

Consistent pattern of higher lability of leaves from high latitudes for both native *Phragmites australis* and exotic *Spartina alterniflora*

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Abstract

1. Global variation in litter decomposition rates is driven by climate, decomposer taxa and litter quality. Most large-scale studies of litter quality have made comparisons across species, rather than within a species sourced from different latitudes. Here, we aim to explore latitudinal variation in leaf litter decomposition rate and litter quality within a species.
2. We investigated whether the typical interspecific pattern of increased litter lability at higher latitudes also holds within plant species, by comparing leaf litter decomposition rates and litter traits from stands of native *Phragmites australis* and exotic *Spartina alterniflora* in Chinese coastal wetlands spanning 20° of latitude using parallel greenhouse and field transplant experiments.
3. We found that leaf litter from high-latitude plants decomposed $46.6 \pm 5.1\%$ faster than that from low-latitude conspecifics, with similar patterns in both plant species in both decomposition experiments. Higher lability of leaves from high latitudes was associated with lower levels of plant defensive compounds (phenolics and tannins) and higher levels of nutrients (Ca, Mg and Na). Litter from the exotic *S. alterniflora* decomposed faster than litter from the native *P. australis*, being consistent with lower defences and higher nutrient concentrations in *S. alterniflora* litter.
4. Our results show that individual species follow the same pattern of increasing litter lability at higher latitudes previously reported in cross-species geographical comparisons. Moreover, this pattern can develop rapidly (<4 decades) in an introduced species, raising the question of whether it is caused by phenotypic plasticity or adaptation.

KEYWORDS

decomposition rate, exotic species, latitudinal gradients, litter traits, *Phragmites australis*, *Spartina alterniflora*

1 | INTRODUCTION

Global variation in litter decomposition rate is driven by three main variables: climate (temperature, precipitation, humidity, etc.), decomposers (micro-, meso-, macro-decomposers) and litter quality

(physical and chemical traits; Bradford et al., 2016; See et al., 2019; Waring, 2012). At small spatial scales, the importance of these three factors varies among studies (Veldhuis et al., 2017; Yue et al., 2016); however, at large spatial scales, climate is typically the most important factor controlling decomposition, with faster decomposition

under hot, wet conditions (Aerts, 1997; Berg et al., 1993; Powers et al., 2009).

Although climatic variation would tend to create a latitudinal pattern of higher in situ decomposition rates at low latitudes, variation in litter quality may oppose this pattern. Studies comparing plants from different latitudes have found that litter from tropical plants is the most recalcitrant (Boyer et al., 2017; Makkonen et al., 2012). Thus, latitudinal patterns in litter quality may dampen the latitudinal pattern in decomposition expected based on climate alone.

Latitudinal studies of variation in litter lability independent of climate have typically focused on cross-species comparisons. Fewer studies have examined intraspecific variation in leaf litter decomposition at large spatial scales. Lecerf and Chauvet (2008) compared decomposition rates of alder leaf litter from five geographical locations in European streams and found a negative relationship between leaf decomposition rate and latitude of leaf origin (i.e. leaves from high latitudes decomposed more slowly). Other studies only have measured how litter decomposition varies based on genotype and litter traits within a single species (Axelsson et al., 2010; Leroy et al., 2007, 2012; Madritch et al., 2006).

Latitudinal variation in decomposition within a species is important for several reasons. First, many plant species are widely distributed, so a single measurement of litter lability may be inappropriate for all populations. Second, intraspecific comparisons are not confounded by many differences among species that may be more related to phylogeny than geography, thereby improving our understanding of geographical patterns. Third, local decomposer taxa may be assembled in response to plant species that occur locally such that cross-site studies with novel plants may be misleading.

Of further interest is the decomposition rate of native versus exotic species. A number of studies have examined the decomposition of native versus exotic species and argued that litter from exotic species decomposes faster than litter from natives (Kennedy & El-Sabaawi, 2017; Liao et al., 2008). For example, Allison and Vitousek (2004) compared leaf litter decomposition rates of five native and six exotic understory Hawai'ian plant species and found that litter from the exotics decomposed faster than that from the natives, and that differences in litter decomposition and nutrient cycling were caused by litter traits of exotic plants. Most of these studies have been conducted on local and regional scales, and we do not know how they generalize across geographical scales.

