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# Early stages of decay of *Lythrum salicaria* L. and *Typha latifolia* L. in a standing-dead position

Maryann Welsch, Joseph B. Yavitt*

*Department of Natural Resources, Cornell University, Ithaca, NY 14850, USA*

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**Abstract**

*Lythrum salicaria* (purple loosestrife) has invaded wetlands across North America and is known to have negative effects on native plant species and diversity. The effects of this invasion on ecosystem processes are less well known. We examined decomposition of *L. salicaria* stems versus that of native *Typha latifolia* (broad-leaved cattail) in a previously cultivated, freshwater marsh in central New York State. We expected different decomposition rates and differences in litter quality of *L. salicaria* stems and *T. latifolia* shoots. We also quantified ergosterol concentration, an index of fungal biomass. However, standing-dead *T. latifolia* shoots and *L. salicaria* stems had lost similar quantities of mass (20–25%) after 1 year. Subsequent heavy snowfall and winter winds caused tissue fragmentation and much greater mass loss, but still similar for both plant species. Ergosterol concentrations were greater in *T. latifolia* shoots than in *L. salicaria* stems; yet, changes in tissue concentrations of nitrogen (N) and Klason lignin were very similar for both plant species. Therefore, although native *T. latifolia* may be more favorable in wetlands, the results of this study suggest that *L. salicaria* stems and *T. latifolia* shoots decompose in a similar fashion and have similar influence on the ecosystem-level processes measured in this study.


*Keywords:* Decomposition; Ergosterol; New York State; Nitrogen; Freshwater marsh

## 1. Introduction

The invasion of exotic plant species is thought to be a major threat to ecosystems by affecting the ecology of native organisms and due to the economic costs of controlling the spread of invasive species and restoring degraded ecosystems (Vitousek et al., 1996; Pimentel et al., 2000). However, there are surprisingly few generalizations about the effects

* Corresponding author. Tel.: +1-607-255-6601; fax: +1-607-255-0349.
*E-mail address:* jby1@cornell.edu (J.B. Yavitt).

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of invasive species on ecosystem processes, such as nutrient cycling, primary productivity, and organic matter decomposition (Ramakrishnan and Vitousek, 1989; Gordon, 1998).

One way that plant species can promote differences in ecosystem processes is through differences in litter quality, defined as the concentrations of nutrients and different classes of organic compounds in litter (Melillo et al., 1982). Litter quality, in part, determines the litter decomposition rate that, in turn, influences the amount of the residue incorporated into soil organic matter with a consequent feedback to soil nutrient availability (Hobbie, 1992). In upland ecosystems, invasive plant species commonly increase net primary productivity and organic matter decomposition to gain an advantage over native species through increased rates of nutrient turnover. However, it is unclear whether this generalization applies to wetlands.

In contrast to that in upland ecosystems, the early stage of decomposition of emergent macrophytes begins in a standing-dead position in which the plant remains upright. As a result, leaching removes soluble carbohydrates and nutrients (Davis and van der Valk, 1978), and microbial decomposers, predominantly fungi, colonize the standing-dead plant (Findlay et al., 1990; Newell et al., 1995). Senesced litter can remain above the soil surface until fragmented or compressed by snow pack (Davis and van der Valk, 1978). Therefore, the traditional method of measuring litter decomposition in which plant tissue is cut into small pieces and placed into a mesh bag (litterbag) on or in the soil can overestimate decay rates of emergent plant tissue by misrepresenting the environment in which the early stages of decay occurs.

The exotic emergent macrophyte, *L. salicaria* was introduced to North America from Europe in the 1800s and is reported to be replacing native plant species such as *T. latifolia* (Mal et al., 1997; Weihe and Neely, 1997) through aggressive competition (Gaudet and Keddy, 1988). Dense stands of *L. salicaria* are undesirable for wildlife as food and habitat (Rawinski and Malecki, 1984; Thompson et al., 1987; Mal et al., 1992), but the effect of *L. salicaria* on ecosystem processes is less well known. In this paper we compare decomposition of aboveground biomass of *L. salicaria* and *T. latifolia* growing in a freshwater marsh in central New York State. We addressed the following questions: Does the chemistry of senesced tissues differ among species and control litter decomposition rates? Do fungi colonize both species equally and if so does fungal colonization account for differences in decomposition rates? We used ergosterol concentration on plant tissue as a way to measure fungal colonization (Newell et al., 1988). By examining the decay of *L. salicaria* stems and *T. latifolia* shoots in an upright, standing-dead position, we obtained a more accurate estimate mass loss and decay rates of emergent plant tissue than studies in which litterbags were employed.

