Dynamics of litter decomposition of dieback *Phragmites* in *Spartina*-invaded salt marshes

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Abstract

Vegetation dieback can alter plant population dynamics and community structure, however, its impact on litter decomposition has been poorly understood. The litterbag method was employed to examine effects of reed dieback on litter decomposition of native *Phragmites australis* in the *Spartina alterniflora*-invaded Chinese salt marshes. Compared with healthy *Phragmites*, the initial C and N contents in leaf, sheath and stem of dieback *Phragmites* were significantly higher (for all $P < 0.001$, except N content in stem $P > 0.05$) and their initial C:N ratios were significantly lower ($P < 0.05$). Moreover, the aerial stem litter of dieback *Phragmites* decomposed significantly faster than that of healthy *Phragmites* ($F_{1,46} = 5.784$; $P < 0.05$). During the 310-day decomposition, the C:N ratio in dieback *Phragmites* was significantly lower than that in healthy *Phragmites* ($F_{1,273} = 28.510$, $P < 0.001$) and the remaining N concentrations of the two types of *Phragmites* were significantly different from each other ($F_{1,270} = 16.316$, $P < 0.001$). Only the N content in leaf tissue of dieback *Phragmites* decreased continuously, while it changed up and down in other tissues. Our results suggest the significance of integrating vegetation dieback into the ecosystem processes and the vegetation and land-surface models, as well as the management strategies on protecting the susceptible ecosystems.

Key words: dieback; *Fusarium*; litter decomposition; *Phragmites australis*; salt marsh; *Spartina alterniflora*

1. Introduction

Vegetation dieback has been observed in various ecosystems, such as stand-level dieback and sudden oak death in forests (Mueller-Dombois, 1986; Rizzo and Garbelotto, 2003), reed dieback and sudden marsh dieback in wetlands (Brix, 1999; Alber et al., 2008). This phenomenon has become more widespread under global change than ever before (Allen et al., 2010; Lloret et al., 2012). Recently, much progress has been made in exploring the mechanisms of vegetation dieback, including the effects of abiotic environment (e.g., Armstrong and Armstrong, 2001; Duarte et al., 2013), biotic factors (e.g., Ahmad et al., 2013; Li et al., 2014) and combined effects associated with human activities (e.g., Altieri et al., 2012; Coverdale et al., 2013). However, the major impacts of vegetation dieback on ecosystems have been far less recognized, although its consequences (e.g., economic and social) are receiving increasing attention (Silliman et al., 2005).

Vegetation dieback can not only affect plant population dynamics through disturbing individual growth and recovery (Swiecki and Bernhardt, 2002; Altieri et al., 2013) and changing soil properties critical to plant survival (Crawford and Stone, 2015), but also change community composition and structure in many different ways, e.g., regulation of species interactions (Hudson and Greenman, 1998; Li et al., 2013) and trophic cascade (Rizzo and Garbelotto, 2003; Altieri et al., 2013). Lately, the results from comparative tests on differences of organic and inorganic components in soil and water at dieback and healthy sites show that vegetation dieback is likely to alter ecosystem processes (Ágoston-szabó and Dinka, 2009). However, experimental

evidence has been still scarce.

Salt marshes providing important ecosystem services have been seriously threatened by vegetation dieback (Alber et al., 2008). The Dongtan wetland in the Yangtze River estuary has recently experienced reed (*Phragmites australis*, hereafter referred as to *Phragmites*) dieback since 2008. Reed dieback leads to the rapid death of *Phragmites* from the top downwards at the end of vegetative growth, which blocks the translocation of photosynthetic production to below-ground tissues, possibly resulting in more carbon retention in above-ground tissues. Moreover, such sudden death of the young tissues at the top can still retain available nutrients (e.g., nitrogen) in the dead tissues, which causes a higher N content in dieback tissues than in senescent ones. Accordingly, litter quality of *Phragmites* may be altered due to the dieback event. Nevertheless, the impacts of reed dieback on litter decomposition have been poorly understood.

