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Decomposition of *Carex* and *Nuphar* Plants in a Subalpine Marsh

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To assess the effect of water depth on the decomposition process, I measured the losses in dry mass of the above- and belowground materials of *Carex utriculata* and *Nuphar luteum* ssp. *polysepalum* as well as cellulose (Whatman filter paper) in the top 10 cm of sediment/soil in a subalpine marsh. Samples were examined by the litter bag technique at three flooding levels (0 to 5, 60, and 100 cm water depth). Over a 374-d period, the % mass losses of cellulose, *Carex* leaves and roots, and *Nuphar* leaves and rhizomes ranged from 98.5 to 99.0, 74.8 to 81.8, 36.3 to 44.9, 95.8 to 97.7, and 78.4 to 91.5%, respectively. Rates for cellulose decay in this study were much higher than for samples from other wetlands; this difference resulted from the location of the litter bag (in the top 10 cm of soil *vs* in the water column). Water depth significantly affected the decomposition of *Carex* roots and *Nuphar* rhizomes. The rate of loss for K was highest in all tissues of *Carex* and *Nuphar*, followed by Na in *Carex* and P in *Nuphar*. N and Ca loss rates generally were low. The C/N ratio tended to converge to a common value over the long term. This convergence has an important implication in the paleoecological interpretation of the C/N ratio change in sediment; i.e., this ratio shift in the sediment core results from a change in the environment, rather than the source material.

Keywords: *Carex*, cellulose, decomposition rate, *Nuphar*, subalpine marsh, water depth

Nuphar and *Carex* are important macrophytes in many subalpine marshes in California, USA, where they often dominate the wetland macrophyte community. These plants are capable of high primary production (Kim and Rejmánková, 2001) with only a small portion of their material being regularly consumed by herbivores (Wetzel, 1975). Therefore, decomposition is a key process in the recycling of nutrients and one of the major factors in the functioning of a wetland ecosystem.

The decomposition rates for plant litter in wetlands is important to ecosystem functions such as soil formation, nutrient cycling, and wastewater treatment. These processes involve nearly all changes in organic matter, e.g., senescence or death, fragmentation, leaching, feeding by detrivores, or changes of component chemistry. In general, decomposition rates are determined by substrate quality, climate, and site factors such as soil type and water quality (Godshalk and Wetzel, 1978; Swift et al., 1979; Kim and Rejmánková, 1999).

Most decomposition studies of vascular plant litter have concentrated on above-, rather than below-, ground plant materials in fens, bogs, and lowland marshes (Thormann and Bayley, 1997). Few studies have been conducted in subalpine marshes. Likewise, studies are lacking that deal with the effect of water depth on the decomposition process, although some have investigated the effect of *soil* depth (Hackney, 1987; Hemminga et al., 1988).

Plant communities in wetlands are determined primarily by water depth (Mitsch and Gosselink, 1993); decomposition of each plant material type occurs in its own particular microenvironment. Therefore, the three sites in the current study were selected for their different water depths and plant communities. The research objectives were to 1) compare cellulose decay rates (i.e., environmental differences) in a subalpine marsh versus those in other wetlands; 2) measure the decomposition rates for above- and belowground materials of the dominant species (*Carex* and *Nuphar*) in this subalpine marsh; 3) assess the effect of water depth on dry-mass loss; 4) compare the changes in C, N, P, Na, K, Ca, and Mg contents; and 4) relate the loss rates for these elements to litter type and water depth.

STUDY AREA AND METHODS

The study was carried out on Pope Marsh, a 70-ha subalpine marsh adjacent to Lake Tahoe, California, USA (38°56'N, 120°02'W). Elevation in this area

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(Tahoe city) is 1885 m, with an average annual temperature of 5.7°C and mean precipitation of 747 mm. The water level for Pope Marsh is largely determined by the water level in Lake Tahoe, and partly by the pumping of water into the Tahoe Keys, a recreational boat dock (Green, 1998). During the study period, the water level changed very little (less than 5 cm). Plant distribution in this marsh is determined primarily by water depth, with the deepest zone dominated by floating-leaved and submersed macrophytes such as water lily (*Nuphar luteum* L. ssp. *polysepalum* Engelman), horse tail (*Hippuris vulgaris* L.), pondweeds (*Potamogeton* spp.), and water milfoil (*Myriophyllum* spp.). The shallow areas are occupied by tule (*Scirpus acutus* Bigelow), sedge (*Carex utriculata* Boott), and rush (*Juncus balticus* Willd) (Rejmánková et al., 1999).

Plant material was collected from *N. luteum* ssp. *polysepalum* in May 1997 and from *C. utriculata* in November 1996. *Nuphar* rhizomes were collected in November 1996, cut into 1-cm-thick sections, then air-dried. The *Carex* samples were washed with tap water, divided into roots and leaves, and air-dried. Approximately 10 g of the dry materials was put into 10 × 10 cm nylon bags (1 mm mesh).