At the latitudinal scale, clines of herbivore pressure on native versus exotic species may not be parallel (Bhattarai et al., 2017). For example, Cronin et al. (2015) found that the latitudinal clines in defence and palatability traits of European invasive genotypes were absent or weak, and thus was non-parallel to gradients for the native genotypes. While previous studies focused on the plant-based food chain (above-ground herbivory and plant palatability), we do not know whether this non-parallel pattern also exists in the debris-based food chain (litter decomposition and litter traits). If there are latitudinal patterns within a species in decomposition, would we expect to see similar patterns in recent invaders? Or will patterns for native and exotic species be non-parallel?

To improve our understanding of latitudinal variation in litter lability, we examined decomposition of leaf litter from two coastal grass species, *Spartina alterniflora* and *Phragmites australis*, collected across a range of 20° latitude along the Chinese coast. These species represent an exotic and a native, respectively. *S. alterniflora* was intentionally introduced into coastal wetlands in China in 1979, and has rapidly spread by natural dispersal and human planting over 20° of latitude along the eastern coast of China (Liu et al., 2018; Zhang et al., 2017). *P. australis* is an important native coastal wetland plant in China. It broadly overlaps in distribution with *S. alterniflora* in salt marshes (Li et al., 2009; Zhang et al., 2019).

Which litter traits best predict latitudinal variation in litter lability at the geographical scale for both species is still unknown. Studies comparing across species disagreed on which traits are best correlated with litter lability (Cornwell et al., 2008; Makkonen et al., 2012; Trofymow et al., 2002). Many studies identified litter C:N as the primary variable predicting litter lability (Duan et al., 2018; Li et al., 2017; Manzoni et al., 2010), but some studies have emphasized the positive role of multiple nutrient elements (Kaspari, Garcia, et al., 2008; Zhang et al., 2008) or the negative effects of secondary compounds such as tannins and phenols (Makkonen et al., 2012). Intraspecific comparisons, such as those we reported here, allowed us to examine variation in traits without confounding effects of plant species identity.

We conducted parallel greenhouse common garden and field transplant experiments in which we compared the decomposition rates of leaf litter of *P. australis* and *S. alterniflora* from sites spanning ~20° of latitude along the Chinese coastline while held climate and detritivore access constant. This comparison of the exotic and native allowed us to address three questions. First, do decomposition rates of exotic species differ from those of natives? In particular, comparisons at one site in China have found that litter of *S. alterniflora* decomposes faster than litter of *P. australis* (Duan et al., 2018; Liao et al., 2008). We do not know if this pattern holds along the entire Chinese coast, but we hypothesized that litter of the introduced species would be more labile than that of the native across the entire latitudinal range. Second, assuming that the native species displays a latitudinal cline in litter lability, does the exotic display a parallel cline? We hypothesized that litter lability of the native, but not the exotic, would increase with latitude, and therefore that there would be a non-parallel pattern in litter lability between the introduced and native species. Third, we hypothesized that intraspecific variation in litter decomposition rates would be correlated with leaf C:N, multiple nutrients and crude measures of chemical defence components (tannin and phenolic concentrations).

2 | MATERIALS AND METHODS

2.1 | Leaf litter collection

We collected leaf litter samples from 12 regions along the Chinese coastline, from 20.89°N to 40.68°N latitude (Figure 1). The regions