Litter decomposition is a pivotal ecosystem process closely tied to carbon transformation and nutrient cycling (Begr and McClaugherty, 2008). It is controlled not only by litter quality but also by characteristics of microbial community and physical environment (Begr and McClaugherty, 2008; LeRoy et al., 2014; Rinkes et al., 2014). In the Yangtze River estuary, the native *Phragmites* communities have been seriously invaded by non-native *Spartina alterniflora* (hereafter referred as to *Spartina*), which has altered the local litter pools and litter decomposition (Liao et al., 2008). Recently, the impacts of *Spartina* invasion on the ecosystem functioning in the Dongtan wetland may become more notable due to the occurrence of reed dieback

which is possibly related to an endophytic fungus *Fusarium palustre* of the invasive *Spartina* (Li et al., 2014). As the reed dieback has continued to spread and accelerated the local community succession via reducing the relative competitive advantage of native *Phragmites* but favoring *Spartina* invasion (Li et al., 2013), studies dealing with the responses of local ecosystem processes to invasion are needed to consider the role of reed dieback. Here, we hypothesized that reed dieback may alter the litter decomposition of native *Phragmites* in the salt marshes invaded by *Spartina*. To test this hypothesis, we addressed the following questions: i) is the litter quality of dieback *Phragmites* different from that of healthy *Phragmites*? ii) Does the litter of dieback *Phragmites* decompose differently from healthy *Phragmites*?

2. Materials and Methods

2.1. Study site

This study was conducted in Dongtan wetland on Chongming Island in the Yangtze River estuary, Shanghai, China (31°25'-31°38'N, 121°50'-122°05'E), which is recognized as a 'Wetland of International Importance' and is set aside as a National Nature Reserve for migratory birds. The island has a northern subtropical monsoon climate with the mean annual temperature of 15.3 °C and the average annual precipitation of 1,022 mm, most of which occurs in the summer (Xu and Zhao, 2005). The whole wetland encompasses a total area of 32,600 ha and consists of shallow water, muddy flats and salt marshes that are dominated by native sedges (e.g., *Scirpus* spp. and *Carex* spp.) and *Phragmites australis*, and non-native *Spartina alterniflora*.

Spartina invades or surrounds native *Phragmites* communities, forming two-species mixtures or mosaics of their pure patches in the salt marshes where *Phragmites* has been experiencing dieback (Li et al., 2013).

2.2. Sampling and litterbag preparation

The aboveground litter samples of dieback *Phragmites* in dieback patches and of healthy *Phragmites* in its pure communities were separately collected on November 24th and on December 24th, 2011, given that the two types of *Phragmites* wilted in early September and mid October, respectively. Senescent *Phragmites* shoots with leaves ready to fall were cut off at ground level. Dieback (or healthy) *Phragmites* litter was collected from a variety of dieback (or healthy) patches in the Dongtan wetland and then mixed. All litter samples were separated into leaf blade, leaf sheath and stem, and carefully washed with tap water immediately after collection. They were cut into 5 cm pieces and oven-dried at 50 °C to constant weight. Random subsamples of the oven-dried leaves, sheathes and stems were used to estimate the initial C and N contents. These subsamples were smashed with a Wiley mill, ground into powder and sieved (mesh size 0.15 mm). The initial C and N contents of litter were analyzed by NC Soil Analyzer (Flash EA 1112 Series; Thermo Finnigan, Elk Grove Village, IL).

The nylon litterbag of 20 cm × 25 cm with a mesh size of 0.3 mm × 0.3 mm was used to quantify litter decomposition. The mesh size was small enough to reduce the physical loss of litter and the intervention of macro-invertebrates (e.g., crabs, spiders

and snails), but water, sediments and microbes could pass through the litterbags freely. Each litter sample of 10.1 g was individually confined in the litterbag which was sealed with nylon strings. All samples were replicated four times and a total of 384 litterbags were prepared.

