cholla) and *Opuntia chlorotica* (pancake prickly pear), which we hypothesized would cause them to differ in decomposition rates and nutrient dynamics. Cholla senesces small, cylindrical cladodes that are typically hard and dry, whereas prickly pear would typically drop in larger, flatter pads that are higher in moisture and lower in structural compounds. We predicted that these characteristics would influence decomposition, including rates of mass loss, nutrient release, and C dynamics, and that soils beneath the decaying cacti would differ in their respiration rates due to the different inputs and microclimate effects from the decaying cacti. Gaining this understanding of cactus decomposition allows us to then compare these results to the previously published studies on shrub and tree leaf litter, to determine how cacti differ from woody and herbaceous leaf litter in their release of chemistry into the ecosystem. The difference in release of chemical constituents at different rates is important to study because it will allow us to expand our knowledge of nutrient recycling in desert ecosystems.

2. Methods

2.1. Study site

This decomposition project was conducted at White Tank Mountains Regional Park, Maricopa County, AZ, USA (33°36' N, 112°30' W; elevation 450 m), at experimental plots maintained by the Central

Arizona-Phoenix Long Term Ecological Research site. The 5-year mean annual precipitation is 185.5 (± 25.7) mm and mean annual temperature is 23.2 (± 0.2) °C (FCDMC, 2019).

2.2. Decomposition study

Cacti cladodes were clipped from two different species of cactus: *Opuntia chlorotica* (pancake prickly pear) and *Cylindropuntia acanthocarpa* (buckhorn cholla). Following other studies of succulent decomposition (Pérez-Harguindeguy et al., 2000; Simões et al., 2011; Martínez-Falcón et al., 2012; Canessa et al., 2021), fresh cacti were clipped to ensure a uniform starting point across replicates, rather than collecting pre-senesced cladodes from the ground that may vary in their degree of initial photodegradation, desiccation, and leaching. The 48 clipped cladodes were taken to the laboratory in plastic clam shell containers, where initial weights of each entire cladode were recorded. Three 1.3-cm diameter cores, totaling approx. 2.5–5 g total wet weight, were taken from each for measurement of initial water content and chemistry. The core weight was subtracted from the overall cladode weight to represent the initial wet weight of each cladode for the onset of the experiment.

Three days after collection, the cactus cladodes were then placed in the field on February 20, 2017. Litter cages (23 × 23 cm) were constructed with 10-cm tall sides made out of 2-mm carbon fiber window mesh, zip-tied around four nails in the ground to make a square perimeter, with an extra 2.5 cm flap nailed flush with the ground to avoid the sides lifting. Cages were topped with a nylon 4.5 × 5 cm mesh lid; the larger mesh was to prevent shading that could decrease natural amounts of photodegradation. Each cage contained one cladode from either species, placed directly in the center of the cage, and the area around the cactus was weeded throughout the study to avoid shading. The cages were arranged in four replicate blocks, with each block containing 12 cages: 6 cages with *O. chlorotica* and 6 with *C. acanthocarpa*. The cages were placed approximately 30 cm apart from each other on bare soil. Throughout the first month of the experiment, the cages were checked regularly, and any attempts at root generation were removed from the cladodes to ensure they died and decomposed.

Decomposing cladodes were collected on 5 different dates spanning 1 year: 39 d, 65 d, 119 d, 221 d, and 354 d. At each collection date, one cladode of each species was randomly chosen from each replicate block, totaling 8 samples per collection date (four of each species). During the summer drought periods, some of the prickly pear cladodes were partially consumed by very persistent herbivores (presumably jackrabbits, *Lepus californicus*) who chewed through the cages, and if the randomly selected cactus had large portions missing with characteristic bite marks, we chose the nearest neighbor that was not. However, at 119–354 d, partially eaten cladodes were unavoidable for some replicate blocks. These replicates were not used in analyses of mass remaining but were included for plant chemistry. Cladodes were returned to the lab in their same plastic clam shell from original collection.

In the lab, the entire fresh mass of each cladode was recorded and approx. 2.5 g of 1.3-cm diameter cores were taken. The cores and the remainder of the cladodes were dried at 60 °C for 72 h and reweighed (the sum of which was the total dry weight of the entire cladode). Cactus % water content was calculated as the percent of the fresh core mass that was lost during drying.

Following protocols common to leaf litter decomposition studies, we measured dry and ash-free dry mass, as well as nutrient content of the cladodes at each time period (e.g., Killingbeck et al., 1982; Day et al., 2007; Hewins and Throop, 2016; Levi et al., 2020). The dried cactus cores and soil samples were prepared for chemical analysis by grinding them to a fine powder using a ball-mill grinder (SPEX Sample Prep Mixer/Mill 8000D). Following Ball and Alvarez Guevara (2015), total P, Na, Mn, Mg, K, and Ca were measured on the cactus samples using the dry ash acid method digestion, by which the cactus samples were ashed in a muffle oven that was gradually brought to 475 °C over 1.5 h, held at

475 °C for 4 h, then dropped to 105 °C. Then the cactus ash was weighed for calculation of percent ash-free dry mass (AFDM; an estimation of organic content of the sample), as:

$$\% \text{ AFDM} = \frac{\text{dry weight} - \text{ash weight}}{\text{dry weight}} \times 100$$

The ashed samples were then digested in 5 mL of 35% HNO₃, centrifuged for 10 min, and the supernatant diluted to 5% HNO₃ for measurement via inductively coupled plasma optical emissions spectroscopy (ICP-OES; Thermo iCAP6300, Hudson NH). Total C and N were measured using an elemental analyzer (PerkinElmer PE2400, Waltham MA).