Dried *Nuphar* leaves and petioles are very fragile and difficult to handle. In addition, the decomposition of aquatic macrophytes is usually characterized by plant material gradually entering senescence and initial decay stages without first drying (Kok et al., 1990). Therefore, fresh *Nuphar* leaves and petioles were used for the litter bags. The collected leaves and petioles were blotted with paper to absorb surface moisture. An approximately 100-g mixture of fresh leaves and petioles was put into each nylon bag. Five of these 1-mm mesh bags were then used to determine the fresh to dry weight ratio. As a final treatment, two Whatman #1 filter papers were placed in each of the same type of mesh bag.

Decomposition rates have been shown to be greatest in the top 10 cm of soil (Hackney and de la Cruz, 1980). Therefore, the litter bags were inserted vertically into shovel slits in the surface soil within the top 10 cm at three water depths: 100 cm (*Nuphar* zone), 60 cm (*Hippuris* zone), and 0 to 5 cm (*Carex* zone) on May 9, 1997. After 113, 238, and 374 d, four litter bags of each type were retrieved from each location. In the laboratory they were washed carefully under running tap water. The contents were then dried at 30°C, weighed, and ground with a mortar and a pestle.

Chemical analyses were performed on subsamples of the ground litter. Ash contents were determined after combustion for 4 h at 550°C in a muffle furnace, then subtracted from dry mass. Hereafter, dry mass means ash-free dry mass. Total carbon (C) and nitrogen (N) were determined on a Carlo-Erba series 5000 CHN-S analyzer. Total phosphorus (P) was determined with ICP-AES (Inductively Coupled Plasma spectroscopy; Thermo Jarrell Ash Corporation, model Atom Scan 25) after microwave acid digestion (Sah and Miller, 1992). The digested solution was used to determine total sodium (Na), potassium (K), calcium (Ca), and magnesium (Mg), using a Perkin-Elmer 2380 Atomic Absorption Spectroscopy and following the methods of Allen (1989).

Duplicate water samples were collected at the interface of the sediment and water columns at each location, placed in a cooler, and filtered through Whatman #44 filter paper in the laboratory on the same day. Water temperature and conductivity were measured with an OMEGA digital thermometer (HH-15TC), a type T thermocouple Cu-CuNi probe, and a HANNA Hi 8633 conductivity meter. Ca, Mg, Na, and K concentrations were determined by a Perkin-Elmer 2380 Atomic Absorption Spectroscopy, following the methods of Allen (1989). Ammonium, nitrate, and soluble reactive phosphorus (SRP; PO_4^-) were analyzed according to the Indophenol, Hydrazine, and colorimetric (molybdenum-antimony solution) methods, respectively (Hunter et al., 1993). The pH of the water samples was measured potentiometrically with a Fisher Scientific Accumet 1003 pH/mV meter and a pH/ATC combination electrode.

Decomposition rates (k) were determined from a single negative exponential model ($Mt = Mo \times e^{-kt}$, Mo: dry mass at t = 0, Mt: dry mass at time t). StatView for Windows (Abacus Concepts, Inc. Version 4.57) and SPSS (Version 10) were used for the statistical analyses.

RESULTS AND DISCUSSION

Water Characteristics

Levels of nitrate, SRP, pH, and Ca from the water samples were highest in August (Fig. 1). Decomposition rates usually would be greater because of high daytime temperatures (Swift et al., 1979), but absorption of nutrients by these plants may have been low in August. In contrast, K, Na, and Mg levels were highest in December. K and Na, in particular, are very labile at that time of year, and are more susceptible to leaching after senescence (Schlesinger, 1997). Water resulting from snowmelt may have been responsible for the higher levels of Mg (Mitsch and Gosselink,