## 2. Methods and materials

### *2.1. Study area*

The study took place in Marten's Tract, part of the Northern Wetlands Complex of the Montezuma Wildlife Management Area, near Savannah, New York. Marten's Tract is located north of the New York State Barge Canal, adjacent to the Seneca River, and is part

of a large area of hydric soils that were drained and put into agriculture approximately 50 years ago. After agriculture was abandoned at this site in 1989 and the dikes were re-built in 1992, *L. salicaria* and *T. latifolia* established and spread, and today the two species make up approximately 80% of aboveground biomass covering the 245-acre tract.

At Marten's Tract, the water table fluctuates in response to seasonal flooding due to snowmelt and gradual water-level drawdown. Since this area was cultivated the soil was relatively uniform at the time of abandonment, and the presence of *L. salicaria* and *T. latifolia* appear to be controlled by the height of the water table. *Typha latifolia* dominates the stand on the wet end closest to the river, whereas *L. salicaria* dominates on the dry end of this marsh, and a mixed stand of fairly equal proportions of each species exists in the intermediate area. The relatively young, mixed stand of *L. salicaria* and *T. latifolia* provided an ideal opportunity to examine the decomposition of each species where long-term effects of monotypic stands had not yet been established and competition between species was in the process of being played out.

### *2.2. Methods*

We carried out two decomposition studies: one was initiated in 1997 and the other in 1998. At the end of October 1997 and again in October 1998, we collected senesced (brown) *L. salicaria* stems and *T. latifolia* shoots from the current years growth. Material was air-dried in the lab and trimmed of branches and flowers (1997 collection) or trimmed to a uniform height of 40 cm (*L. salicaria*) and 50 cm (*T. latifolia*) (1998 collection). We shortened the plant heights in 1998 to reduce the top-heaviness of the plant stake samples, thus decreasing the chances for plant samples to be knocked down, which greatly affected the previous years samples (see results). Trimmed plants were weighed and attached to tagged-wooden stakes (tomato stakes) with cable ties. Forty plant stakes per species were placed in each of six experimental plots (10 m $\times$ 12 m) at Marten's Tract in a random arrangement (at least 1 m apart) at the beginning of November 1997 and 1998. The six plots were part of an on-going experiment created in the summer of 1997 with three treatments and two replicate plots each in which (1) *L. salicaria* was removed and only *T. latifolia* remained (*T. latifolia*-only), (2) *L. salicaria* and *T. latifolia* were both removed (bare) and, (3) a mixed stand of fairly equal proportions of *L. salicaria* and *T. latifolia* existed (control). The cut end of each shoot or stem was placed in contact with the soil (buried ca. 5 cm). A subset of recently senesced stems and shoots from each cohort (1997 and 1998) was retained to determine moisture and tissue chemistry analysis.

Subsets of plant stakes were collected during the following year at the start of the growing season (end of May 1998 and 1999), the middle of the growing season (end of July 1998 and 1999), and 1 year after the start of the experiment (November 1998 and 1999). Samples from each collection (approximately 10 stakes per species from each plot) were air-dried and weighed to determine mass loss and combusted at 450 °C for 5 h to determine ash-free dry mass. A subset from each collection was used for analysis of moisture content, tissue quality, and ergosterol concentration.

The 1997 cohort of plant stake samples was partitioned into two sections by height: base (0–30 cm for *T. latifolia* and 0–60 cm for *L. salicaria*) and top (>30 cm for *T. latifolia* and >60 cm for *L. salicaria*). Height sections were determined by the average height of *T.*

*latifolia* shoots (approx. 90 cm) and *L. salicaria* stems (approx. 110 cm) and by the amount of sample necessary for tissue chemistry analyses. The 1998 cohort of samples for tissue chemistry was not divided into height intervals. Individual plants were ground to pass through a #40 mesh screen, and a subset was analyzed for Klason lignin using the method of Wieder and Starr (1998). Total carbon (C) and N were determined on pooled samples (three plants per plot) of plant tissue. The pooled samples were ground and mixed in a ball mill (SPEX 8000). Samples (1–1.5 mg) were processed for total C and N by combustion (Roboprep–CN Biological Sample Converter, Europa Scientific).

A pooled subset of three to five plants (per species) from each collection in 1998–1999 was analyzed immediately (same day) for ergosterol concentration, using the methodology of Newell et al. (1988). Approximately 1.5 g (cut into 2–4 cm length pieces) were extracted in methanol and alcoholic KOH and the extract was partitioned into pentane fractions and evaporated under $N_2$. Samples were re-dissolved in 3 ml of methanol, sonicated and then filtered through a 0.45-μm membrane filter (Acrodisc). Ergosterol concentrations were determined using high-pressure liquid chromatography (Varian Instrument Co.) with an UV detector wavelength of 282 nm and a reverse phase column (Dynamax C18, 5 μm, 4.6 mm i.d. × 250 mm).