2.3. Litter decomposition

In order to minimize the effects of environmental heterogeneity on litter decomposition, two types of community with three replicates (six plots in total) which possessed similar environmental variables (e.g., oxidation reduction potential, electric conductivity, pH, water content and light intensity) (Li et al., 2013) were established at the same elevation in February 13th, 2012, including the dieback community with dieback *Phragmites* and healthy *Spartina*, and the healthy community with both healthy *Phragmites* and *Spartina*. The nearest distance between the plots was c. 20 m which was distant enough to minimize the spatial autocorrelation between these plots. A few crabs, spiders and snails were found in all the plots. The dieback and healthy *Phragmites* litterbags were accordingly laid in the dieback and healthy communities. To fix litterbags for aerial decomposition in each plot, two 1.5 m long bamboo rods with a distance of 1.5 m were inserted into the sediment, on which one 1.7 m long bamboo rod with 1.5 m height above the sediment surface was fixed. A nylon string bound with litterbags was tied onto the two 1.5 m long bamboo rods at ground level in each plot and used for surficial decomposition.

Litterbags of leaf, sheath and stem in the air or on the surface in each plot were

randomly collected on March 4th, March 24th, April 14th, May 3rd, June 13th, August 3rd, October 3rd and December 20th, which means that litters experienced 20, 40, 60, 80, 120, 170, 230, 310 days' decomposition. Reed dieback in the dieback communities started to occur in July (Fig. 1). The litterbags of healthy *Phragmites* stem were lost for unknown reason at the last sampling time. Retrieved litters were carefully rinsed with tap water and collected in clean paper bags, and then oven-dried at 50 °C to constant weight. The remaining dry mass was measured at each sampling time and the litter mass remaining (%) was calculated as the percentage of the initial dry mass. The amounts at the beginning of the experiment were considered as original values (100%). After the mass loss was measured, these litters with three replicates were used to determine the C and N contents. The litter C or N remaining (%) were expressed as the percentage of the initial C or N contents.

2.4. Statistical analysis

Expectations of normality and statistical analyses were performed in R software (version 2.12.2, R Development Core Team, 2011). Data of initial C, N contents and C:N ratios were cubic-root transformed to meet normality and homogeneity. Analysis of variance (ANOVA) and a post hoc Tukey's HSD test were used to examine the effects of two types of *Phragmites* (i.e., dieback and healthy *Phragmites*) and three tissues (i.e., leaf, sheath and stem) on initial C, N contents and C:N ratios. Analysis of covariance (ANCOVA) with time as a covariate and a post hoc Tukey's HSD test were applied to examine the effects of two types of *Phragmites*, three tissues and two

positions (i.e., in the air and on the soil surface) on the remaining litter mass, litter C and N concentrations and C:N ratio.

The decomposition rate (k) was determined by an exponential equation as

$$M_t = M_0 \times e^{-kt} \quad (1)$$

where M_t is the mass remaining at time t , M_0 is the initial mass before decomposition and k (year⁻¹) is the exponential decomposition constant (Graca et al., 2005). The exponential decay equation can be rewritten as

$$\ln M_t = -kt + \ln M_0 \quad (2)$$

Eq. 2 was used to fit decomposition data. The slope of the regression line was the decomposition constant k . Linear regression model was used to calculate the value of k and two way ANOVA was used to estimate the difference of k between dieback and healthy *Phragmites*.

3. Results

3.1. Initial litter quality

The initial C contents in leaf, sheath and stem of dieback *Phragmites* were significantly higher than those of healthy *Phragmites* (Table 1, 2; leaf: $P<0.001$; sheath: $P<0.001$; stem: $P=0.013$). The initial N contents in leaf and sheath of dieback *Phragmites* were also significantly higher than those of healthy *Phragmites* (Table 1, 2; leaf: $P<0.001$; sheath: $P=0.0043$), except that in stem ($P=0.090$). Compared with those of healthy *Phragmites*, the initial C:N ratios in the three tissues of dieback *Phragmites* were significantly lower (Table 1, 2; leaf: $P<0.001$; sheath: $P=0.025$; stem:

$P=0.042$).

3.2. Litter decomposition

Changes in dry mass of dieback and healthy *Phragmites* in terms of leaf, sheath and stem were presented in Figure 2. The data of litter decomposition are fit well to Eq. 2 (Table 1). The two types of *Phragmites* decomposed significantly faster in the air than on the soil surface (for all, $P<0.001$). The stem of dieback *Phragmites* decomposed faster than that of healthy *Phragmites* in the air (Table 1; $F_{1,46}=5.784$; $P=0.020$) but not on the soil surface ($F_{1,40}=2.297$; $P=0.138$). However, there was no significant difference of decomposition rates of leaf and sheath between the two types of *Phragmites* (Table 1; for all, $P>0.05$).

