1 **Interactive effects of elevated CO₂ and nitrogen deposition accelerate**
2 **litter decomposition cycles of invasive tree (*Triadica sebifera*)**

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12 **Running head:** Combined CO₂ and N effects on litter cycling

ABSTRACT

Litter decomposition is an important component of forest nutrient recycling potentially impacted by elevated CO₂, nitrogen (N) deposition, and biological invasions. Each can affect decomposition indirectly via changes in litter quantity, litter quality, and soils, which may increase or offset direct effects of elevated CO₂ on decomposition. To date, no study has examined how elevated CO₂ and N deposition interact to determine exotic plant litter cycling or the importance of variation among native and invasive populations of exotic plants for these effects.

In this study, we examine elevated CO₂ and N deposition effects on litter production and decomposition of native (China) and invasive (USA) populations of tallow tree (*Triadica sebifera*). First, we investigated litter production in greenhouse chambers. Then, we conducted three additional experiments using experimentally created litter and soils to examine CO₂ and N effects on litter decomposition via changes in litter quality, soils, and atmospheric environment.

Elevated CO₂ and N deposition increased litter production with their combined effects more than additive. Nitrogen deposition increased litter production of native populations more than that of invasive populations. Litter produced in elevated CO₂ had higher C:N and decomposed more slowly than litter produced in ambient CO₂ but N deposition weakened these effects. Decomposition was slower in soils with histories of N deposition or plant association. Elevated CO₂ had no direct effects on litter decomposition.

The net effect of elevated CO₂ alone on litter decomposition throughputs was

35 negative for invasive populations due to strong reductions in litter decomposability.

36 The net effect of elevated CO₂ and N deposition together on litter throughputs was

37 positive, especially for native populations due to strong litter production increases.

38 Results suggest that elevated CO₂ and N deposition impact litter cycling primarily

39 through changes in litter quantity and quality with smaller effects via soils. Elevated

40 CO₂ and N deposition had strong positive effects on litter throughputs together due to

41 synergistic positive effects on litter production and offsetting effects on

42 decomposability. Although elevated CO₂ and N deposition had consistent effects on

43 native and invasive populations, the relative magnitudes of their effects on litter

44 quantity and quality impacted litter cycling, suggesting the importance of considering

45 plant trait variation in an overall estimation of global change effects on nutrient

46 dynamics in forests and other ecosystems.

47 *Keywords:* EICA, global change, plant invasions, plant–soil interactions, soil effects,

48 structural equation model

1. Introduction

Increasing atmospheric carbon dioxide (CO₂), anthropogenic nitrogen (N) deposition, and exotic plant invasions are aspects of global change threatening biodiversity and functioning of forests and other ecosystems (Vitousek et al., 1996; Mack et al., 2000; Luo et al., 2006; Bellard et al., 2013). Elevated CO₂ provides more carbon (C) for plant photosynthesis and soil N availability can be directly increased by N deposition. Plant traits such as growth rates, secondary metabolism, and interactions with the soil biota vary between exotic and native species and among native and invasive populations of exotic species (Kemp et al., 1994; Bradford et al., 2007; Liu et al., 2015). Therefore, the effects of elevated CO₂ and N deposition on litter production and decomposition may vary as well. However, no study has examined how elevated CO₂ and N deposition interact to determine exotic plant litter cycling or the importance of variation among native and invasive populations of exotic plants for these effects.

Some successful exotic invaders may have a competitive advantage over native plants in their introduced ranges in part because they experience little herbivore attack and so reduce their chemical defenses and increase their growth rates through an evolutionary response (Blossey and Nötzold, 1995). These traits may not only be important for their invasion success but also for their potential impacts on ecosystem processes (Genton et al., 2005; Zou et al., 2007; Li et al., 2014; Kleunen et al., 2015). For instance, elevated CO₂ often enhances plant growth as CO₂ availability may limit photosynthesis when soil resources are abundant, especially for plants with high

maximal growth rates (Cotrufo et al., 1998; Norby et al., 2001). But litter quality may also vary with maximal growth rate so that CO₂ affects not only invasion success but also litter production and litter quality (Cotrufo et al., 1998; Norby et al., 2001). But, to date, there have only been two studies that compared growth of exotic plants from invasive and native populations in ambient and elevated CO₂ and neither included replicate populations, which limits the strength of conclusions about genetic variation in traits between ranges. In the first study with the herbaceous invader *Eupatorium adenophorum*, plants from the invasive population grew faster than ones from the native population in both ambient and elevated CO₂ (Lei et al., 2011). In the second study with the grass *Phragmites australis* that also included N deposition, plants from the native population had a larger percent increase in growth with CO₂ and/or N addition but plants from the invasive population grew larger than ones from the native population in all conditions (Mozdzer and Megonigal, 2012). Therefore, effects of elevated CO₂ could potentially be stronger in the presence of invasive populations, which could create a greater quantity of litter. This litter may potentially be different quality for decomposition as well but neither study examined litter decomposition. However, plant growth responses to elevated CO₂ may be limited by N availability (Luo et al., 2004; Hu et al., 2006), so it is important to include N deposition in studies of CO₂ impacts on litter cycling.