In 1999, we also followed changes in tissue chemistry and ergosterol concentrations of standing-dead *L. salicaria* stems and *T. latifolia* shoots (1998 years growth) to compare to the plant stake samples. These plants were located outside the experimental plots and were collected on the same dates as plant stakes. Each standing-dead plant was divided into three height intervals: base (0–30 cm), middle (30–60 cm), and top (>60–90 cm). Replicates were pooled and analyzed immediately for ergosterol, as described above. In addition, we measured $CO_2$ evolution from standing-dead plants, using the method of Newell et al. (1985). Portions were incubated in acid-washed glass jars after wetting with de-ionized, distilled water for 15 min and pouring off excess water. The jars were sealed, and a gas sample was withdrawn from the headspace after a 2-h period and analyzed for $CO_2$ concentration by gas chromatography using a thermal conductivity detector (Varian 3400 CX). We also used standing-dead plants for tissue chemistry analyses to assess relative changes in litter quality of plant stake samples and standing-dead samples after 1 year of decay. Tissue chemistry analyses included total C and N and Klason lignin and were determined according to methods described above and compared among the three height sections of standing-dead samples.

Because *L. salicaria* leaves drop off the plant at senescence, whereas *T. latifolia* shoots do not, we determined decomposition rates of *L. salicaria* leaves in litterbags over 7 months. Recently, senesced (brown) *L. salicaria* leaves were collected in early September 2000 from plants outside the experimental plots at Marten's Tract and were air-dried before 4–5 g were placed into litterbags (12 cm × 12 cm, 2 mm mesh), weighed and tagged. The litterbags were tethered with fishing line to PVC stakes and placed on top of the litter layer (consisting of mostly stems and leaves) in a patch of predominantly *L. salicaria* at Marten's Tract on 15 September 2000. Litterbags were collected three times over 7 months: 15 October (1 month), 15 December (3 months), and 13 April (7 months). The experiment was terminated after 7 months because little material remained in the litterbags.

The experimental design included three treatments with two replicate plots each. The decomposition of *L. salicaria* stems and *T. latifolia* shoots (stakes and litterbags) was analyzed

with the general linear model (GLM) with species, treatment, height (1997 cohort only), and sampling date used as the main effects in an analysis of variance (ANOVA) model with interactions. The same statistical design was used for standing-dead data except species, height, and sampling date were used as main effects. The comparison of standing-dead plants and plant stake samples after 1 year of decay involved the calculation of weighted averages of measured parameters in which concentrations of ergosterol, N, C, and lignin of standing-dead samples were weighted according to the height of the plant stakes. Significant interaction terms were further investigated with Tukey's pairwise comparisons with a family error rate of 0.05.

## 3. Results

### 3.1. Mass loss

For the 1997 cohort, mass loss after 1 year was 50% for *L. salicaria* stems and 40% for the *T. latifolia* shoots (Fig. 1). A heavy, wet snowfall of 30.5 cm on 14 November 1997 caused the majority of these samples to be knocked over. Subsequently, we observed significant fragmentation, especially on the *L. salicaria* stems, which apparently contributed to mass loss. In an attempt to account for fragmentation, we tracked changes in specific density (mass/volume) of the *L. salicaria* samples. Following a slight increase from an initial value of 0.345 to 0.36 g $cm^{-3}$ after 6 months, mean stem density decreased back to the initial value for the remaining time. The small change in *L. salicaria* stem density suggests that the mass loss of *L. salicaria* stems, reported in Fig. 1, was over-estimated by fragmentation during the winter months of 1998.

For the 1998 cohort, mass loss after 1 year was 20% for *L. salicaria* stems and 25% for the *T. latifolia* shoots (Fig. 1). Therefore, mass loss was significantly less for the 1998 cohort than for the 1997 cohort, per species. Moreover, the 1998 cohort had a significant treatment effect for mass loss in which *T. latifolia* shoots lost more mass than *L. salicaria* stems when placed in the bare plots. This was the only significant treatment effect observed. Finally, *L. salicaria* leaf litter decayed rapidly showing 58% mass loss in 7 months (data not shown).