During the decomposition, the litter C contents of dieback and healthy *Phragmites* in the air and on the soil surface decreased continuously. The three tissues of the two types of *Phragmites* decomposed differently at the two positions (Table 2; $F_{2,274}=29.93$, $P<0.001$). The remaining C concentrations in all tissues on the soil surface were lower than those in the air (for all, $P<0.001$). However, no significant difference of the remaining C concentration between dieback and healthy *Phragmites* was found ($F_{1,262}=1.268$, $P=0.261$).

The remaining N concentration in dieback *Phragmites* was significantly different from that in healthy *Phragmites* (Table 2; $F_{1,270}=16.316$, $P<0.001$). The remaining N concentration in leaf of dieback *Phragmites* was lower than that of healthy *Phragmites* (Fig. 3; $P<0.001$, but $P>0.05$ for both in sheath and stem). The remaining

N concentrations in leaf litter of dieback *Phragmites* continuously decreased at the two decomposition positions, however, the remaining N concentrations of the aerial and surficial leaf litter of healthy *Phragmites* increased to $133.2 \pm 4.73\%$ (means $\pm$ se) after 120 days and $117.5 \pm 2.26\%$ after 20 days, respectively (Fig. 3). Moreover, the sheath and stem remaining N concentrations of the two types of *Phragmites* changed up and down during aerial and surficial decomposition (Fig. 3).

Compared with healthy *Phragmites*, the remaining C:N ratio in dieback *Phragmites* was significantly lower (Table 2; $F_{1,273}=28.510$, $P<0.001$). The remaining C:N ratio in leaf was the lowest and that in stem was the highest (Table 2; $F_{1,273}=337.639$, $P<0.001$). The remaining C:N ratios of stem were different at the two positions ($P<0.001$).

4. Discussion

This study demonstrated that dieback *Phragmites* differed from healthy *Phragmites* not only in initial litter quality, but also in the litter decomposition processes. Litter quality is a critical determinant of decomposition rate at a regional scale or smaller spatial scales (Aerts, 1997). Generally, plant tissues with higher initial N concentration (Witkowski, 1991; Rothstein et al., 2004) or lower C:N ratio (Enríquez et al., 1993; Gholz et al., 2000) are believed to have greater decomposition rates. Our findings showed that the litter tissues of dieback *Phragmites* contained higher initial C and N contents but lower initial C:N ratios than those of healthy *Phragmites*, which should result in different decomposition rates. However, only stem litter of dieback

Phragmites decomposed faster than healthy *Phragmites*, while there was no significant difference of decomposition rates in leaf and sheath between the two types of *Phragmites*. Wang et al. (2014) reported that litter quality played an important role in early stage decomposition. Besides litter quality, the decomposition rate is determined by decomposers and climate (Aerts, 1997; Chapin et al., 2012). Accordingly, the decomposition rates in this study may also be strongly affected by microbial decomposers, considering that the environmental conditions between dieback and healthy plots were similar. The reed dieback here has been found to be associated with *Fusarium* infection (Li et al., 2014), which probably changes the plant physiological (e.g., pH and water content) (Zheng, 2007) and biochemical traits (e.g., releasing toxins) (Shi et al., 1997; Marike and Wilhelm, 2011), and may not favor colonization of other saprophytes that are responsible for decomposition (Yu, 2010). As we observed in the field, the severity of dieback on leaf and sheath was greater than that on stem, suggesting that the leaf and sheath quality of dieback *Phragmites* may be changed to the extent that limits the litter decomposition. The experiment did not include reciprocal incubation of litter, which is the limitation of this study because it was impossible to separate the impacts of litter quality from abiotic environmental conditions (e.g., available N and other nutrients) and biotic factors (e.g., microbial decomposer communities) on decomposition processes. However, efforts were deliberately concentrated on testing whether there was any significant difference of litter decomposition between dieback and healthy *Phragmites*.