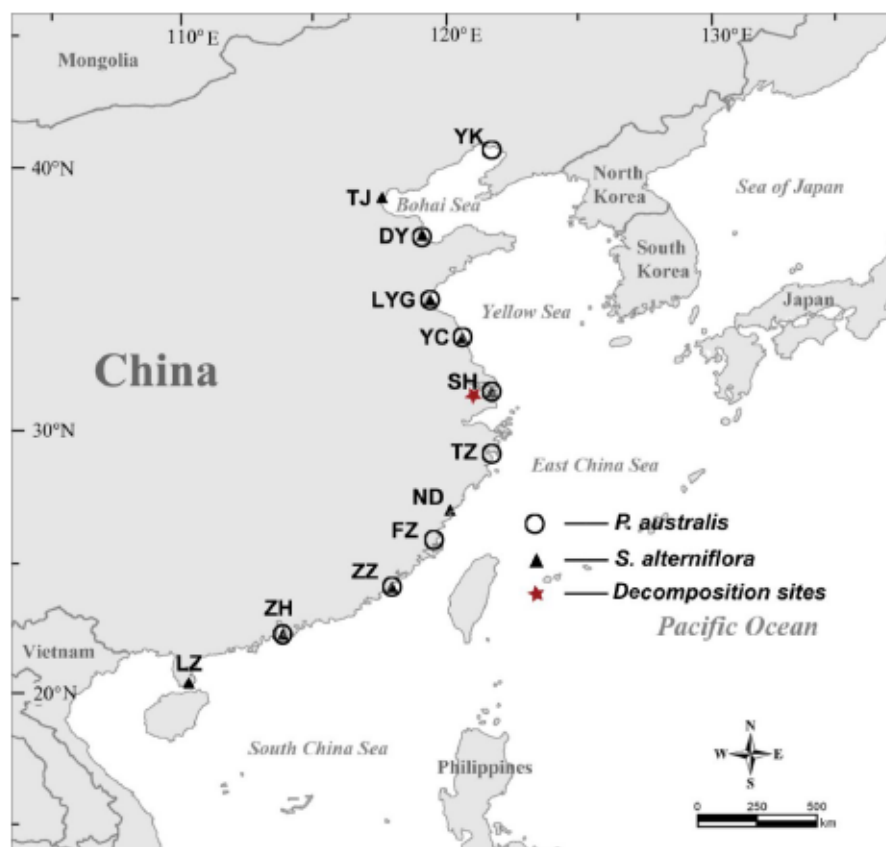


FIGURE 1 Map of eastern China showing the regions where leaf litter from *Phragmites australis* and *Spartina alterniflora* were collected, and the locations of the two decomposition experiments (shown with a single star) at Shanghai Fudan University Jiangwan campus (greenhouse) and Chongming salt marsh (field)

Region	Site abbreviation	Latitude (°N)	Longitude (°E)	<i>Spartina alterniflora</i>	<i>Phragmites australis</i>
YingKou	YK	40.68	122.18		✓
TianJin	TJ	39.15	117.70	✓	
DongYing	DY	37.72	119.04	✓	✓
LianYunGang	LYG	34.58	119.18	✓	✓
YanCheng	YC	33.23	120.74	✓	✓
ShangHai	SH	31.50	121.96	✓	✓
TaiZhou	TZ	28.86	121.66		✓
NingDe	ND	26.62	119.61	✓	
FuZhou	FZ	26.06	119.61		✓
ZhangZhou	ZZ	24.52	117.40	✓	✓
ZhuHai	ZH	22.43	113.63	✓	✓
LeiZhou	LZ	20.89	110.17	✓	

TABLE 1 Regions where leaf litter from the two plant species were collected

were chosen to span as large a latitudinal range as possible for the two study species, *S. alterniflora* and *P. australis*, on the coast of China. Because the two plant species do not have identical distributions, each was collected from 9 of the 12 regions (Table 1). These nine regions were chosen to exclude sites where a species was rare (did not occur in multiple patches >5 m in diameter), or had been present for <5 years. For each plant species that was sampled at a site, we selected five, 5 × 5 m plots, at least 1 km apart from each other. Plots were in the middle of monospecific stands of the species of interest.

We collected leaf litter between November 2015 and February 2016, with one visit to each region for each plant species, timed according to the phenology of each plant at that region. We collected freshly senesced leaves that were yellow and still attached to the plant stalk. We collected senesced leaves from all parts of plant stalks from five 1 × 1 m subplots within the 5 × 5 m plot and then mixed leaf litter well and pooled it into a single sample per species, for a total of 45 samples (9 regions × 5 plots). The litter samples were oven-dried at 60°C for 72 hr to a constant weight.

2.2 | Litter traits

In order to determine which litter traits best predicted decomposition rates, we measured several physical and chemical traits of the dried leaf litter, using standard methods (Appendix S1). We measured three physical traits: specific leaf area, leaf toughness and leaf thickness. We measured 12 chemical traits: C, N, P, K, Ca, Na, Mg, lignin, tannin, cellulose, hemicellulose and total phenol content. Because the ratios of some of these traits may be more important for explaining decomposition rates than individual concentrations (Currie et al., 2010; He et al., 2019; Pei et al., 2019), we calculated four ratios found important in other studies to include in the analysis: C:N, N:P, lignin:N and tannin:N.