### 3.2. Plant stake tissue chemistry and ergosterol concentrations

Mean C concentrations were consistently greater in *L. salicaria* stems than in *T. latifolia* shoots in both the 1997 cohort (Table 1) and the 1998 cohort (Table 2). In contrast, Klason lignin concentrations were similar among species. Carbon content decreased during decay, approximately paralleling mass loss, whereas Klason lignin content increased slightly between November and July for both species, particularly for *L. salicaria* stems in the 1998 cohort.

Mean N concentrations were greater in *T. latifolia* shoots than in *L. salicaria* stems, particularly in the 1997 cohort (Tables 1 and 2). Overall, both species accumulated N during decay, which subsequently influenced C:N and lignin:N ratios. Moreover, in the 1997 cohort, *T. latifolia* shoots accumulated significantly more N than *L. salicaria* stems.

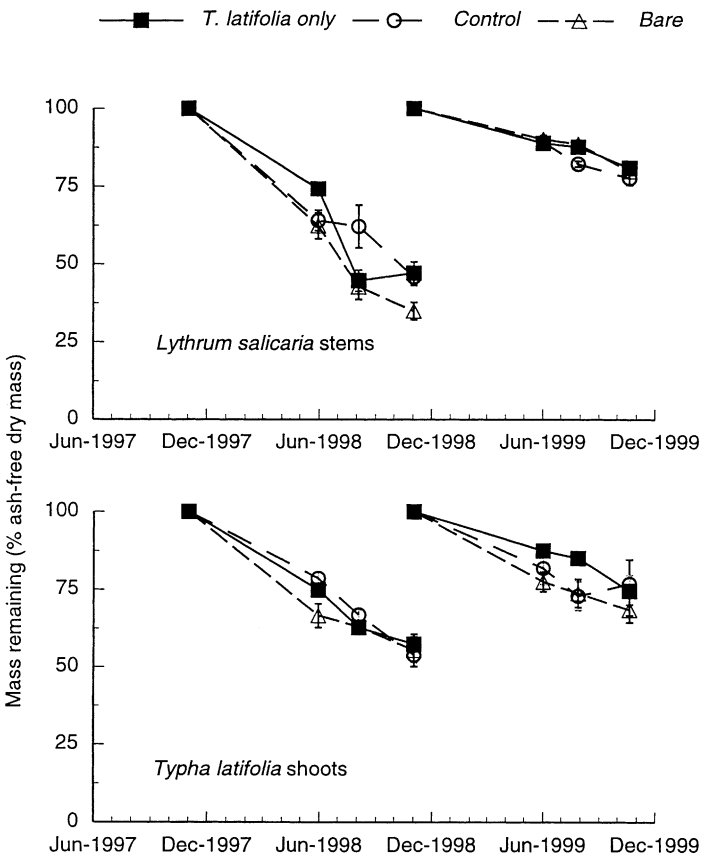


Fig. 1. Mean mass remaining of plant stake *L. salicaria* stems and *T. latifolia* shoots decomposing in three treatments for experiments started in 1997 and again in 1998. Control treatment had both plant species growing; *Lythrum salicaria* plants had been remove from *T. latifolia* only plots; bare plots had no plant growth. Bars are standard errors.

In the 1998 cohort, however, *L. salicaria* gained more N than *T. latifolia* shoots after 1 year of decay.

Because the 1997 cohort had been partitioned into two height segments, we found that Klason lignin and C concentrations remained fairly constant as a function of plant height during decay (Table 1). In contrast, mean N concentration was two times greater in the tips of *L. salicaria* stems than in the stem base in November 1997. With further decay, N concentrations in the tips of *L. salicaria* stems decreased noticeably and eventually were similar to that in the base of the stems. *Typha latifolia* shoots were not analyzed for tissue chemistry in November 1997; however, N concentrations were fairly homogeneous as a function of plant height for the remainder of the sampling dates.

Ergosterol concentrations were significantly greater in *T. latifolia* shoots than in *L. salicaria* stems on all dates, except 31 May (Table 2). Overall, ergosterol concentrations of

Table 1
Litter quality of plant stake samples per each collection date for the 1997 cohort