Elevated CO₂ and N deposition will likely alter litter quality (e.g., N concentration, C:N ratio and lignin:N ratio, here estimated as C:N), impacting decomposition rates via these litter mediated effects. Indeed, elevated CO₂ can decrease N concentrations

in senesced leaves, which generally lead to decreased litter quality and hence slow litter decomposition rates (Ball, 1997; Cotrufo et al., 1998; Norby et al., 2001). However, N deposition might impose opposing positive effects on litter quality, potentially increasing N stocks in plant litter and litter decomposition rates (Lei et al., 2012). In part due to their rapid growth rates, foliage of plants from invasive populations may have higher C:N (Wang et al., 2012) which could reduce decomposability of their litter compared to that produced by plants from native populations. However, selection for lower chemical defense production in the absence of specialist herbivores may lead to foliage with lower concentrations of secondary compounds such as tannins in invasive populations (Wang et al., 2012) which could increase decomposability of their litter compared to that produced by plants from native populations. Therefore, the decomposition rate of litter produced by plants grown with elevated CO₂ and N deposition will likely reflect the balance between these two global change factors and population variation in traits that impact litter quality.

In addition, elevated CO₂, N deposition, and variation in plant traits can impact litter decomposition by changing soil environmental factors and the soil biota. For example, C allocated belowground and soil acidity could be altered by elevated CO₂ and N deposition, potentially changing soil C pools and microbial activities (Jones, 1998; Kandeler et al., 1998), both of which are positively correlated with litter decomposition. Invasive and native populations of exotic species may also differ in their impacts on soil characteristics that may impact litter decomposition. For instance,

invasive *Triadica sebifera* populations create more biologically active soils that mineralize more N than soils associated with *T. sebifera* plants from native populations (Zou et al., 2006; Zhang et al., 2013). In addition, plants from invasive *T. sebifera* populations have higher rates of mycorrhizal association than plants from native *T. sebifera* populations which may impact soil physical and chemical properties (Yang et al., 2015). Moreover, litter and soil C:N may interact to determine litter decomposition rates (Finn et al., 2015). Because N deposition will increase soil N availability this may alter soil C:N and hence the composition of litter decomposer communities and litter decomposition rates (Ågren et al., 2013; Finn et al., 2015). Therefore, elevated CO₂ and N deposition may alter litter decomposition rates via soil mediated effects that may vary among populations of plants.

In addition to indirect effects of elevated CO₂ and/or N deposition on litter cycling via changes in the quantity and quality of litter produced or soil physical and biotic properties, CO₂ can affect litter decomposition directly via atmospheric effects (Angelis et al., 2000; Carney et al., 2007; Liu et al., 2015). However, no study reports the contributions of these different effects to the net impact of CO₂ and N deposition on litter cycling. Moreover, no study reports the interactive effects of plant genetic variation, elevated CO₂, and N deposition on the performance of an exotic plant species, and subsequent litter decomposition, despite its importance for understanding the potential impacts of elevated CO₂ and N deposition on ecosystem C and N processes.

Here, we conducted experiments in replicate chambers to explore the effects of

elevated CO₂, N deposition, and their interactions on the morphological traits, litter production, and litter decomposition of native and invasive populations of *T. sebifera*. We hypothesized that: (1) Invasive populations will have higher growth rates, lower root:shoot ratio (R:S), and higher foliar litter production than native populations, especially with elevated CO₂ and N deposition. (2) Invasive populations will produce lower quality litter and cultivate soils that enhance litter decomposition. (3) The net effects of elevated CO₂ and N deposition alone and in combination on litter production and decomposition will be larger for invasive versus native populations.

2. Material and methods

2.1. Seed collections

Triadica sebifera (Chinese tallow tree) is aggressively invading forests, grasslands, and wetlands in the southeastern USA (Bruce et al., 1997; Henkel et al., 2016). It was first introduced into Georgia in the late 18th century from China as a potential oil seed crop and subsequently introduced along the Gulf coast (Bruce et al., 1997). We hand collected *T. sebifera* seeds from eight populations in China (native populations) and eight in the USA (invasive populations) in November and December 2012 (Table S1). In each population, we collected seeds from at least five trees. Seed masses of populations were independent of population origin ($P=0.16$) which suggests that potential seed provisioning effects on seedling performance were not strong. We removed the waxy seed coat by soaking in water with lab detergent, surface sterilized seeds with a 10% bleach solution, and we planted seeds in plastic pots filled with soil

sterilized in an autoclave. We placed pots in a greenhouse at Rice University (Houston, TX) where all the experiments took place.