The reed dieback might alter the litter nitrogen dynamics as a result of the higher

initial N contents and lower remaining N contents at the end of decomposition as well as the lower C:N ratios all along in dieback *Phragmites*, compared with those of healthy *Phragmites*. The loss of N from dieback *Phragmites* provides a possible explanation for the biomass increase of non-native *Spartina* in patches with co-existing dieback *Phragmites* (Li et al., 2013), which is likely to promote the invader's growth and spread (Minchinton and Bertness, 2003; Tyler et al., 2007). The loss of N and the lower C:N ratio as well as the higher initial C content in dieback *Phragmites* leaf indicated that the C content changed considerably during the decomposition, suggesting that reed dieback might also affect carbon turnover. Considering that reed dieback can potentially reduce the C and N stocks in tissues in one growing season due to its negative impacts on the growth of *Phragmites* (Li et al., 2013), whether reed dieback changes the C and N pools in the long term is still unknown.

Theoretically, the net N release in the decomposition process is mainly affected by the litter C:N ratio or N content (Frey et al., 2000; Parton et al., 2007). Berg and McClaugherty (1987) find that the net N release occurs when the C:N ratio is between 20 and 80. Berg and Laskowski (2006) and Moore et al. (2006) have reported that the critical condition for the net N release is that the C:N ratio was between 20 and 30, and the initial N content was 20 mg/g. Parton et al. (2007) also suggest that N is released when the C:N ratio is below 40. In this case, the C:N ratios were in the range of 32.20 (± 0.42) to 105.91 (± 6.18) and the lowest C:N ratio was in leaf litter of dieback *Phragmites* (Fig. 4), indicating that the net N release possibly occurred in the

leaf litter of dieback *Phragmites*. Interestingly, the epiphytic N fixation has been observed in leaf, sheath and stem of healthy *Phragmites* during the decomposition, probably due to the colonization of N-fixation organisms (Rice and Tenore, 1981; Bowden, 1986), which was not found in leaf and surficial sheath of dieback *Phragmites*. This might be associated with the higher initial N content and the unsuitable microenvironment of these tissues related to infection of the endophytic fungus *F. palustre* (Li et al., 2014).

While previous studies have reported that reed dieback can change plant community composition and structure in the invaded salt marsh (Li et al., 2013), this study further showed that the dieback caused by *Spartina* invasion also altered the litter quality and litter decomposition of the native *Phragmites*. Although these results came from the short-term investigation, they implicate the significance of reed dieback in affecting vegetation cover and nutrient cycling in the salt marsh. Vegetation dieback such as reed dieback in this case and forest dieback in other parts of the world (e.g., Anderegg et al., 2012) can change the vegetation cover which can significantly affect the climate system. Thus, this study also provides the guidance on the vegetation and land-surface models which might have neglected potential changes in vegetation cover before. At present, plants may become more vulnerable and susceptible to the human-driven global changes (e.g., climate warming, biological invasion and pathogen disease), therefore, it is necessary to consider vegetation dieback from an ecological perspective to predict the future changes of fragile ecosystems and manage the ecosystems.

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Figure legends

Figure 1 The decomposing litters in the dieback community suffering reed dieback (A) and the healthy community (B). Photos were taken on July 3rd, 2012.

Figure 2 Litter mass remaining (%) of leaf, sheath and stem of dieback (D) and healthy (H) *Phragmites* during aerial and surficial decomposition. The vertical bars represent standard errors (n=3).

Figure 3 Litter nitrogen remaining (% initial) of leaf, sheath and stem of dieback (D) and healthy (H) *Phragmites* during aerial and surficial decomposition. The vertical bars represent standard errors (n=3).

Figure 4 C:N ratio changes of leaf, sheath and stem of dieback (D) and healthy (H) *Phragmites* during aerial and surficial decomposition. The vertical bars represent standard error (n=3).

Table 1 Initial litter C and N contents, C:N ratios in leaf, sheath and stem, and decomposition rate per year (k) of dieback and healthy *Phragmites*. The values of all the parameters represent means $\pm$ se (n=3). Different letters indicate significant differences within one tissue type ($P<0.05$).