Other metabolic and structural compounds were analyzed using pyrolysis-gas chromatography and mass spectrometry (py-GCMS). Samples were first pyrolyzed on a CDS Pyroprobe 5150 pyrolyzer at 600 °C for 20 s (CDS Analytical, Inc., Oxford, PA, USA). Pyrolysis products were then transferred automatically to a Thermo Trace GC Ultra gas chromatograph (Thermo Fisher Scientific, Austin, TX, USA) and Polaris Q ion trap mass spectrometer (Thermo Fisher Scientific). Mass spectra were analyzed using Automated Mass Spectral Deconvolution and Identification System, (AMDIS, V 2.65) and the National Institute of Standards and Technology (NIST) compound library. Compound relative abundances were calculated relative to the total ion signal from all detected and identified peaks. Individual compounds were analyzed separately and also arranged into the following functional groups: lignin, aromatic, phenols, polysaccharides, proteins, other nitrogen-bearing compounds, lipids, and compounds of unknown functional origin (Grandy et al., 2009; Wickings et al., 2011). Given the time and labor expenses of py-GCMS, samples were only run at specific sampling periods (days 0, 39, and 119) representing 100%, 75%, and 50% mass remaining.

2.3. Decomposition data analysis

Percent of initial fresh weight remaining was calculated for each time period by dividing the measured fresh weight (FW_t) by the initial fresh weight (FW_i) of the same cladode, as $\frac{FW_t}{FW_i} \times 100$. The measured % water was used to convert this fresh weight into dry weight, and then the AFDM of the cores was used to estimate the AFDM of the entire cladode at each time point ($AFDM_t$) to similarly calculate percent AFDM remaining at each collection period as $\frac{AFDM_t}{AFDM_i} \times 100$.

The nutrient content of each sample was used to calculate the mass of nutrients lost at each time point by subtracting the total nutrient content of each sample from the initial content. Because the individual prickly pear cladodes were double the mass of cholla cladodes (averaging 45.1 ± 1.6 g vs 19.3 ± 1.5 g dry weight, initially), the prickly pear would obviously release more total nutrients over one year than the cholla. Therefore, this mass of released nutrients was divided by the initial dry mass of the cladode to express nutrient release in terms of mass lost per g initial dry weight.

All statistical analyses were conducted in R (version 4.0.2). Initial litter chemistry was compared between the two species using a one-way Analysis of Variance (ANOVA) for each chemical parameter with Species (2 levels) as the main effect. A two-way Analysis of Covariance (ANCOVA) was run for each measurement of mass loss and nutrient release, testing the impact of Species, Time (as days of decomposition, a continuous variable), and their interaction. For mass loss, an additional three-way ANCOVA was run testing each measured chemical parameter as a potential covariate to explain mass loss, along with Species and Time. In addition to each chemical parameter, we also tested the potential impact of nutrient ratios that are commonly shown to influence mass loss: C:N, C:P, N:P, and Lignin:N. Finally, we tested the impact of precipitation as a potential covariate using two calculations of precipitation, which was collected as daily precipitation amounts from the nearest county-run weather station (FCDMC, 2019). To understand the influence of recent vs. seasonal precipitation on decay rates, we

calculated both the precipitation received in the interval between each sampling point (e.g., total precipitation between days 0–39, 40–65, 66–119, etc.), and the total accumulated precipitation at each time period since the onset of the experiment (e.g., total precipitation between days 0–39, 0–65, 0–119, etc.).

2.4. Soil CO₂ flux

To estimate how resources released by decomposing cacti influenced soil biological activity, *in situ* soil CO₂ flux beneath decomposing cacti was measured. In the field, cladodes from both species were located near or beneath living cacti and categorized by color, wrinkles, and moisture into decomposition stage on a scale of 1–5, representing a gradient from freshly fallen cacti (1) through advanced (5) decomposition levels. These cladodes were not caged once located. Fresh cladodes (1) were found or clipped and left in place for the duration of the measurement period and characterized by a bright green color with all spines attached, firm and heavy from moisture. A lightly decomposed cladode (2) was still green but missing some spines with a wrinkled skin. Moderately decomposed cladodes (3) were yellowing, wrinkled and beginning to harden. A score of (4) was assigned to browning, heavily wrinkled, and dry cladodes, and (5) to heavily decomposed cladodes that were entirely brown with much of the internal structures revealed, and very dry and brittle. These criteria were used for both species as a relative age scale to compare respiration rates across decay stages. Three control sites on bare desert soil were included for comparison as baseline conditions.