2.2 Experiments

In the first experiment, we investigated effects of elevated CO₂ and N deposition on litter production of native (China) and invasive (USA) populations of *T. sebifera* in replicated greenhouse chambers. Then, we conducted three additional experiments using experimentally created litter and soils to examine CO₂ and N effects on litter decomposition via changes in litter decomposability, soils, and atmospheric environment. Finally, we used structural equation modelling (SEM) to examine the overall effects of CO₂, N deposition, and variation among populations of *T. sebifera* on litter cycling.

2.3. Growth experiment

We randomly assigned 16 chambers (1 m × 1 m × 1.2 m tall) to ambient (~400 ppm, 8 chambers) or elevated CO₂ (800 ppm, which approximates predicted levels in the year 2100, 8 chambers;(IPCC, 2014). Each chamber was covered by clear plastic that was perforated at the top to allow air to readily exit the chamber and each received air from an 8 mm inner diameter plastic tube through the bottom of the chamber. We placed two pumps outside the greenhouse (Pondmaster AP-100, Danner Manufacturing, Islandia, NY USA) to draw in air unaffected by the experiment. One pumped air into a system of pipes and tubes that supplied the 8 ambient chambers and a chamber without plants. The other pump supplied an identical set of pipes, tubes, and 9 chambers (8 experimental plus a plant free one). In the elevated CO₂ plant-free

chamber we placed a CO₂ monitor/controller (Atlas 3, Titan Controls, Vancouver, WA USA) that regulated a valve that injected CO₂ from a compressed gas cylinder such that the air supply was kept at 800 ppm CO₂. Chambers had approximately one air change per hour. Each chamber had four racks for holding containers (D20T, Stuewe & Sons, Corvallis, OR, USA).

For each chamber, we filled thirty-four 656 ml deepots (D40, Stuewe & Sons) with soil collected from a recently tilled fire break at Justin Hurst Wildlife Management Area (Jones Creek, TX USA). We transplanted two seedlings from each of the eight native and eight invasive populations into 32 of the pots and left the other two with no plants. We randomly deployed seedlings within each chamber into 34 of the 80 spaces so that plants were not in adjacent locations in racks. We assigned one plant from each population, and one of the plant-free pots, to the N deposition treatment and kept the other plant of each population (and plant-free pot) as an unfertilized control. We simulated N deposition by adding NH₄NO₃ solutions at a rate of 2 g N m⁻² to pots monthly starting four weeks after transplanting and lasting for four months, which amounted to 8 g N m⁻². This rate was based on N deposition levels in *T. sebifera*'s native range which currently average around 3 g N m⁻² and are predicted to be 8 g N m⁻² in the year 2100 (Liu et al., 2013). We applied an equivalent quantity of deionized water to N control pots. In total, there were 512 pots with plants (16 chambers × 16 populations × 2 nitrogen treatments) and 32 pots without plants (2 nitrogen treatments per chamber). We kept pots well-watered and hand weeded them throughout the experiment.

At the end of the experiment in October 2013, we cut plants at ground level and separated stems and leaves. We removed soil from the pots, took a soil sample from each which was stored at 4°C in the dark, and then gently washed roots from the soil. We air dried plant samples to constant weight to obtain dry litter mass.

We ground litter sub-samples for C and N estimation. We analyzed three samples per each of the 64 combinations of population×CO₂×fertilization (N=192). We combined samples of the same treatment combination among chambers. We then analyzed samples for C and N content by a CNS elemental analyzer (Variomax CNS Analyser, Elementar GmbH, Hanau, Germany; Zhang *et al.*, 2014).

Because we manipulated CO₂ in multiple replicated chambers and had multiple plants in each chamber that received an N deposition treatment, our design was split-plot with CO₂ as the whole-plot factor and simulated N deposition, population origin, and interactions as split-plot factors. We used mixed model ANOVAs (Proc mixed in SAS 9.4) to determine the responses of mass, R:S, foliar C:N, and height to the whole-plot factor CO₂ treatment and the split-plot factors fertilization, population origin, and interactions in the growth experiment. We included chamber (CO₂) as the whole-plot error (except for foliar C:N for which we had to pool samples among chambers). We included population (origin) as a random effect in these and other analyses to test for effects of origin. For significant terms with more than two levels, we used adjusted means partial difference tests to examine differences among treatment means. Data met the assumptions of normality and homogeneity of variances.

2.4. Soil mediated effects on decomposition experiment

To study the effects of elevated CO₂, N deposition, and plant population origin on litter decomposition via changes in soil characteristics, we placed randomly selected leaves from pots in the growth experiment into a petri dish containing soil from a single pot in that experiment (including plant-free pots so that there were 544 dishes). This design with a constant amount of an average litter but soils from individual pots allowed us to examine effects of CO₂ and N deposition via soil effects independent from their effects via quantity and quality of litter produced.