| Date | Height | C | N | Klason lignin | C:N ratio | Lignin:N ratio |
|---|---|---|---|---|---|---|
| *Lythrum salicaria* | | | | | | |
| 1 November 1997 | Base | 45.8 ± 0.5 | 0.20 ± 0.03 | 39.1 ± 0.7 | 243 ± 32 | 208 ± 29 |
| | Top | 45.4 ± 0.8 | 0.44 ± 0.06 | 42.9 ± 0.9 | 108 ± 15 | 101 ± 13 |
| 29 May 1998 | Base | 44.8 ± 0.3 | 0.23 ± 0.01 | 43.4 ± 1.1 | 198 ± 10 | 179 ± 8 |
| | Top | 43.4 ± 0.4 | 0.38 ± 0.03 | 46.5 ± 1.8 | 117 ± 10 | 112 ± 10 |
| 3 August 1998 | Base | 44.7 ± 0.4 | 0.29 ± 0.02 | 41.4 ± 1.2 | 155 ± 9 | 146 ± 6 |
| | Top | 44.9 ± 0.4 | 0.33 ± 0.03 | 41.6 ± 2 | 139 ± 11 | 119 ± 7 |
| 1 November 1998 | Base | 43.3 ± 0.6 | 0.29 ± 0.02 | 42.8 ± 1.9 | 154 ± 12 | 151 ± 10 |
| | Top | 44.6 ± 0.2 | 0.31 ± 0.02 | 42.2 ± 1.3 | 145 ± 8 | 135 ± 11 |
| *Typha latifolia* | | | | | | |
| 29 May 1998 | Base | 40.6 ± 0.6 | 0.29 ± 0.01 | 40.3 ± 0.7 | 142 ± 8 | 152 ± 9 |
| | Top | 41.9 ± 0.7 | 0.33 ± 0.03 | 41.4 ± 1.0 | 133 ± 11 | 150 ± 19 |
| 3 August 1998 | Base | 40.1 ± 1.5 | 0.41 ± 0.03 | 42.6 ± 1.5 | 101 ± 9 | 106 ± 10 |
| | Top | 42.0 ± 0.6 | 0.41 ± 0.02 | 39.5 ± 1.2 | 104 ± 6 | 103 ± 7 |
| 1 November 1998 | Base | 40.0 ± 1.0 | 0.45 ± 0.01 | 42.7 ± 1.2 | 89 ± 4 | 94 ± 6 |
| | Top | 41.6 ± 0.4 | 0.45 ± 0.05 | 42.2 ± 1.4 | 97 ± 9 | 99 ± 9 |

Plant stake samples in 1998 were divided into two height classes: base (0–60 cm for purple loosestrife and 0–30 cm for cattail) and top (>60 cm for purple loosestrife and >30 cm for cattail). Values are the means + 1 standard error. Units for C, N, and Klason lignin are % ash-free dry mass.

plant stake stems and shoots decreased from November 1998 to May 1999, then increased for the remaining sampling dates.

### 3.3. Standing-dead material

Ergosterol concentrations were measured as a function of height of standing-dead plants for each collection date (Fig. 2). For *T. latifolia* shoots, ergosterol concentrations were

Table 2
Litter quality and ergosterol content of plant stake samples per collection date for the 1998 cohort

| Date | C | N | Klason lignin | C:N ratio | Lignin:N ratio[a] | Ergosterol |
|---|---|---|---|---|---|---|
| *Lythrum salicaria* | | | | | | |
| 1 November 98 | 46.5 ± 0.4 | 0.18 ± 0.04 | 38.7 ± 1.8 | 288 ± 56 | 238 ± 23 | 76.5 |
| 31 May 1999 | 44.1 ± 0.4 | 0.32 ± 0.02 | 48.1 ± 1.5 | 141 ± 8 | 151 ± 11 | 25.7 ± 0.6 |
| 27 July 1999 | 44.2 ± 0.7 | 0.32 ± 0.02 | 47.8 ± 2 | 142 ± 10 | 151 ± 12 | 37.1 ± 1.8 |
| 19 October 99 | 44.4 ± 0.8 | 0.42 ± 0.02 | 38.0 ± 0.5 | 108 ± 5 | 92 ± 6 | 49.3 ± 2.8 |
| *Typha latifolia* | | | | | | |
| 1 November 1998 | 44.5 ± 0.1 | 0.20 ± 0.03 | 40.3 ± 2.6 | 228 ± 35 | 206 ± 16 | 126.3 |
| 31 May 1999 | 41.9 ± 0.5 | 0.34 ± 0.012 | 41.6 ± 0.9 | 124 ± 5 | 123 ± 5 | 24.7 ± 3.7 |
| 27 July 1999 | 41.2 ± 0.4 | 0.39 ± 0.02 | 47.3 ± 1.2 | 107 ± 7 | 122 ± 6 | 68.8 ± 4.1 |
| 19 October 1999 | 42.8 ± 0.5 | 0.35 ± 0.02 | 42.6 ± 0.9 | 125 ± 9 | 124 ± 9 | 79 ± 4.2 |

[a] Values are the means and (standard error). Units are % ash-free dry mass for C, N, and Klason lignin, and $\mu g\, g^{-1}$ dry mass for ergosterol.