To measure the CO₂ flux, a Li-COR 8100 Infrared Gas Analyzer (IRGA; LI-COR Biosciences, Lincoln, NE) was used in addition to a moisture Delta theta probe (Delta-T Devices) to measure soil water content (SWC) and a thermistor temperature probe inserted into the soil beneath the uncaged decaying cactus cladodes. The cladode was temporarily moved, and a PVC collar was inserted into the soil with a 10-cm survey chamber fitted over top. The height of the collar aboveground (offset) was measured for calculation of volume of the headspace in each PVC ring. Once the sealed chamber was placed over the collar, CO₂ flux was recorded for 60 s intervals after a 10 s deadband. These measurements were repeated three times for each cladode weekly for 6 weeks of the late autumn (dry period) and early winter (rainy season) in November–December.

CO₂ flux data analyses were also conducted in R. A five-way Analysis of Covariance (ANCOVA) was used to test the impact of species, decay stage, date, moisture and temperature and their interactions on CO₂ flux across the six weeks of measurements. Following Ball and Virginia (2015), regression tree analysis was performed using the rpart package in R. Regression trees describe the relationship between a response variable (CO₂ flux) and multiple predictor variables of a range of data types by progressively splitting the data into dichotomous branches (Logan, 2010; Kelsey et al., 2012). A model including temperature and SWC as continuous predictor variables, and cactus species and decay stage as categorical predictor variables, was employed to explain CO₂ flux.

3. Results

3.1. Cactus decomposition dynamics

The two cactus species differed significantly in initial chemistry, with prickly pear pads being slightly but significantly higher in %C, N, K, Mg, Mn, Na as well as % water content, proteins, and compounds of unknown functional origin (Table 1). The species did not differ significantly in their % P, Ca, or other structural and metabolic compounds. However, while the differences in initial chemistry were statistically significant, they were not great in magnitude. Their largest initial difference was in water content, with prickly pear having about 10% greater water content than cholla.

Table 1

Initial chemistry and water content for the two species of cactus decomposed during this study: *Opuntia chlorotica* (pancake prickly pear) and *Cylindropuntia acanthocarpa* (buckhorn cholla). Values are the average $\pm$ SE (n = 24). P-values from the one-way ANOVA comparing the two Species are denoted as * (<0.05), ** (<0.01), *** (<0.001), or n.s. (not significant, >0.05).

	<i>O. chlorotica</i>	<i>C. acanthocarpa</i>	P-value
%C	35.4 $\pm$ 0.4	34.6 $\pm$ 0.3	*
%N	1.39 $\pm$ 0.04	1.28 $\pm$ 0.03	*
%P	0.102 $\pm$ 0.005	0.092 $\pm$ 0.007	n.s.
%K	1.93 $\pm$ 0.08	1.15 $\pm$ 0.08	***
%Mg	1.53 $\pm$ 0.07	1.16 $\pm$ 0.05	**
%Mn	0.018 $\pm$ 0.002	0.011 $\pm$ 0.001	*
%Na	0.128 $\pm$ 0.010	0.091 $\pm$ 0.005	**
%Ca	5.67 $\pm$ 0.30	5.70 $\pm$ 0.23	n.s.
%Water	81.2 $\pm$ 0.6	71.8 $\pm$ 1.2	***
%Aromatic	6.78 $\pm$ 1.79	4.07 $\pm$ 0.56	n.s.
%Lignin	14.3 $\pm$ 3.1	10.2 $\pm$ 2.8	n.s.
%Lipids	22.5 $\pm$ 7.5	32.3 $\pm$ 5.1	n.s.
%Polysaccharides	21.5 $\pm$ 2.6	24.9 $\pm$ 0.7	n.s.
%N-Bearing	6.21 $\pm$ 1.50	3.87 $\pm$ 0.28	n.s.
%Protein	6.73 $\pm$ 0.87	3.50 $\pm$ 0.70	*
%Phenols	10.7 $\pm$ 2.2	12.5 $\pm$ 1.6	n.s.
%Unknown	11.2 $\pm$ 1.0	5.6 $\pm$ 1.7	*

Throughout one year in the field, both species showed a precipitous decrease in fresh mass (Fig. 1a), but most of that was through water loss. Both species lost almost all of their water over the duration of spring and summer, with <1% of their initial water remaining at 221 days (Appendix A). The concurrent decrease in AFDM, representing loss of the organic cactus biomass beyond desiccation, and associated release of C was much slower, with prickly pear losing about 50% of its original AFDM and cholla only about 30% (i.e., 70% remaining) after one year