We placed dishes in ambient CO₂ chambers (racks had been cleaned and the plastic covering and tubing had been replaced after the growth experiment). Litter samples were ~0.8g of leaves placed on nylon mesh laid on the soils. During decomposition, we maintained soil moisture by weighing the dishes at least every three days and spraying them with deionized water to maintain constant mass. We retrieved half the samples after one month and the rest after two months of decomposition except dishes from bare soil plots which were only retrieved at the second time. For each retrieve, we carefully collected litter from the mesh, cleaned soil off, dried litter and weighed it. We estimated decomposition as litter mass loss rate with time.

We first examined litter mass loss rate in an ANOVA with the fixed effects CO₂, fertilization, population origin, retrieve time, and their interactions that excluded dishes with soil from pots without plants. Then, we performed an additional ANOVA using only dishes at the second retrieve time and had plant presence, population origin nested in plant presence, CO₂, fertilization, and their interactions as fixed effects.

2.5. Litter decomposability effects on decomposition experiment

To study the effects of elevated CO₂, N deposition, and plant population origin on litter decomposition via changes in litter quality, we placed leaves from single pots in the growth experiment into petri dishes containing soil that was a mix of soils from the pots with plants in that experiment. There was not enough litter for 58 plants so there were 454 dishes in total (range 5 to 8 replicates per treatment combination). We placed dishes with litter and soil in ambient CO₂ chambers and employed the same methods as in the soil effects decomposition experiment. This design with a common soil but a constant mass of leaves from individual pots allowed us to examine effects of CO₂ and N deposition via litter quality effects independent from their effects via soils and quantity of litter produced.

We examined litter mass loss rate in an ANOVA with the fixed effects CO₂, fertilization, population origin, retrieve time, and their interactions.

2.6. Atmospheric effects on litter decomposition experiment

To study the effects of elevated CO₂ on litter decomposition via atmospheric effects, we placed randomly selected leaves from plants in the growth experiment into 128 petri dishes containing soil that was a mix of soils from the pots with plants in that experiment. We placed 8 dishes in each of the chambers used for the growth experiment. Methods followed those used for the other decomposition experiments. This design with constant amount of an average litter and a common soil allowed us to examine direct environmental effects of CO₂ independent from CO₂ effects via soils or the quantity and quality of litter produced.

We examined litter mass loss rate in an ANOVA with the fixed effects CO₂, time, and their interaction.

2.7. Structural Equation Models

We used structural equation models (SEM) to examine effects of CO₂, N fertilization, presence of plants and their population origin (separate analyses for invasive vs. native populations) on the rate of leaf litter decomposition as mass per unit time. We assumed that the overall rate of mass throughput from litter decomposition depended on litter quantity, litter quality, soil effects, and atmospheric effects as a multiplicative process. The models included: separate error terms for each variable; paths from dummy variables for CO₂, fertilization, and plant origin to litter quantity (growth experiment) and rate of litter mass loss in the litter effects experiment; paths from CO₂, fertilization, plant presence, and plant origin and rate of mass loss in the soil effects experiment; and a path from CO₂ to rate of mass loss in the atmospheric effects of experiment. We checked the fit of each model by examining chi squared values. In the first estimate of net effects, we only included significant effects in our calculations and expressed standard effect sizes compared to the unfertilized, ambient CO₂ rate. We repeated those estimates including all effects regardless of significance.

3. Results

3.1. Interactive effects of CO₂ and N on plant growth

Leaf, root and total mass, and leaf C:N all depended on CO₂, fertilization, and their

interactions (Table 1). Specifically, elevated CO₂ increased leaf, root, and total mass but the increases were significantly larger with N addition than those without N addition (leaves: +53.6% vs. +27.3%, Fig. 1A; roots: +83.5% vs. +76.1%, Fig. S1A, total: +53% vs. +46%, Fig. 2). Elevated CO₂ and fertilization each significantly increased stem mass (CO₂: +15.3%; N: +48.3%; Table S2, Fig. S2) and R:S ratio (CO₂: +43.2%; N: +11.8%; Table 1, Fig. S3). Fertilization increased height (+11.1%; Table S2; Fig. S4). Leaf C:N increased with elevated CO₂ but these increases were smaller with fertilization (Table 1; Fig. 3A).

Fertilization increased root mass (native +67.9% vs. invasive +54.7%; Fig. S1B) and leaf mass more strongly for native populations than for invasive populations (Table 1; Fig. 1A). Fertilization effects on stem mass, R:S, and height did not vary with population origin (Tables 1 and S1). Total mass varied with origin and fertilization but native and invasive populations were not significantly different in mass with or without N addition (Table 1; Fig. 2). Increases in leaf C:N with CO₂ depended on population origin but native and invasive populations did not differ significantly in either ambient or elevated CO₂ (Table 1; Fig. 3B).