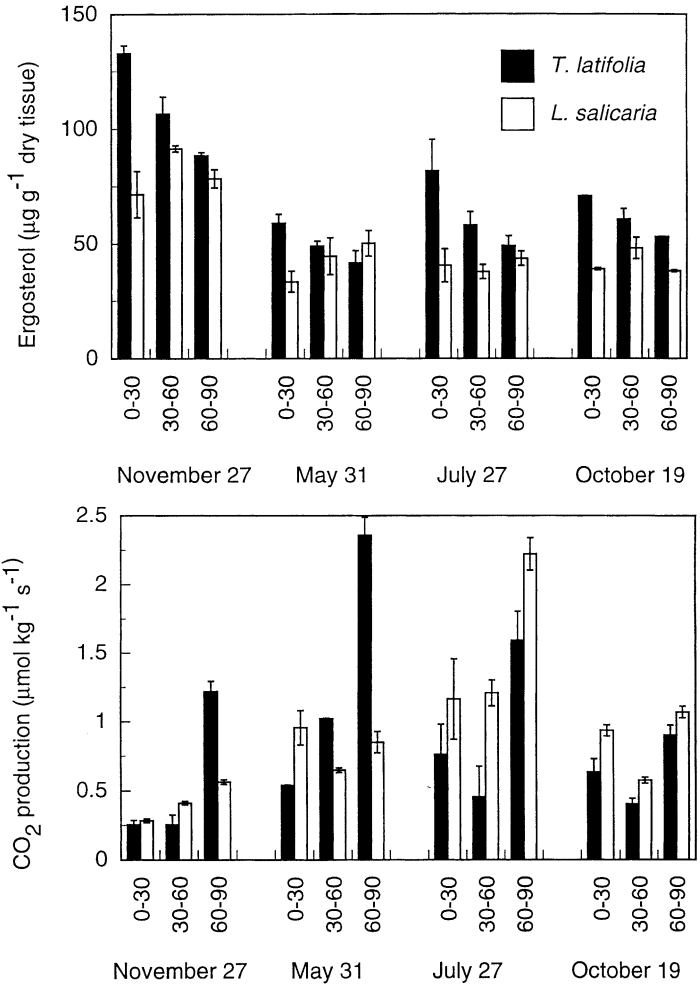


Fig. 2. Mean ergosterol concentrations and $CO_2$ production of standing-dead *L. salicaria* stems (white) and *T. latifolia* shoots (black) of the 1998 cohort. Bars are standard error.

greater in the base of the plants, whereas ergosterol concentrations were very similar between heights of *L. salicaria* stems. As a result, ergosterol concentrations were greater in *T. latifolia* shoots than *L. salicaria* stems. Overall, ergosterol concentrations of standing-dead plants decreased from November 1998 to May 1999 and remained fairly constant after that. The production of $CO_2$ from *L. salicaria* stems and *T. latifolia* shoots varied temporally (Fig. 2) and was greater in the tips of the plants. In contrast to ergosterol concentrations, $CO_2$ production was generally greater in *L. salicaria* stems than *T. latifolia* shoots.

After 1 year of decay, C concentrations were slightly greater in standing-dead plants than plant stakes (Table 3). Klason lignin concentrations were greater in standing-dead *L. salicaria* stems than plant stakes, but the reverse was true for *T. latifolia* shoots. However,

Table 3
Comparison of decomposition parameters of plant stake and standing-dead *L. salicaria* stems and *T. latifolia* shoots after 1 year of decay

| | Ergosterol | $CO_2$ production | C | N | Klason lignin | C:N ratio | Lignin:N ratio |
|---|---|---|---|---|---|---|---|
| *L. salicaria* | | | | | | | |
| Plant stake | 49.3 ± 2.8 | 1.91 ± 0.10 | 44.4 ± 0.8 | 0.42 ± 0.02 | 37.8 ± 0.7 | 108 ± 6 | 92 ± 6 |
| Standing-dead | 41.28 | 0.82 | 46.1 | 0.31 | 45.0 | 148 | 145 |
| *T. latifolia* | | | | | | | |
| Plant stake | 79 ± 4.2 | 1.12 ± 0.08 | 42.7 ± 0.4 | 0.35 ± 0.02 | 42.5 ± 1.2 | 125 ± 9 | 124 ± 9 |
| Standing-dead | 66.8 | 0.74 | 44.1 | 0.25 | 36.1 | 179 | 147 |

Values for plant stake samples are the mean and (standard error). Values for standing-dead samples are the means weighted according to plant stake height. The units are % ash-free dry mass for C, N, and Klason lignin. The units for ergosterol are $\mu g\, g^{-1}$ dry mass. The units for $CO_2$ production are $\mu mol\, kg^{-1}\, s^{-1}$.