2.3 | Decomposition experiments

We compared decomposition rates of litter by greenhouse common garden and field transplant experiments in Shanghai, China. The common garden experiment was done in the greenhouse of Fudan University, Jiangwan campus (31.34°N; 121.50°E). In order to confirm whether the latitudinal patterns of litter decomposition observed in the greenhouse also hold in the field under more natural abiotic and biotic conditions (in the presence of natural decomposer communities), we set up an additional transplant experiment in the field, at Chongming salt marsh (31.67°N; 121.66°E) of the Yangtze River estuary. In both cases, we incubated leaf litter in 1-mm mesh fiberglass litterbags which allow the entry of microbes, microfauna and mesofauna. Yangtze River's sediment load is the fourth largest in the world and delivers a large amount of sediment to the estuary area every year, with an average annual accretion of about 10 cm on the estuarine marshes (Hu et al., 2019; Yang et al., 2002). Although grass leaves partially decompose in place before falling to the ground, leaf litter that falls to the sediment surface at our site can be quickly buried by sediment (Duan et al., 2018; Li et al., 2009). Therefore, we buried litterbags ~10 cm deep in the soil to mimic decomposition under these conditions. In addition, burying litterbags underground circumvented interference of tidal scouring, which may bias the decomposition rate.

For the greenhouse experiment, we collected field soil from Chongming Island in September 2016, from an area with a mixture of *S. alterniflora* and *P. australis* plants. We filled pots (15 × 1 × 15 cm) with 2 cm of soil, laid a litterbag with ~5 g dry litter flat on top of the soil and then added an additional 8 cm of soil above the litter bag. Each treatment combination was replicated three times, for a total of 270 pots (2 litter types × 45 plots × 3 replicates). Pots were placed in a climate-controlled greenhouse at 20°C and 75% humidity and were watered daily to maintain damp conditions. Litter was incubated for 94 days, from 1 October 2016 to 2 January 2017.

For the field transplant experiment, we incubated litter in six 5 × 5 m plots, three each within monospecific stands of *S. alterniflora* and *P. australis*. We excavated soil to a depth of 10 cm, laid litterbags

filled with ~15 g of litter flat in the soil and replaced the upper 10 cm of soil above the litter bags. Litter from *S. alterniflora* was incubated in stands of *S. alterniflora*, and litter from *P. australis* was incubated in stands of *P. australis*. Each treatment combination was replicated three times, once per plot, for a total of 270 litter bags (2 litter types × 45 plots × 3 replicates). Litter was incubated for 88 days, from 4 August 2017 to 30 October 2017. Eight bags were lost upon retrieval, for a final sample size of 262.

At the end of both experiments, we retrieved the samples, washed soil from the litter over a 0.1 mm screen and removed all visible soil fauna and small stones. The remaining litter was dried to a constant weight at 60°C for 72 hr and weighed. We calculated the litter decomposition rate represented by litter mass loss (%) as

$$\text{Litter mass loss} = \frac{M_0 - M_t}{M_0} \times 100\%,$$

where M_t was the final mass of the sample, and M_0 was the initial mass of the sample, and we calculated the litter decomposition rate constants (k) as

$$k = -\frac{\ln(M_t/M_0)}{t},$$

where M_t was the final mass of the sample, M_0 was the initial mass of the sample and t was expressed as days. Data from the three (or two, in cases where bags were lost) replicates were averaged to give a single k value for each treatment combination.

2.4 | Data analysis

All statistical analyses were conducted in R version 3.6.3 (R Core Team, 2019). We compared k values, litter mass loss and litter traits among plant species and across latitude using general linear mixed models, with 'plot' as a random effect, and 'latitude' and 'plant species' as fixed effects, in the nlme package, and we assessed homogeneity and normal distributed errors by checking residual plots and data of leaf litter C, N, P, Na, lignin, cellulose content, C:N, lignin:N, toughness and thickness were log-transformed to improve the homogeneity. Since collinearity among explanatory variables could bias the interpretation of the results, we analysed Spearman rank-order correlations between litter traits to identify and exclude traits that were strongly correlated (correlations with coefficients >0.70) with each other (Dormann et al., 2013; Appendix S2). When two variables were highly correlated (correlations with coefficients >0.70), we kept the variable more related to litter k value according to the bivariate regression plots in Figures S8 and S9 (Appendix S3), and excluded the other one. Based on the analysis, we selected specific leaf area, leaf toughness, C, P, K, Ca, Na, Mg, lignin, tannin, cellulose, hemicellulose and total phenol content, C:N and N:P to explain leaf litter decomposition patterns in *S. alterniflora* (Appendix S2). We selected specific leaf area, leaf thickness, C, P, Ca, Na, Mg, lignin, tannin, hemicellulose and total phenol content, and C:N to explain leaf litter decomposition patterns in *P. australis*

(Appendix S2). We determined which litter traits best predicted k values for each species using multiple regression in the STAT package, and selected the best model with smallest AIC value based on AIC analysis, which we used stepwise backwards method in the model, and we assessed the model with the threshold that AIC value between the AIC of best model and null model was higher than 2 (Burnham & Anderson, 2002).