3.2. Litter, soil and CO₂ atmospheric mediated effects on decomposition

Litter decomposability shown by litter mass loss rate depended on CO₂, time, and the interactions of time×fertilization, CO₂×fertilization, and CO₂×time×fertilization (Table 2; Fig. 4). Specifically, litter mass loss at the first retrieve was lower for seedlings grown in elevated CO₂ but it was only lower at the second retrieve for plants grown in elevated CO₂ without fertilization (Fig. 4).

Soil history effects on litter mass loss rate depended on time and fertilization with lower decomposition in fertilized soils (Table 2, Fig. 5). Litter mass loss was significantly greater for soils that came from pots without plants ($F_{1,251}=27.95$, $P<0.0001$) but there were significant interactions among CO₂, fertilization, and plant presence (CO₂×fert: $F_{1,251}=8.56$, $P<0.01$; plants×CO₂×fert: $F_{1,251}=8.60$, $P<0.01$). This reflected more rapid mass loss for ambient CO₂ & fertilized soils in the absence of plants but no effect of CO₂ or fertilization when plants were present (Fig. 5).

In the atmospheric effects experiment, mass remaining only depended on retrieve time (Table 2).

3.3. Structural equation modeling

The amount of leaf litter produced was increased by CO₂ and fertilization more than additively, especially for native populations (“Litter Quantity”, Fig. 6). Litter was less decomposable when plants were grown in elevated CO₂, especially for invasive populations, though this effect was not as strong when plants were fertilized (“Litter Decomposability”, Fig. 6). This mitigating effect of fertilization was stronger for native populations. The only significant effect via soils was a history of presence of plants which decreased the rate of litter loss (“Soil Effects”, Fig. 6). Elevated CO₂ did not directly impact the rate of litter mass loss (“Atmospheric Effects, Fig. 6). The overall rate of mass input to soil from litter decomposition was decreased by elevated CO₂ alone for invasive populations, weakly increased by fertilization alone, and strongly increased by CO₂ and fertilization together, especially for native populations (Fig. 5). These reflected CO₂’s weak positive effect on litter quantity and strong

negative effect on decomposability, fertilization's weak positive effect on litter quantity, and fertilization amplifying CO₂'s effect of litter quantity while weakening its effect on decomposability.

4. Discussion

This study revealed that both elevated CO₂ and N deposition increased plant growth and synergistically enhanced the growth of *T. sebifera*. However, elevated CO₂ and N addition impacted subsequent litter decomposition in opposite ways. Specifically, elevated CO₂ slowed litter decomposition by strongly decreasing litter quality, especially for invasive populations, while N attenuated this CO₂ effect. In addition, the presence of plants or N addition negatively impacted litter decomposition via soil mediated effects. The relative magnitudes, but not directions, of CO₂ and N effects varied among invasive and native populations so that the overall impacts of CO₂ and N deposition on litter cycling also varied among populations. There were no atmospheric effects of elevated CO₂ on litter decomposition.

4.1. Effects of elevated CO₂ and N on plant mass growth

Plant growth responses to elevated CO₂ and N deposition vary among plant populations. For instance, one study reported 28% and 36% increases in the mass growth of invasive and native *Eupatorium adenophorum* with elevated CO₂ (Lei et al., 2011). In another study, a native genotype of *Phragmites australis* had larger proportional mass growth responses than an invasive genotype to elevated CO₂ (+98% vs. +47%), N addition (25 g m⁻² yr⁻¹; +254% vs. +136%), or CO₂ with N (+510% vs.

+319%) though absolute growth was always higher for the invasive genotype (Mozdzer and Megonigal, 2012). But, the positive effects of elevated CO₂ or N deposition, alone or in combination, on total plant mass we observed here were smaller than those on *Phragmites* (Fig. 2). Moreover, the responses of invasive and native populations of *T. sebifera* varied less than those of the invasive population and native population of *Phragmites* (Table 1; Fig. 2). In part this may reflect limitations from the use of only a single native population and a single invasive population in the *Phragmites* study. But no *T. sebifera* population responses to CO₂ (maximum=+75%), N (maximum=+98%), or CO₂ & N (maximum=+162%) were as large as those in the *Phragmites* study and no populations in our study differed two-fold in their growth responses to elevated CO₂ (maximum difference=1.8 times), N (maximum difference=1.5 times), or CO₂ & N (maximum difference=1.5 times). We did find that for *T. sebifera* the amount of leaf litter produced, the decomposability of litter produced, and properties of soil relevant to litter decomposition, which are critical response variables for litter cycling varied with population origin in interaction with elevated CO₂ and N deposition.