N concentrations were greater in plant stakes than standing-dead stems and shoots. This difference in N subsequently resulted in lower C:N and lignin:N values in the plant stake samples than the standing-dead samples. In addition, ergosterol concentrations were greater in the plant stakes than the standing-dead samples and $CO_2$ evolution from plant stakes samples was higher than standing-dead samples, especially for *L. salicaria*.

## 4. Discussion

We suspect that mass loss rates were elevated in the 1997 cohort by the heavy snowfall in early November of 1997 that knocked over all vegetation in the marsh. These samples were clearly in contact with standing water and the soil surface, making the decomposition measurement more akin to a litterbag study. In addition, winter winds and heavy snowfall fragmented tissue, which increased mass loss rates. Notably, decay rates of *T. latifolia* shoots in the 1997 cohort were comparable to rates reported in other studies that used litterbags (Brinson et al., 1981; Nelson et al., 1990; Van der Valk et al., 1991; Harris et al., 1995; Emery and Perry, 1996).

The 1998 cohort did not fall over, except for a few *T. latifolia* stems in the bare plots. However, decay rates might have been slowed by early water-level drawdown in 1999, which resulted in lower moisture content of the stems and shoots. For example, mean water content of *T. latifolia* shoots was 76% in the 1997 cohort versus 22% in the 1998 cohort. Likewise, mean water content of *L. salicaria* stems was 61% in the 1997 cohort versus 14% in the 1998 cohort. Presumably, there is a quadratic relationship between decay rates and water content, but only a controlled experiment using prescribed water content can determine the shape of the relationship. Notably, the faster decay rates of *T. latifolia* shoots than *L. salicaria* stems in the bare plots (Fig. 1) was due to *T. latifolia* shoots being more top-heavy and a few shoots that fell over with no adjacent vegetation for support.

The decay of *L. salicaria* leaf litter was similar to the estimate of Emery and Perry (1996), but much lower than that observed by Grout et al. (1997). However, Grout et al.

Table 4
ANOVAs for the litter quality of plant stack samples for both the 1997 cohort and the 1998 cohort

| Source | Nitrogen | | | Carbon | | | Klason lignin | | | Ergosterol | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | d.f. | %TSS | *P* | d.f. | %TSS | *P* | d.f. | %TSS | *P* | d.f. | %TSS | *P* |
| 1997 Cohort | | | | | | | | | | | | |
| Species | 1 | 20.75 | <0.001 | 1 | 51.15 | <0.001 | 1 | 5.76 | 0.081 | | | |
| Height | 1 | 5.66 | 0.005 | 1 | 2.82 | 0.005 | 1 | 0.08 | 0.764 | | | |
| Treatment | 2 | 0.01 | 0.656 | 2 | 4.47 | 0.001 | 2 | 6.49 | 0.162 | | | |
| Date | 2 | 11.32 | 0.001 | 2 | 0.71 | 0.677 | 2 | 4.20 | 0.278 | | | |
| Error | 49 | 32.07 | | 49 | 21.38 | | 50 | 61.16 | | | | |
| 1998 Cohort | | | | | | | | | | | | |
| Species | 1 | 1.07 | 0.199 | 1 | 31.94 | <0.001 | 1 | 0.03 | 0.843 | 1 | 22.14 | <0.001 |
| Treatment | 2 | 2.57 | 0.326 | 2 | 6.24 | 0.002 | 2 | 1.69 | 0.363 | 2 | 5.86 | 0.002 |
| Date | 3 | 69.81 | <0.001 | 3 | 38.68 | <0.001 | 3 | 38.55 | 0.001 | 3 | 48.15 | <0.001 |
| Error | 28 | 14.56 | | 28 | 11.73 | | 28 | 27.30 | | 24 | 9.12 | |

%TSS: % total sum of squares.

(1997) examined decay rates in estuaries where they attributed high decay rates in some of their sites to wave action and current energy.

The relatively minor differences in litter quality that we observed among plant stakes and standing-dead samples suggests that the plant stake method accurately represented the early stages of emergent macrophyte decomposition. Moreover, the subtle differences in C and Klason lignin concentrations in *T. latifolia* shoots versus *L. salicaria* stems (Table 4) suggest that these two species were relatively similar in different classes of organic compounds in litter. The spatial patterns of N in standing-dead *L. salicaria* demonstrated that N was not homogeneous throughout the height of the plant. Regardless for the reason, these results suggest that concentrations of N in senescing plant tissue may be spatially explicit and confound measurements of decomposing tissues within litterbags.