3 | RESULTS

In the greenhouse common garden experiment, leaves of *S. alterniflora* decomposed faster than those of *P. australis* (Figure 2a). Decomposition rates of both plant species varied as a function of latitude of origin (provenance), with leaves from high latitudes having k values 34.6%–52.4% higher than leaves from low latitudes, depending on species (Figure 2a). The slope of this relationship appeared higher for *S. alterniflora* than for *P. australis*, but this difference was not statistically significant ($p = 0.06$). Leaves from high latitudes had mass loss 21.2%–25.2% higher than leaves from low latitudes for both species (Appendix S3, Figure S1A); however, the conclusions drawn from the analysis of mass loss were the same as from analysis of k values (Latitude: $p = 0.003$; Plant species: $p < 0.001$; Latitude $\times$ plant species: $p = 0.53$).

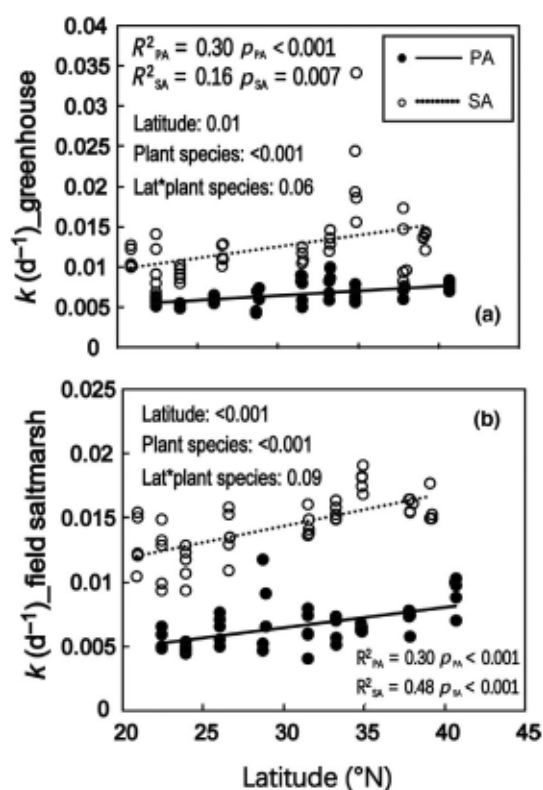


FIGURE 2 Effects of latitude and plant species on leaf litter decomposition rate k of native *Phragmites australis* and invasive *Spartina alterniflora* incubated in common garden and field transplant experiments at Fudan University greenhouse (a) and Chongming salt marsh (b). Lines were fit by least-squares regression

Results from the field transplant experiment were similar to those from the greenhouse common garden. Leaves of *S. alterniflora* again decomposed faster than leaves of *P. australis* (Figure 2b). Decomposition rates of both plant species again varied as a function of provenance, with leaves from high latitudes having k values 42.3%–57.1% higher than leaves from low latitudes, depending on species (Figure 2b). The slope of this relationship again tended to be higher for *S. alterniflora* than for *P. australis*, but this trend was again not statistically significant ($p = 0.09$). Leaves from high latitudes had mass loss 18.9%–37.3% higher than leaves from low latitudes for both species (Appendix S3, Figure S1B), but the difference in this case was not as striking as in the greenhouse experiment. Likewise, the conclusions drawn from analysis of mass loss did not differ from conclusions drawn from analysis of k values (Latitude: $p < 0.001$; Plant species: $p < 0.001$; Latitude $\times$ plant species: $p = 0.68$).

Leaf litter traits varying with latitude differed between the two plant species. For the exotic *S. alterniflora*, only 8 of the 19 litter traits examined varied with latitude (Appendix S3). With increasing latitude, leaf Ca, Mg and Na concentrations and the N:P ratio increased, whereas leaf tannin and phenolics concentrations and tannin:N ratio decreased. In contrast, for the native *P. australis*, 18 of the 19 litter traits examined varied with latitude (Appendix S3). With increasing latitude, leaf N, Ca, K, Mg, Na concentrations and the N:P ratio increased, whereas leaf thickness, SLA, C, P, tannin, total phenols, lignin, cellulose and hemicellulose concentrations decreased, and the C:N, tannin:N and lignin:N ratios also decreased.