As proposed by the evolution of increased competitive ability (EICA) hypothesis, exotic plants are not attacked by specialist insects and so reduce their allocation to anti-herbivore defenses, and increase their growth rate (Blossey and Nötzold, 1995). Indeed, invasive *T. sebifera* has been demonstrated to have higher rates of mycorrhizal colonization, greater N or P exploration ability, more rapid growth, higher foliar C:N, and lower R:S and so typically have greater responses to increased

soil resources than do *T. sebifera* from native populations (Siemann and Rogers, 2003; Zhang et al., 2013; Yang et al., 2015). However, in this study we found that litter production was greater for native populations with N deposition which was unexpected based on these other studies. This difference in N deposition effects on invasive vs. native *T. sebifera* populations among studies suggests that some aspects of the experimental set-up associated with the plant populations that vary across studies are important for variation in growth responses to increased soil resource availability. In addition, N deposition levels are higher on average in the native range of *T. sebifera* (Liu et al., 2013) than those in the invasive range (Thomas et al., 2010). Alteration of plant root morphology and production as well as stimulation of soil microbial community by elevated CO₂ and N deposition have been reported (Lipson et al., 2014; Dawes et al., 2015; Liu et al., 2015; Nie et al., 2015). Therefore, CO₂ and N could impact litter quality, growth and mass allocation, which might further regulate the litter decomposition process associated with C and nutrient release.

4.2. Effects of elevated CO₂, N addition, and population origin on litter decomposition

The decomposability of invasive *T. sebifera* litter was slightly higher than native origin litter (Table 2) even though no significant differences were observed in litter C:N between origins (Table 1; Fig. 3). This suggests that differences in chemical composition, such as secondary chemical concentrations, may have influenced decomposability because invasive populations generally have lower amounts of defense chemicals (Wang et al., 2012). Additionally, litter decomposition was also affected by elevated CO₂ and N deposition, mainly via litter and soil effects,

respectively (Table 2; Figs. 3 and 4). Indeed, litter decomposition might differ between native and invasive genotypes due to differences in competitive ability and photosynthetic capacity and divergent responses to elevated CO₂ and N deposition. Higher litter quality and/or faster litter decomposition rates of invasive plants has been reported in previous studies (Ehrenfeld, 2003; Allison and Vitousek, 2004; Liao et al., 2008). This may lead to more readily decomposing litter and hence faster nutrient turnover rate in the invaded area (Cameron and Spencer, 1989). Indeed, both higher nutrient (N and P) and soil biota using ability by invasive *T. sebifera* have been reported by previous studies (Zou et al., 2006; Nijjer et al., 2007; Zhang et al., 2013). These abilities would generally lead to larger nutrient stocks in plant residues and hence subsequent litter decomposition (Cameron and Spencer, 1989). In addition, subsequent litter decomposition of *T. sebifera* could also be altered in response to litter, soil or atmospheric environment effects imposed by elevated CO₂ and N addition.

Our SEM results showed that elevated CO₂ and N deposition in interaction impacted litter decomposability with opposing effects and their interaction also was important for positive effects on litter quantity (Fig. 5). However, while N addition enhanced litter decomposability under elevated CO₂ treatment, no fertilization effects on litter decomposability were observed in ambient CO₂ (Figs. 3 and 5), indicating the effects of N deposition on litter decomposability might be enhanced by increased atmospheric CO₂ conditions. In addition, no significant interactive effects of elevated CO₂, N addition and origin were observed on litter decomposability (Table 2), which

might have implications for the consistent effects of these two global change factors on the decomposability of *T. sebifera* litter via changes in litter quality though SEM results suggested that negative effects of CO₂ were stronger with invasive *T. sebifera*.

Litter decomposition could also be regulated by changes in soil environmental factors caused by elevated CO₂ and N addition (*e.g.*, acidity, nutrient levels or microbial community) (Carney et al., 2007; Finn et al., 2015; Hasegawa et al., 2015; Liu et al., 2015). However, except for the positive effects of N addition on litter mass remaining via soil effects, no soil effects of elevated CO₂ or its interaction with N were observed in our study (Table 2; Fig. 5). Indeed, the effects of elevated CO₂ on litter decomposition via soil effects might be associated with changes in soil moisture, soil acidity or even microbial biomass (Liu et al., 2015). However, soil moisture was maintained at the same level throughout our study, which might have excluded the effects of potential changes in soil moisture in response to elevated CO₂ (Liu et al., 2015). Even though not examined by this work, the maintenance of similar soil moisture might have prevented changes in soil acidity and microbial biomass and thereby diminish the soil effects induced by CO₂. Meanwhile, negative effects of N addition on litter decomposition have been reported by previous studies (Micks et al., 2004; Mo et al., 2006; Fang et al., 2007) but positive and neutral effects have also been seen (Downs et al., 1996; Vitousek, 1998). Various mechanisms underlying the negative effects of N deposition on decomposition rate have been proposed, including interactions between N and enzymes associated with cellulose and lignin degradation (Carreiro et al., 2000), increasing the efficiency of recalcitrant material formation

(Sun et al., 2016) and decreasing decomposer growth (Ågren et al., 2013).