Plant	Tissue	Initial C content	Initial N content	Initial C:N	Aerial		Surficial	
		(mg/g)	(mg/g)	ratio	k	R^2	k	R^2
Dieback	Leaf	41.370 $\pm$ 0.0381 ^a	1.285 $\pm$ 0.0161 ^a	32.204 $\pm$ 0.418 ^a	0.461 $\pm$ 0.035 ^a	0.961	1.897 $\pm$ 0.216 ^a	0.917
	Sheath	39.479 $\pm$ 0.107 ^a	0.822 $\pm$ 0.056 ^a	48.503 $\pm$ 3.545 ^a	0.306 $\pm$ 0.024 ^a	0.960	1.491 $\pm$ 0.127 ^a	0.952
	Stem	43.083 $\pm$ 0.114 ^a	0.490 $\pm$ 0.0160 ^a	88.089 $\pm$ 2.989 ^a	0.212 $\pm$ 0.010 ^a	0.984	0.566 $\pm$ 0.043 ^a	0.962
Health	Leaf	39.695 $\pm$ 0.133 ^b	0.797 $\pm$ 0.018 ^b	49.858 $\pm$ 1.204 ^b	0.460 $\pm$ 0.028 ^a	0.975	1.998 $\pm$ 0.172 ^a	0.952
	Sheath	38.456 $\pm$ 0.036 ^b	0.625 $\pm$ 0.004 ^b	61.534 $\pm$ 0.417 ^b	0.343 $\pm$ 0.015 ^a	0.987	1.503 $\pm$ 0.148 ^a	0.936
	Stem	42.539 $\pm$ 0.050 ^b	0.404 $\pm$ 0.022 ^a	105.905 $\pm$ 6.176 ^b	0.192 $\pm$ 0.008 ^b	0.989	0.428 $\pm$ 0.052 ^a	0.913

Table 2 ANOVA and ANCOVA with time as a covariate of litter decomposition parameters of dieback and healthy *Phragmites*. ^a After cubic-root transformation. *df* shows the numerator degrees of freedom/denominator degrees of freedom. ns, not significant. * $P<0.05$; ** $P<0.01$; *** $P<0.001$.

Parameters	Plant		Tissue		Position		Plant × Tissue		Plant × Position		Tissue × Position		Covariate	
	<i>df</i>	<i>F</i>	<i>df</i>	<i>F</i>	<i>df</i>	<i>F</i>	<i>df</i>	<i>F</i>	<i>df</i>	<i>F</i>	<i>df</i>	<i>F</i>	<i>df</i>	<i>F</i>
<i>Initial</i> ^a														
Carbon content	1/12	222.920 ***	2/12	935.550 ***	-	-	2/12	21.040 ***	-	-	-	-	-	-
Nitrogen content	1/12	104.110 ***	2/12	220.290 ***	-	-	2/12	12.070 **	-	-	-	-	-	-
C:N ratio	1/12	59.845 ***	2/12	214.241 ***	-	-	2/12	2.196 ^{ns}	-	-	-	-	-	-
<i>Remaining</i>														
litter mass	1/264	0.162 ^{ns}	2/264	16.911 ***	1/264	27.976 ***	2/264	0.560 ^{ns}	1/264	0.003 ^{ns}	2/264	1.323 ^{ns}	1/264	37.242 ***
Carbon concentration	1/262	1.268 ^{ns}	2/262	151.388 ***	1/262	586.412 ***	2/262	0.149 ^{ns}	1/262	0.488 ^{ns}	2/262	29.996 ***	1/262	2332.399 ***
Nitrogen concentration	1/262	16.781 ***	2/262	27.246 ***	1/262	2.215 ^{ns}	2/262	6.202 **	1/262	0.152 ^{ns}	2/262	17.684 ***	1/262	32.665 ***
C:N ratio	1/262	28.422 ***	2/262	336.597 ***	1/262	33.948 ***	2/262	2.565 ^{ns}	1/262	0.400 ^{ns}	2/262	5.322 **	1/262	42.253 ***