The best multiple regression model predicting decomposition rates (k values) for *S. alterniflora* in the common greenhouse experiment included five predictor variables. The decomposition rate was negatively related to the leaf toughness, tannin concentration and lignin concentration, and positively related to Ca and Mg concentrations (Table 2). More complicated models for *S. alterniflora* decomposition added Na(+) and C:N(-) (Table 2). The best multiple regression model predicting k values for *P. australis* in the common greenhouse experiment included three predictor variables. The decomposition rate was negatively related to leaf C and lignin, and positively related to Ca concentrations (Table 2). More complicated models for *P. australis* decomposition added Na(+) and Mg(+) concentration.

The best multiple regression model predicting k values for *S. alterniflora* in the field experiment included four predictor variables. The decomposition rate was negatively related to C, tannin, total phenols, and positively related to Na concentrations (Table 2). More complicated models for *S. alterniflora* decomposition added C:N(-) and toughness(-). The best multiple regression model predicting k values for *P. australis* in the field experiment included six predictor variables. The decomposition rate was negatively related to leaf C:N ratio and total phenols, and positively related to P, Ca, Na and SLA (Table 2). More complicated models for *P. australis* decomposition added hemicellulose(-) and tannin(-). Plots showing how selected leaf litter traits varied with latitude, and bivariate plots for decomposition rates in the

TABLE 2 The three best regression models for decomposition rates of litter from *Spartina alterniflora* and *Phragmites australis* in greenhouse and field transplant experiments. (+) and (–) indicates that traits were positively or negatively related to decomposition rates

Model	AIC	ΔAIC	N	R ²	p
Greenhouse					
<i>S. alterniflora</i> leaf litter decomposition rate <i>k</i>					
tannin(–) lignin(–) toughness(–) Ca(+) Mg(+)	–505.51	0	45	0.46	<0.001
tannin(–) lignin(–) toughness(–) Ca(+) Mg(+) Na(+)	–505.36	0.15	45	0.47	<0.001
C:N(–) tannin(–) lignin(–) toughness(–) Ca(+) Mg(+) Na(+)	–504.12	1.39	45	0.47	<0.001
Null model	–481.98	23.53	45	0	<0.001
<i>P. australis</i> leaf litter decomposition rate <i>k</i>					
C(–) lignin(–) Ca(+)	–614.73	0	45	0.34	<0.001
C(–) lignin(–) Ca(+) Na(+)	–613.05	1.68	45	0.33	<0.001
C(–) lignin(–) Ca(+) Mg(+) Na(+)	–612.64	2.09	45	0.33	0.001
Null model	–599.07	15.66	45	0	<0.001
Field					
<i>S. alterniflora</i> leaf litter decomposition rate <i>k</i>					
C(–) tannin(–) total phenols(–) Na(+)	–587.49	0	45	0.66	<0.001
C(–) tannin(–) total phenols(–) C:N(–) Na(+)	–587.43	0.06	45	0.67	<0.001
C(–) tannin(–) total phenols(–) C:N(–) toughness(–) Na(+)	–586.71	0.78	45	0.67	<0.001
Null model	–542.31	45.18	45	0	<0.001
<i>P. australis</i> leaf litter decomposition rate <i>k</i>					
C:N(–) total phenols(–) P(+) Ca(+) Na(+) SLA(+)	–615.80	0	45	0.66	<0.001
C:N(–) total phenols(–) hemicellulose(–) P(+) Ca(+) Mg(+) SLA(+)	–615.44	0.36	45	0.66	<0.001
C:N(–) total phenols(–) hemicellulose(–) tannin(–) P(+) Ca(+) Mg(+) SLA(+)	–614.05	1.75	45	0.66	<0.001
Null model	–572.90	42.90	45	0	<0.001

greenhouse and field experiments as a function of selected predictor variables are shown in Appendix S3.

Three of the leaf litter traits that were repeatedly associated with faster decomposition—leaf Ca, Mg and Na concentrations—were consistently higher in *S. alterniflora* than in *P. australis* (Appendix S3). Conversely, three of the leaf litter traits that were repeatedly associated with slower decomposition—leaf tannin, phenol and hemicellulose concentrations—were consistently higher in *P. australis* than in *S. alterniflora* (Appendix S3).