Examination of soil enzyme activity and changes in soil microbial community composition in response to CO₂ and N were not included in this study. However, our study highlights the possibility of soil effects on subsequent litter decomposition and the importance of measuring soil microbial communities in future work studying the effects of elevated CO₂ and N deposition on invasive plants and the subsequent litter decomposition.

4.3. Atmospheric effects of elevated CO₂ on subsequent litter decomposition

The third experiment examining the direct, atmospheric effects of elevated CO₂ on litter decomposition showed no effects by CO₂ (Table 2; Fig. 5). While effects of atmospheric conditions with elevated CO₂ on litter decomposition have been suggested to be as important as the atmospheric environment under which litter was produced (Hall et al., 2006), our results indicated that these effects might vary with focal species and study time scale. In comparison to effects via litter production and soils, direct atmospheric effects appeared to be minor.

4.4. Management implications

One of the major ecosystem level impacts of *T. sebifera* invasions is that *T. sebifera* litter has low C:N and decomposes rapidly compared to native prairie plants that it displaces which causes increases in soil fertility (Cameron and Spencer, 1989). These higher levels of soil fertility accelerate *T. sebifera* invasions and complicate restoration efforts (Siemann and Rogers, 2003). But, our results suggest that elevated CO₂ may lessen the effects of *T. sebifera* invasions on soil fertility by reducing *T.*

sebifera litter quality. However, the positive growth responses we observed also suggest the potential for elevated CO₂ and N deposition to increase the difficulty of managing *T. sebifera* invasions. In fact, another study found that increases in *T. sebifera* growth with elevated CO₂ were larger than for three co-occurring native tree species dominant in forests in the southeastern USA (Wang *et al.*, unpublished data). Finally, the potential for more rapid growth with elevated CO₂ and N deposition may limit the impact of biocontrol agents that might be introduced to control *T. sebifera*.

5. Conclusions

In conclusion, these results increase our understanding of the effects of elevated CO₂ and N deposition on invasive plant growth and subsequent litter decomposition. While CO₂ and N synergistically impacted the biomass production of *T. sebifera*, their effects were opposite for subsequent litter decomposition. On average, elevated CO₂ slowed litter decomposition through reduced litter decomposability and sped up decomposition through soil effects. In contrast, N deposition offset CO₂ effects on decomposability and significantly slowed decomposition through soil effects. Although CO₂ and N had consistent effects on native and invasive populations, the relative magnitudes of their effects on litter quantity and quality impacted litter cycling, suggesting the importance of considering plant trait variation in an overall estimation of global change effects on ecosystem nutrient dynamics. Specifically, the net effect of CO₂ alone on litter decomposition outputs was negative but this effect was stronger for invasive populations with stronger decomposability reductions. The net effect of CO₂ and N was positive but this effect was stronger for native

populations with stronger litter production increases. Since litter decomposition is an important process associated with nutrient releasing and recycling, altered litter decomposition under global change conditions might also have implications for the persistence and expansion of invasive plant species.

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650 **Table 1** The dependence of leaf, root, total mass, root to shoot ratio (R:S) and leaf C:N in the growth experiment on CO₂, N fertilization (Fert),
651 population origin and their interactions in ANOVAs. Only fixed effects are shown. Significant results are shown in bold. * $P<0.05$, ** $P<0.01$,
652 *** $P<0.001$, **** $P<0.0001$.

653

Effect	df	Leaf mass		Root mass		Total mass		R:S		df	Leaf C:N	
		F	P	F	P	F	P	F	P		F	P
CO ₂	1,14	27.4	****	58.4	****	59.7	****	21.8	***	1,14	277.6	****
Fert	1,476	99.3	****	445.0	****	553.6	****	12.4	***	1,170	4.3	*
CO ₂ ×Fert	1,476	23.4	****	26.6	****	30.6	****	0.8	0.38	1,170	6.4	*
Origin	1,14	2.2	0.16	1.9	0.20	0.6	0.46	2.0	0.18	1,14	0.3	0.57
CO ₂ ×Origin	1,14	2.6	0.13	4.0	0.07	2.5	0.14	0.1	0.81	1,14	9.8	**
Origin×Fert	1,14	8.0	*	5.4	*	5.7	*	<0.1	0.87	1,14	3.3	0.09
CO ₂ ×Origin×Fert	1,14	0.2	0.71	1.6	0.23	0.1	0.76	2.5	0.14	1,14	0.1	0.81

654

655 **Table 2** The dependence of litter mass remaining in the litter decomposability, soil effects, and atmospheric effects experiments on CO₂, retrieval
656 time, N fertilization (Fert), and their interactions in ANOVAs. Pots without plants in the soil effects experiment are not included. Only fixed
657 effects are shown. Significant results are shown in bold. * $P<0.05$, ** $P<0.01$, **** $P<0.0001$.