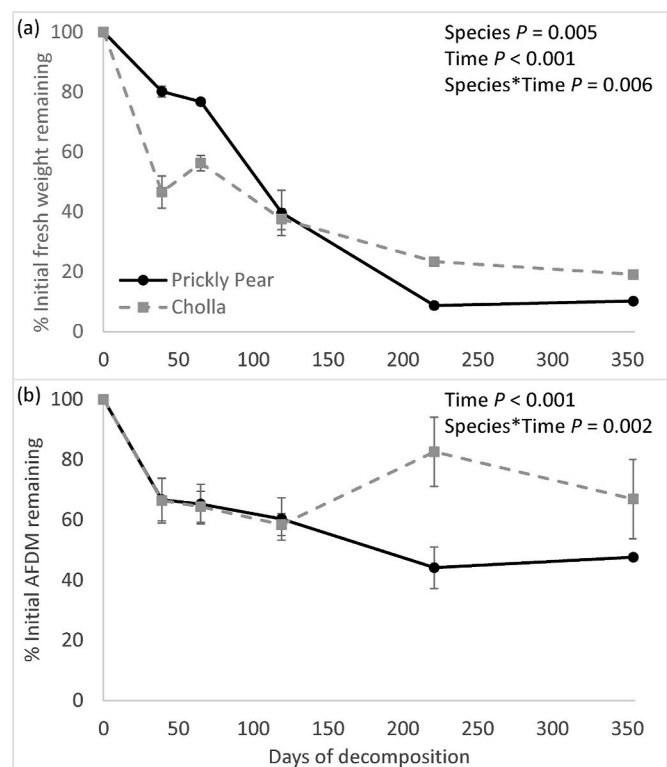


Fig. 1. Mass loss of two cactus species decomposed for one year: *Opuntia chlorotica* (pancake prickly pear) and *Cylindropuntia acanthocarpa* (buckhorn cholla). Mass loss is expressed as both (a) percent of fresh mass remaining and (b) percent of ash-free dry mass (AFDM) remaining. Values are the average $\pm$ SE (n = 4). P-values from the two-way ANCOVA are provided for all significant main effects and interactions.

(Figs. 1b and 3b). Initially, cholla lost fresh mass more quickly due to its faster water loss, but AFDM loss was equivalent in the two species. After 4 months, both species had lost equivalent proportions of their initial water, and prickly pear continued losing AFDM while cholla increased, representing a gain in organic mass between 119 days (June) and 221 days (October) that then decreased again by 354 days (February). Of all of the chemical properties measured, the only properties that significantly covaried with %AFDM remaining were % water ($P = 0.032$), % lignin ($P = 0.029$), Lignin:N ratio ($P = 0.026$), and marginally % polysaccharides ($P = 0.048$). The total accumulated precipitation since day 0 ($P = 0.017$) also correlated with AFDM loss, with the periods of greatest mass loss corresponding to intervals of measurable precipitation increase (Appendix B). Other individual chemical properties or ratios were not significant covariates with mass loss.

Over the 354 days, the decomposing cacti released not only water, but also C and Ca in the largest amounts (approx. 3–4 g water, 100–200 mg C, and 25–50 mg of Ca released per g of initial dry weight; Fig. 2). Nitrogen, Mg, and K were mineralized in the range of 1–10 mg per g dry weight. Less abundant were P and Na, which were an order of magnitude lower in their mineralization, and Mn at two orders of magnitude lower. Both species released most nutrients at a statistically equivalent rate ($P > 0.05$ for Species and Species*Time for most elements). Only water, C, and K were released in statistically greater proportions by prickly pear. For all other nutrients, both species tended to release equivalent proportions of their nutrients for the first four months, diverge at 221 days when cholla immobilized nutrients (concurrent with its increase in dry

mass), then return to a similar nutrient content by 354 days. Notably these patterns over time are not statistically significant ($P > 0.05$ for Time and Species*Time for all except water and C) given the high variability that persists in the later sampling periods for both species. These temporal patterns are significant, though, when considering the % of initial nutrient remaining instead of mineralization per g dry weight (Appendix A).

Structural and metabolic compounds could only be analyzed on a percent content basis, given that the values are expressed as their percent of all compounds measured, not percent of overall litter mass. Only protein content changed significantly over the course of decay, with a slight increase in concentration as they approached 50% AFDM remaining (Appendix C). Both proteins and the unknown compounds remained significantly higher in prickly pear throughout the first 50% of mass loss. There were no significant patterns over time or between species for all other compounds measured by py-GCMS (data not shown).

3.2. Soil CO_2 flux

Soil CO_2 flux rates were more strongly influenced by soil moisture ($P < 0.001$) and temperature ($P < 0.001$) than they were by the species ($P = 0.146$) or decay stage ($P = 0.051$) of the overlying cacti. Most noticeably, CO_2 flux rates were much greater after the onset of the winter rains, when soil temperatures were more moderate and soil water content was higher (Fig. 3a). The regression tree illustrates that flux