4 | DISCUSSION

In this study, plants growing at high latitudes produced leaves that decomposed more readily than those from low-latitude plants. We found strong latitudinal patterns of leaf litter decomposition rate in both the exotic *S. alterniflora* and the native *P. australis*. This general pattern was similar in both the greenhouse and the field transplant experiments. This result is consistent with those of previous cross-species studies that have consistently found that, if abiotic conditions are held constant, as in a common garden, litter originating from plant species characteristic of subarctic, temperate or Mediterranean biomes decomposes rapidly, whereas litter originating from plant species characteristic of tropical forests tends to

decompose slowly (Boyer et al., 2017; Makkonen et al., 2012). Our results show that the same pattern of increasing litter lability at high latitudes also holds within a species.

Because plant chemical defences against herbivores or other enemies also slow decomposition (Grime et al., 1996; Moretto et al., 2001), one possible explanation for increased litter lability at high latitudes is that plant defences are lower at high than at low latitudes. Consistent with this possibility, both tannins and phenols were lower in leaf litter from high- versus low-latitude plants in both species. Tannins and phenolics in particular are known to slow decomposition as they can be unpalatable to decomposers (Coq et al., 2010; Coulis et al., 2009; Loranger et al., 2002). Previous studies in coastal wetlands have found that a variety of plants from high latitudes, including *S. alterniflora*, have a higher palatability to herbivores and lower levels of chemical defences than conspecifics at low latitudes (Pennings et al., 2001, 2007; Siska et al., 2002), being consistent with this hypothesis.

Another possible explanation for increased litter lability at high latitudes is that important nutrients occur at higher concentrations in high-latitude litter. We found that concentrations of Ca, Mg and Na were higher in high- versus low-latitude litter samples of both plant species. A number of studies have found that multiple nutrient concentrations of litter correlate with decomposition rate (Kaspari, Garcia, et al., 2008; Makkonen et al., 2012; Zhang

et al., 2008), possibly because the multiple nutrients increase abundance of decomposers, thereby increasing overall decomposition rates (Kaspari, Yanoviak, et al., 2008; Reich et al., 2005). It remains to be determined what mechanisms explain higher nutrient concentrations at high latitudes, and whether this is a general pattern.

An additional potential driver is variation in the growing season length across latitude. A shorter growing season at high latitudes can lead to a shorter leaf life span, with leaves that are higher in nitrogen and softer, and consequently grow faster, die younger and decompose faster (Reich et al., 1999). In our study, leaf litter nitrogen increased significantly with increasing latitude (Appendix S3, Figure S3), which may correspond to the declining leaf life span. In addition, a more hazard-filled environment including higher herbivore pressure at lower latitude sites may require tougher leaves to achieve the same mean leaf life span (Pennings et al., 2001; Siska et al., 2002). While we did not observe tougher leaves at low latitudes, we did find thicker leaves of native *P. australis* at lower latitudes which may be a similar response leading to a longer life span.

Different from those herbivory studies that observed non-parallel patterns (Bhattarai et al., 2017; Cronin et al., 2015), we found a parallel latitudinal pattern of leaf litter decomposition rates between native *P. australis* and exotic *S. alterniflora*. This is contrary to the prediction of our second question, and suggested that geographical clines may vary between the 'green' world (palatability for herbivory) and the 'brown' world (lability for decomposition). We speculate that the consistent latitudinal patterns of leaf lability for native *P. australis* and exotic *S. alterniflora* may be mainly related to the parallel patterns of nutrient elements (Ca, Mg and Na).

Although we confirmed that the intraspecific variation in litter decomposition rates was correlated with a set of parameters including multiple nutrients and defence components as in our third question, the main predictors for explaining the decomposition rates were not identical between the two plant species and between the two experiments. For example, C:N was included in the best models for *S. alterniflora* in greenhouse and *P. australis* in field transplant experiment, and C concentration in the best models for *S. alterniflora* in the field and *P. australis* in the greenhouse. Other studies have also found that litter traits predicting decomposition rate vary between different decomposition environments (Makkonen et al., 2012). It is therefore important to consider both the environment and species and genetic identities when we study the traits that drive decomposition rates.