Changes in N concentrations of the decomposing tissues of both species were much less than in other studies of emergent macrophyte decomposition in which litterbags were employed, particularly for *T. latifolia* (Morris and Lajtha, 1986; Findlay et al., 1990; Vargo et al., 1998; Gessner, 2000). Rather, our findings were in line with Newell et al. (1995), who compared changes in concentration of N between standing-dead and fallen leaves of *Carex walteriana*. Moreover, several studies have shown that litterbags suspended in the air without contact with the soil loose N in contrast to litterbags on the soil or peat surface (Boyd, 1970; Davis and van der Valk, 1978; Bruqueta de Zozaya and Neiff, 1991). In particular, Findlay et al. (1990) concluded that fungal biomass and mass loss alone could not explain a large increase in N content of *Typha* tissue in litterbags, suggesting that N adsorption from soil accounted for much of the N accumulation.

Although ergosterol concentrations differed among the two species we must conclude that ergosterol was a poor index of decomposition and tissue decomposability. The largest difference was found in ergosterol concentrations of standing-dead and plant stakes, but only in samples collected in May (Fig. 3). This suggests that fungal decomposers readily colonize newly senesced plant material in late autumn, and decline after that, presumably, as

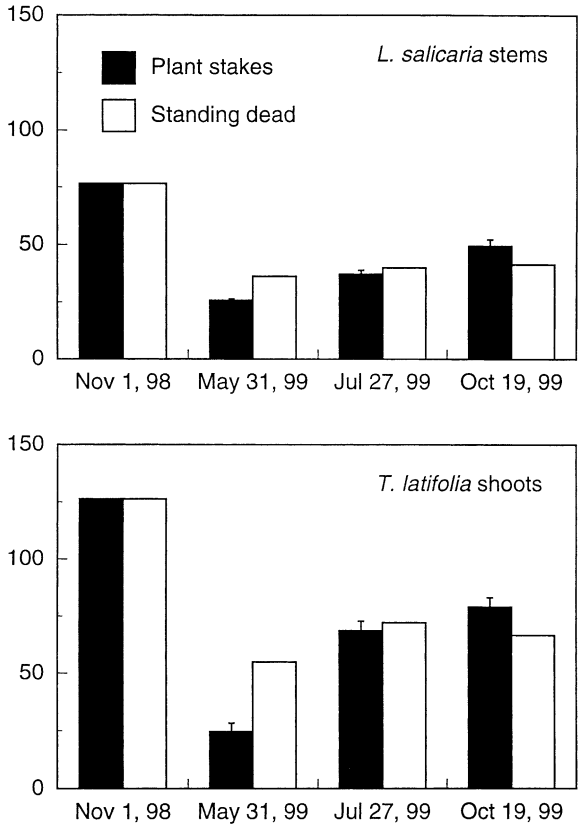


Fig. 3. Ergosterol concentrations of plant stake (black) and standing-dead (white) *L. salicaria* stems and *T. latifolia* shoots of the 1998 cohort. Values for plant stake samples are the mean and bars are standard errors. Ergosterol concentrations of standing-dead samples were weighted according to the height of the plant stake samples.

plant material is depleted of more labile carbon compounds and only recalcitrant substances remain (Barlocher and Biddiscombe, 1996; Kuehn et al., 1999).

The poor correlation between rates of $CO_2$ evolution and ergosterol has been found in a few other studies (e.g. Newell et al., 1995; Kuehn et al., 1999; Hackney et al., 2000). Apparently, fungi with differing proportions of ergosterol decompose plant tissue. In addition, studies have shown that the distribution of fungal communities changes with plant age as changing nutrient levels due to senescence and translocation, and harsh physical conditions such as desiccation influence the colonization of varying fungal species (Dix and Webster, 1995).

The heavy snowfall in 1997 did provide an opportunity to examine emergent decay when the standing-dead plants do fall over and are partially to totally submerged and compare it with aerial decomposition. We suggest that the litterbag method largely over-estimates rates of decay of emergent macrophytes due to the contact of senescing tissue with sediments and water, enhancing nutrient availability, and microbial activity. However, standing-dead

plants are subject to adverse weather conditions, such as heavy snowfall and winter winds. Thus, fragmentation can influence the absolute mass loss of a stem or shoot, as well as promote increased decay as the plant material is broken apart and delivered to the soil surface where decay rates are more rapid.

When standing after 1 year of decay, tissue of both species still had 80% mass remaining. Since much of this residue was recalcitrant material, decay, even on the soil surface, would likely be slow. The slow decay of remaining material could eventually lead to a substantial input to the sediment organic matter pool.

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