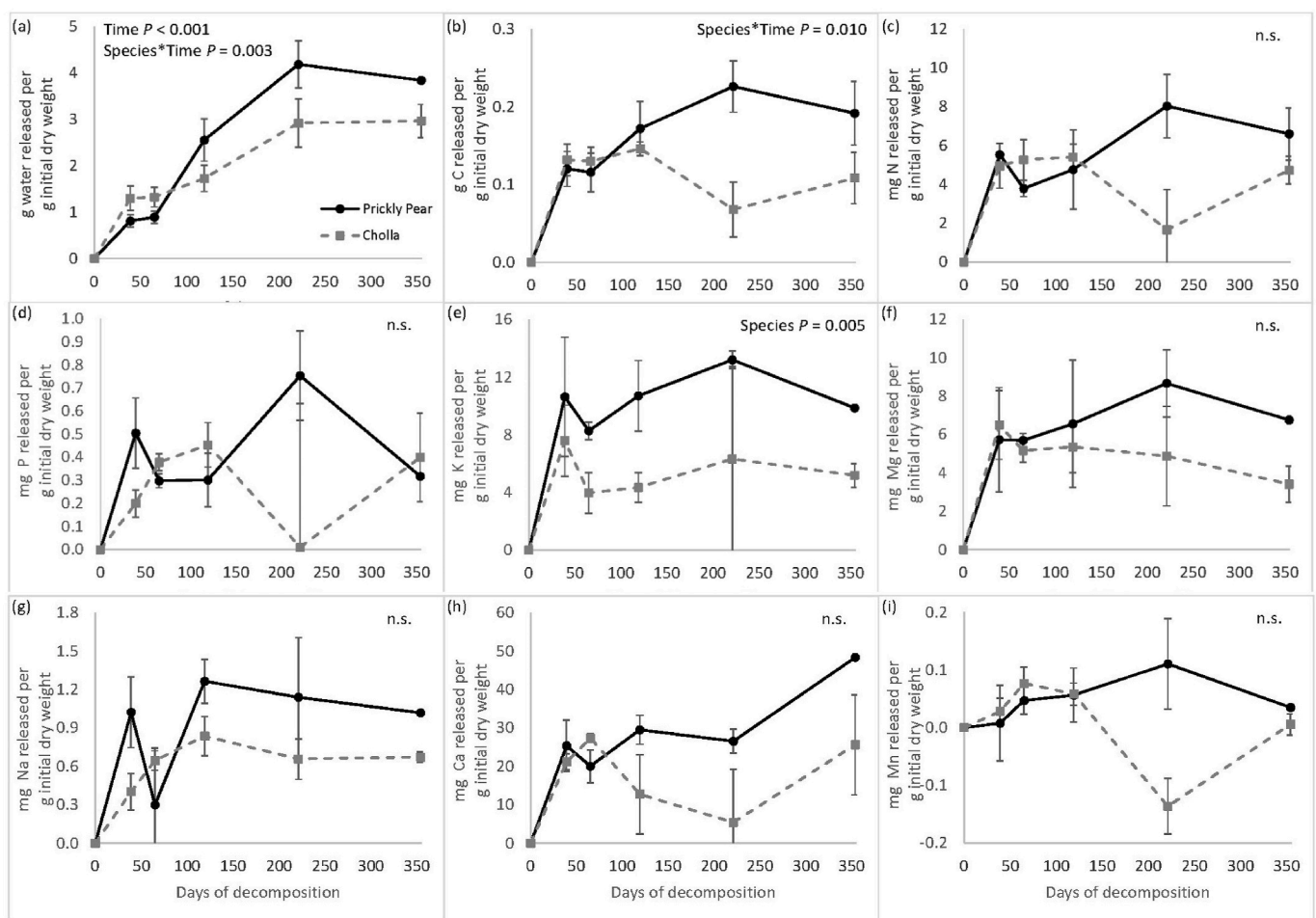


Fig. 2. Water, carbon, and nutrient release from two cactus species decomposed for one year: *Opuntia chlorotica* (pancake prickly pear) and *Cylindropuntia acanthocarpa* (buckhorn cholla). Chemical release is standardized across the two species as the mass released per g of initial dry weight. Values are the average $\pm$ SE ($n = 4$). P-values from the two-way ANCOVA are provided for all significant main effects and interactions (n.s. = not significant, $P > 0.05$ for all factors).