Factor	Litter Decomposability			Soil Effects			Atmospheric Effects		
	df	F	P	df	F	P	df	F	P
CO ₂	1,14	6.3	*	1,14	1.2	0.29	1,124	1.5	0.22
Time	1,410	220.9	****	1,454	293.4	****	1,124	74.3	****
CO ₂ ×Time	1,410	2.4	0.12	1,454	0.6	0.46	1,124	0.5	0.48
Fert	1,410	3.1	0.08	1,454	4.4	*			
CO ₂ ×Fert	1,410	7.4	**	1,454	1.0	0.32			
Fert×Time	1,410	4.0	*	1,454	1.2	0.28			
CO ₂ ×Fert×Time	1,410	5.0	*	1,454	0.5	0.48			
Origin	1,14	4.4	0.05	1,14	2.4	0.15			
CO ₂ ×Origin	1,14	0.7	0.43	1,14	2.6	0.13			
Origin×Time	1,14	<0.1	0.98	1,14	0.1	0.81			
CO ₂ ×Origin×Time	1,14	0.1	0.75	1,14	<0.1	0.91			
Origin×Fert	1,14	0.6	0.44	1,14	2.8	0.12			
CO ₂ ×Origin×Fert	1,14	<0.1	0.88	1,14	<0.1	0.95			
Origin×Fert×Time	1,14	<0.1	0.86	1,14	0.5	0.48			
CO ₂ ×Origin×Fert×Time	1,14	0.1	0.76	1,14	0.3	0.60			

Table 3 The dependence of litter mass remaining in the soil effects experiment on CO₂, N fertilization (Fert), plant presence (Plants) and their interactions in ANOVAs (second retrieve only). Only fixed effects are shown. Significant results are shown in bold. **** $P < 0.0001$.

Effect	Litter mass remaining (%)		
	df	F	P
CO ₂	1,14	1.5	0.24
Fert	1,233	0.3	0.61
CO ₂ ×Fert	1,233	3.5	0.06
Plants	1,233	20.6	****
CO ₂ ×Plants	1,233	1.2	0.27
Fert×Plants	1,233	0.7	0.41
CO ₂ ×Fert×Plants	1,233	3.1	0.08
Origin (plants)	1,14	1.3	0.28
CO ₂ ×Origin (plants)	1,14	0.8	0.38
Origin×Fert (plants)	1,14	2.2	0.16
CO ₂ ×Origin×Fert(plants)	1,14	0.1	0.79

Fig. 1. The dependence of leaf mass (means + 1 se) in the growth experiment on (A) CO₂ (ambient or elevated) and fertilization treatments (Control or N addition) and (B) population origin (native or invasive) and fertilization treatments. Means with the same letter were not significantly different in post-hoc tests ($P < 0.05$).

Fig. 2. The dependence of total mass (means + 1 se) in the growth experiment on (A) CO₂ (ambient or elevated) and fertilization treatments (Control or N addition) and (B) population origin (native or invasive) and fertilization treatments. Means with the same letter were not significantly different in post-hoc tests ($P < 0.05$).

Fig. 3. The dependence of leaf C:N (means + 1 se) in the growth experiment on (A) CO₂ (ambient or elevated) and fertilization treatments (Control or N addition) and (B) CO₂ (ambient or elevated) and population origin (native or invasive) treatments. Means with the same letter were not significantly different in post-hoc tests ($P < 0.05$).

Fig. 4. The dependence of litter mass remaining (means $\pm$ 1 se) at the first and second retrieve time on CO₂ (ambient or elevated) and fertilization treatments (Control or N addition) in the litter decomposability experiment. Data points with the same letter were not significantly different in post-hoc tests ($P < 0.05$).

Fig. 5. The dependence of litter mass remaining (means $\pm$ 1 se) on CO₂ (ambient or elevated) and fertilization treatments (Control or N addition) at the first and second retrieve time in the soil effects experiment. Litter decomposing with soil that had plants present in the growth experiment are shown with filled symbols and litter decomposing with soil that did not are shown with open symbols (second retrieve only).

Fig. 6. SEMs for the effects of elevated CO₂, N fertilization, their interaction and plant presence on litter decomposition input via changes in the quantity of litter produced, the quality of litter produced, and the properties of soils and direct effects of elevated CO₂ on decomposition for (A) native (China) populations versus (B) invasive (US) populations. Significant results are shown in black and non-significant results are shown in grey. Negative relationships are denoted by dotted lines and positive relationships are denoted by solid lines. The coefficient next to a line indicates the relative strength of the effect. Stronger effects are represented by thicker lines. The total effects of elevated CO₂, nitrogen deposition, and CO₂ and nitrogen together are shown next to the output arrows. For CO₂ and fertilization, the coefficient represents the size of the effect compared to controls and the significance denotes whether this effect was non-additive. ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$.