Even if litter originating from high latitudes is more labile than litter from low latitudes in a common garden, it may not decompose faster in situ because of lower temperatures in high-latitude habitats (Parton et al., 2007). Climate, decomposer groups and intrinsic litter traits affecting lability are all important in influencing variation in litter decomposition rates at large spatial scales (Aerts, 1997; Bradford et al., 2016; Silver & Miya, 2001; Waring, 2012). Previous studies of litter lability have mostly been of two types. The first compared litter from different plant species that was incubated at the same site, thereby exploring the effects of plant species traits on litter

decomposition. These studies have found a 10.5-fold difference in decomposition rates among species (Cornwell et al., 2008). The second focused on the effects of climatic variables on litter decomposition, and found that the same litter incubated at different sites varied 5.5-fold in decomposition rates (e.g. Currie et al., 2010; Parton et al., 2007). Here, by collecting leaf litter of the same plant species from different latitudes and incubating them at a single site, we add to a small body of studies representing a third type of decomposition experiment exploring how intraspecific variation affects decomposition (e.g. Lecerf & Chauvet, 2008; LeRoy et al., 2006). To do this, we collected leaf litter of the same plant species from different latitudes and incubating them at a single site. We found a 1.5-fold latitudinal variation in litter lability within a species. Although these various types of studies have identified the importance of different single drivers on decomposition, ultimately, in nature, in situ decomposition rates depend on how litter lability, climate and decomposers interact.

In relation to question about the difference in decomposition rates between invasive and native species, we found that the leaf litter of exotic *S. alterniflora* decomposed faster than that of the native *P. australis* regardless of the latitude origin. Although we only compared two species, this pattern is consistent with previous comparisons of native and exotic species, in which litter of exotics tended to decompose more rapidly than that of natives (Bray et al., 2017; Liao et al., 2008). This difference between native and exotic species is likely due to variation in their leaf traits. Invasive plants may have low concentrations of chemical defences because they experience lower herbivore pressure in the novel habitats due to the enemy release (Keane & Crawley, 2002). Invasive species may also have high nutrient levels since they usually have higher competitive abilities for getting nutrients than the natives (Blossey & Notzold, 1995; Funk, 2005; Rothstein et al., 2004). These differences in leaf traits, and especially higher foliar nutrient levels and lower chemical defence levels, are generally thought to promote faster decomposition in exotics than natives (Braun et al., 2019; Liao et al., 2008; Rothstein et al., 2004).

The faster cycling of nutrients from the litter of exotic plants may help exotic species invade new habitats (Aerts et al., 2017; Ashton et al., 2005). For example, exotic *Typha x glauca* does not replace native species through resource competition, but its litter changes the soil in ways that benefit itself, with a positive feedback that facilitates its own further invasion (Farrer & Goldberg, 2009). Similarly, the rapid decomposition of *S. alterniflora* litter has been suggested to facilitate its invasion along the Chinese coast (Liao et al., 2008), but the definitive experiments testing this hypothesis have not been done.

One possible caveat for our study is that both decomposition experiments involved burying leaf litter, whereas in nature most of the leaf litter of both species decomposes while leaves are still attached to stems, or on the soil surface. Some leaf litter, especially of the native *P. australis*, however, does fall to the soil surface and become buried by sediment, so our methodology was not completely unrealistic. Nevertheless, our intent was not to measure

actual decomposition rates in nature, but simply to provide a set of standard conditions where decomposition could be compared among species and provenances. It would be meaningful for future studies to use surface-deployed litter bags, and to extend our work by deploying litter bags at multiple common gardens across latitude.

Another potential caveat is that our decomposition experiments were relatively short (88–94 days). This time period was sufficient for significant mass loss (on average 56% over all samples), but this loss would have represented the more labile organic material in the leaves. Whether our results would have been similar for the more recalcitrant organic matter is an open question.

We demonstrated similar latitudinal clines in litter lability for a native and an exotic plant, but the exotic has only been present in China for four decades (Liu et al., 2018; Zhang et al., 2017), raising the question of whether the cline in the exotic has a genetic basis or was produced by phenotypic plasticity. Studies of some traits (e.g. seed set) in *S. alterniflora* in China using a combination of field sampling and common garden experiments have shown that some traits that vary across latitude in China have a genetic basis, indicating strong selection in the four decades since *S. alterniflora* was introduced to China (Liu et al., 2017). For other traits (e.g. plant height), however, the latitudinal clines observed in the field disappeared in common gardens, indicating that they are produced by phenotypic plasticity. Further studies are needed to determine whether the latitudinal clines in decomposition rates and plant traits that we observed in both *S. alterniflora* and *P. australis* have a genetic basis or are the result of plastic responses to the varying environment.

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AUTHORS' CONTRIBUTIONS

J.W. and Y.Z. designed the study; Y.Z. collected litter samples and conducted the greenhouse common garden work and analysed the data; Z.L. conducted the field decomposition experiment; all authors wrote the manuscript. The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.9ghx3ffdx> (Zhang et al., 2021).

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SUPPORTING INFORMATION

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