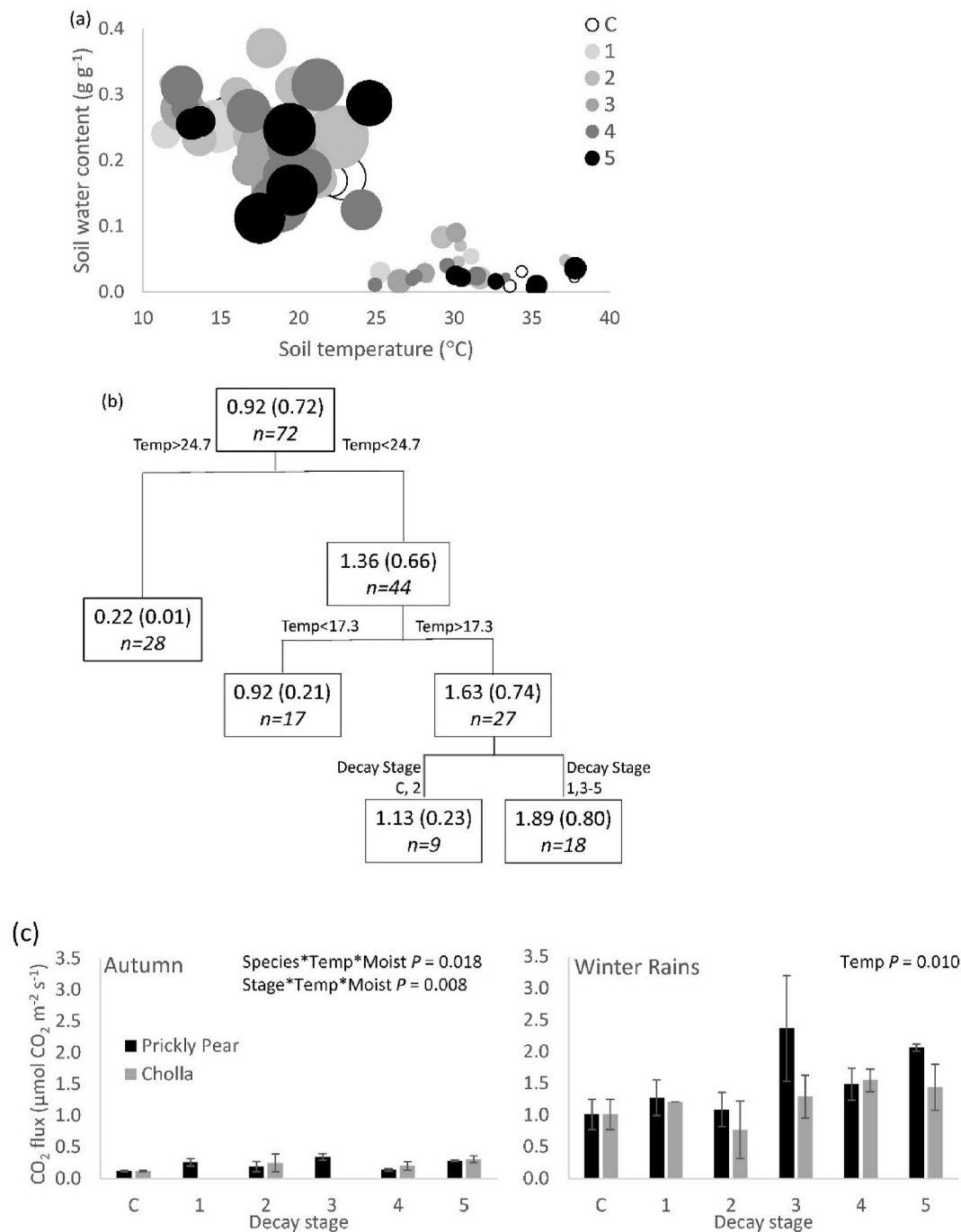


Fig. 3. (a) CO_2 flux rates from soil beneath decaying cactus cladodes, in relationship to soil temperature and moisture at the time of measurement. Size of the bubble is relative to the magnitude of the flux. Data are presented according to a gradient of decay stage of the overlying cactus, with 1 comprising freshly fallen cactus and 5 representing the most advanced, heavily decayed; C = control soils with no overlying cactus. (b) Results of the regression tree analysis predicting soil CO_2 flux with soil temperature, moisture, cactus species, and decay stage. Boxes at each node list the mean CO_2 flux ($\mu\text{mol CO}_2/\text{m}^2/\text{s}$) with standard deviation in parentheses, followed by the number of observations. The lines between boxes show the thresholds of soil temperature ($^{\circ}\text{C}$) and decay stage specified by the regression tree analysis that dichotomize the data. (c) Soil CO_2 flux rates from beneath decaying cacti (average $\pm$ SE) for hot, dry weather in autumn (early November) and cooler, wetter weather after the onset of winter rains (late November into December). P-values from the four-way ANCOVA, testing effects of temperature, moisture, cactus species, and decay stage are provided for the highest-order significant interactions or main effects.

rates were an order or magnitude lower when temperatures were greater than $\sim 25^{\circ}\text{C}$ (Fig. 3b). Decay stage of the cactus was a secondary influence to that of temperature and moisture. Specifically, under moderate temperatures (~ 17 – 25°C), CO_2 flux rates diverge by decay stage, where control soils (without cacti) and those under lightly decomposed cacti were lower in flux than freshly fallen cacti and the other more advanced decay stages. Again, the species of the cactus was not a

significant factor. While soils under prickly pear tended to have higher CO_2 flux rates than under cholla and control soils after the winter rains began, the difference is small in comparison to the effect of overall weather and decay stage (Fig. 3c).

4. Discussion

In both species, fresh mass loss was largely due to water loss, but with a concurrent loss of ~30–50% of AFDM (and therefore C) in the first 100 days, after which the loss of AFDM declined more slowly. Near the one-year mark, the prickly pear had lost approximately 50% of its initial AFDM, while the cholla had lost only approximately 30%. [Martínez-Falcón et al. \(2012\)](#) also saw similar mass loss rates over the first ~100 days of cactus decay when the insect decomposer community was excluded. This is comparable to our data, as we saw no visible evidence of macroscopic insects colonizing the cholla or prickly pear during our study, suggesting they are not a large component of decay for these non-columnar species at this site. The chemical properties that correlated with AFDM loss were limited to lignin, lignin:N, and polysaccharide content. Lignin is commonly documented as a predictor of decay rates across species and ecosystems, given that the higher lignin content leads to a more recalcitrant litter to be decomposed (e.g., [Melillo et al., 1982](#); [Talbot and Treseder, 2012](#); [Talbot et al., 2012](#); [Walela et al., 2014](#); [Hall et al., 2020](#)). Polysaccharides may represent compounds that are easily broken down by decomposers, increasing decay rates. Seasons, including our wet winters and the continual wet-dry weather cycle occurring in the summer monsoon season in the Sonoran Desert, also played a key role in determining the pattern of mass loss. We observed faster C and AFDM loss during the spring, particularly during the intervals with noticeable precipitation accumulation, that slowed with the onset of late spring and early summer droughts before the monsoon season begins. During periods of rain, soluble minerals and compounds would be leached, as evidenced in both cactus and leaf litter decomposition studies. The water limitation of decomposition explains why % water and total accumulated precipitation were significantly correlated with AFDM decay.

Despite the differences in initial chemistry between the two species, the initial stage of desiccation, mass loss, and nutrient release was similar in the two cactus species. This reflects the fact that the chemical properties correlated with AFDM loss (lignin and polysaccharides) did not differ between the two species. After four months of decay, though, prickly pear continued to decrease in AFDM (and therefore mineralize more C), while cholla temporarily gained mass. The increase in mass can potentially be attributed to a spike in microbial biomass, given the visual observation of hollow yet necromass-filled cholla cladodes at these later collection dates that could have led to an overall increase in mass. However, a 20% increase in AFDM (corresponding to roughly 3 g) is a sizable amount of microbial biomass, particularly given the assumption that the C comprising their biomass would have come from the cholla. Abundant bacterial and yeast necromass growing in cactus 'rot pockets' is well-described in the literature from a taxonomic perspective ([Starmer and Phaff, 1983](#); [Fogleman and Foster, 1989](#); [Foster and Fogleman, 1993](#); [Ganter and Quarles, 1997](#)), but we found no published quantifications of overall biomass, so we are unable to conclude whether such an sizable increase in organic mass is attributable to necromass. Though we did not specifically measure microbial biomass, the additional biomass would correspond with the nutrient immobilization that occurred, particularly notable in C, N, P, and Mn after 125 d of mineralization, when cholla began to immobilize nutrients while mineralization continued in prickly pear. Organic sedimentation is also a possible explanation for the increase in AFDM, though it seems unlikely that the two species would differ in their collection of deposited sediment to explain the increase seen in cholla but not prickly pear. Similarly, deposition of geologic minerals such as Mn in dust is well documented globally in deserts, including notably high levels of MnO the Sonoran Desert ([Péwé et al., 1981](#); [Eltayeb et al., 1993](#); [Gunawardena et al., 2013](#); [Zhang et al., 2014](#)), which could account for the increased mineral content in cholla, though again it seems unlikely that dust deposition on the two species would differ. Other than greater amounts of C and K released from prickly pear, there was not a significant difference in total amount of nutrients released by the two cacti, reflecting the fact that

their initial nutrient chemistry was only moderately different. Though the total amount of nutrients released is similar between the two species, the timing of release differs, and the mechanisms that explain why cholla increased in mass and nutrient immobilization while prickly pear continued to decrease warrants further exploration.

In comparison to the more commonly-studied woody and herbaceous plant litter decomposition, the rate of mass loss we measure for these two cactus species is slightly slower than the decay rates published for a drought-deciduous shrub leaf litter of relatively high initial leaf litter quality in nearby sites ([Ball et al., 2019](#)), but faster than low-chemical-quality creosote leaves ([Day et al., 2018](#)). The influence of available water and precipitation that we measured is also common in the literature (e.g., [Aerts, 1997](#); [Hewins and Throop, 2016](#); [Du et al., 2020](#); [Wu et al., 2020](#)), as is the relationship with lignin and lignin:N mentioned above, but interestingly initial nutrient content, including the elements that differed between the two species, did not influence decay rate as has been demonstrated for leaf litter (e.g., [Aber et al., 1990](#); [Hobbie and Vitousek, 2000](#); [Pérez-Harguindeguy et al., 2000](#); [Martínez-Yrizar et al., 2007](#)). A similar lack of nutrient effect on decomposition has been recorded for other species in this area ([Ball et al., 2019](#)).

Macronutrient dynamics during decay are also similar to what is demonstrated in the literature for woody and herbaceous leaf litter. A commonly-documented pattern of leaf litter decomposition is for an initial period of net nutrient immobilization by the microbial biomass and decay products followed by net mineralization, where the occurrence and extent of that immobilization is dependent on leaf chemistry, as some litters may require more immobilization than others. This is well-documented for N and P, but also other nutrients such as Ca for some species (e.g., [Post et al., 1985](#); [Blair, 1988](#); [Koukoura et al., 2003](#); [Parton et al., 2007](#); [Moore et al., 2011](#)). In the limited number of Sonoran Desert decomposition studies that measure nutrient dynamics, there are examples of initial N immobilization early in Sonoran Desert leaf litter decay ([Day et al., 2015](#); [Predick et al., 2018](#); [Levi et al., 2020](#)), but often arid ecosystems are an exception to this pattern ([Parton et al., 2007](#)). Desert soils tend to have low C:N ratios, due to water limitation of plant N uptake and an accumulation of insoluble N salts that are not leached from the soil ([Post et al., 1985](#)). Thus, N is not likely a limiting factor in Sonoran Desert decomposition, particularly with additional anthropogenic N inputs into the system from the Phoenix metropolitan area, leading to N mineralization throughout decomposition, causing phosphorus to be limiting and require immobilization ([Ball et al., 2019](#)). Net mineralization was the dominant pattern for both cactus species, regardless of a modest difference in initial %N, except for one period of immobilization in cholla associated with the increase in AFDM remaining and not likely the result of nutrient limitation of breaking down the cactus material itself. The C:N of the cacti decomposed here was consistently around 25–28 throughout the study (below the common thresholds around 30–50; [Parton et al., 2007](#)), yet immobilization occurred. Despite this altered timing for immobilization, the cacti lost comparable proportions of their initial N and P over one year of decay as did shrub leaves at other Sonoran Desert sites near Phoenix ([Ball et al., 2009](#)). Therefore, the release patterns of N and P during cactus decomposition did not appear to differ substantially from leaf litter decomposition, and the main variation from what is understood about leaf litter decay is the amount of certain micronutrients being recycled.

Nutrient cycling was particularly high in both cactus species for C and Ca compared to the other nutrients that were released from the cacti. Both species contained a substantial quantity of Ca, due to the calcium oxalates abundant in cacti, with significant rates of Ca released during decay at levels one or two orders of magnitude greater than the other nutrients. Studies of saguaro decay suggest that the chemistry of this release will be in the slow transformation of calcium oxalate into calcite, constituting an inorganic form of C inputs into the soil ([Garvie, 2006](#)). Our data quantify the rapid rate at which that may be occurring, given the order(s) of magnitude greater release of Ca compared to other

nutrients being recycled. Studies reporting Ca dynamics during decomposition are lacking for the Sonoran Desert, but the prickly pear and cholla contained 2–10 times more Ca initially than woody plant leaf litter in other ecosystems, and therefore mineralized 20–50 mg Ca per g of cactus dry mass during a year of decomposition, as opposed to the immobilization that is often seen in woody plant leaf litter (Killingbeck et al., 1982; Zou et al., 1995; Berg et al., 2010; Lovett et al., 2016; Yue et al., 2020).

We hypothesized that the decomposing cacti would provide a favorable microclimate and inputs of nutrients to stimulate biological activity in the underlying soil. The soil CO₂ flux data demonstrate that temperature and water availability were the most important factors that affect respiration, more so than the inputs from the decaying cactus overlying the soil. The dual control of temperature and moisture on aridland soil respiration has been described elsewhere (Wildung et al., 1975). Decay stage only had a secondary effect on respiration under optimum microclimate conditions for soil respiration. Lightly decomposed cacti grouped with control soils not beneath a cactus, likely reflecting the limited water and nutrient release at that stage. Freshly fallen cacti, however, grouped with the moderate and advanced decay stages, possibly due to the shaded and moist microclimate it provides until decay begins.

Differences between the two species, particularly the greater shading effect of prickly pear compared to cholla cladodes, did not significantly alter soil respiration. Both prickly pear and cholla initially contained a large quantity of water leading to a high percentage of water loss over the first several months of decomposition in spring and summer that could create a cooler, shaded microclimate in the soil beneath them. This is particularly true of prickly pear, with larger cladodes with higher initial water content that evaporates a notable ~3–4 g of water per g of dry mass. While the differences in C release rates during decay would suggest the species differ in litter respiration rates, that did not translate to soil respiration rates in an *in situ* field setting, despite the physical differences. There tended to be higher soil CO₂ flux rates beneath prickly pear in the optimal climate conditions after the winter rains began, but this small difference was overshadowed by other ecosystem factors. It is possible that a larger accumulation of prickly pear pads, such as an entire fallen arm or accumulation directly beneath the plant, would provide sufficient mulching to create a noticeable difference in CO₂ flux.

5. Conclusion

Our data demonstrate the role of cacti in Sonoran Desert elemental cycles, contributing not only to the carbon cycle, but also to macro- and micronutrient cycles during desiccation and early-stage decay. In particular, the calcium oxalate stored within cacti allows them to contribute significantly to the Ca and C cycles at levels 2–10 times greater than leaf litter decay. While the two cactus species did not strongly differ from each other, immobilization within the cholla did lead to some retention of nutrients within the first year of decomposition. Overall, prickly pear has the potential to contribute more towards ecosystem C and K dynamics than cholla, but otherwise both species decompose similarly. The patterns we observed during cactus decomposition were also similar to other studies of leaf litter decomposition. With the addition of anthropogenic produced greenhouse gases, the climate is changing the habitat suitability for cacti (Albuquerque et al., 2018). Limiting the habitats that these cacti can survive will impact biogeochemical cycling in desert ecosystems where they were once abundant, particularly in water and Ca dynamics. Thus far, there is still limited information represented within the scientific community on the biogeochemistry of decomposing cacti, however, leaf litter decomposition studies provided insights with similar patterns.

CRedit authorship contribution statement

Anna H. Bilderback: Writing – original draft, Formal analysis.

Alexander J. Torres: Investigation, Writing – review & editing. **Miranda Vega:** Conceptualization, Investigation, Data curation, Writing – review & editing. **Becky A. Ball:** Conceptualization, Methodology, Data curation, Visualization, Writing – original draft, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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