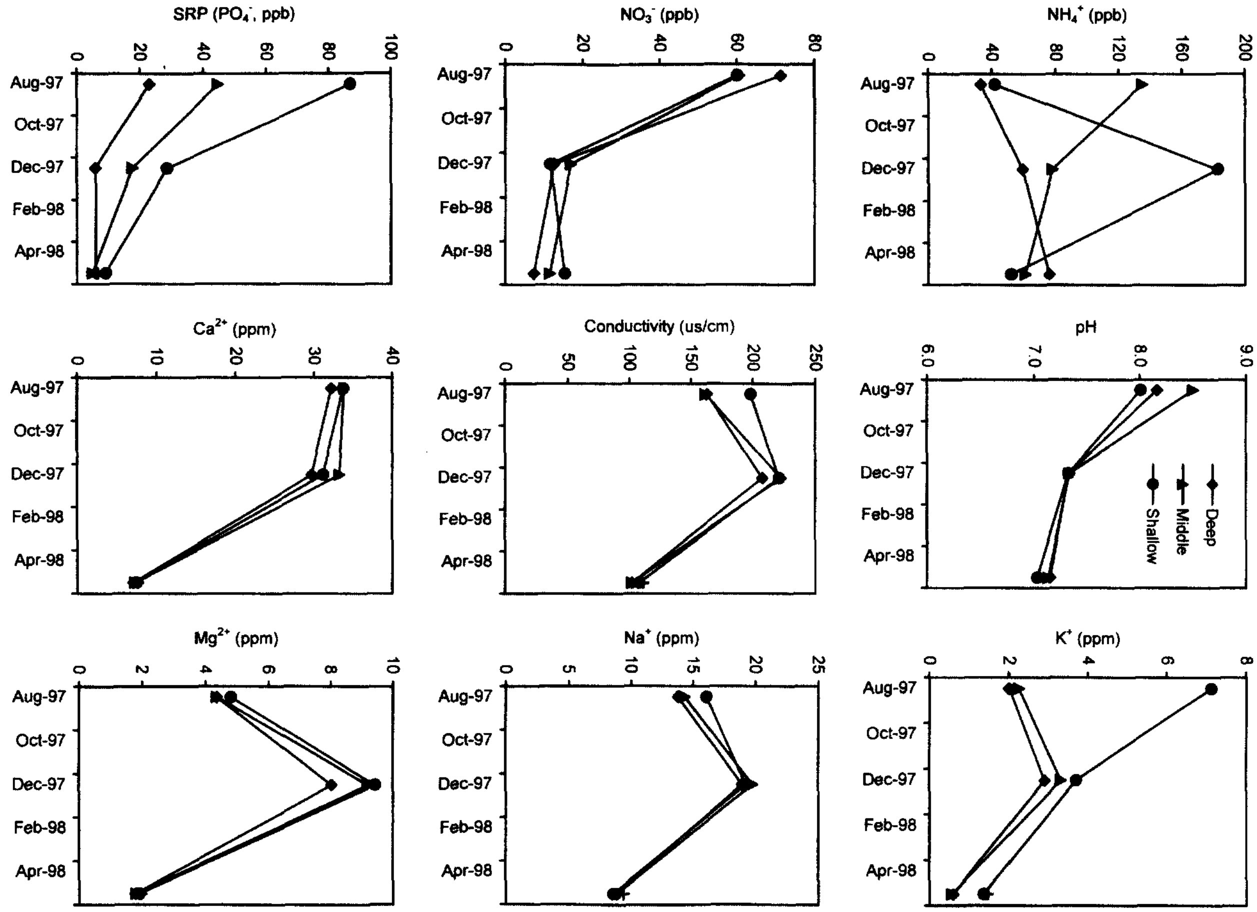

Figure 1. Changes in soil surface water parameters at three water depths in a subalpine marsh: deep (100 cm), middle (60 cm), shallow (0 - 5 cm).

1993). Ammonium contents showed no seasonal trends.

Levels of SRP in August varied by location, with amounts being greatest in the shallow areas and lowest in the deeper zones. Soluble reactive phosphorus in the water column originated primarily from decomposition of plant materials, whereas in sediment, the less decomposed organic material was an important source of SRP. Deep locations were dominated by *Nuphar*, while the middle zones were more heavily populated by *Hippuris*. Both species have softer stems and leaves than do *Carex* and, therefore, generally have higher decomposition rates (Brock et al., 1985; Kok et al., 1990; Kok and van der Velde, 1994). Thus, SRPs in middle and deep locations should have been higher in the fall because decomposition of *Nuphar* and *Hippuris* was greater after senescence. However, actual phosphorus concentrations did not support that hypothesis, indicating that another mechanism must govern underwater phosphorus levels. In general, ion concentrations were lowest in deeper locations and highest in shallow zones, with the exceptions being Ca and ammonium.

Decomposition of Cellulose, *Carex*, and *Nuphar*

The mass of all materials declined significantly over 113 d, averaging 76% for cellulose, 64% for *Carex* leaves, 30% for *Carex* roots, 90% for *Nuphar* leaves, and 62% for *Nuphar* rhizomes (Fig. 2). Over 374 d, % losses in mass for cellulose, *Carex* leaves and roots, and *Nuphar* leaves and rhizomes ranged from 98.5 to 99, 74.8 to 81.8, 36.3 to 44.9, 95.8 to 97.7, and 78.4 to 91.5%, respectively.

The pattern of decomposition in aboveground plant material generally can be divided into three phases, with different processes dominating each time period. The initial phase is characterized by rapid weight loss from the litter caused by leaching of soluble compounds. This phase is followed by an extended period

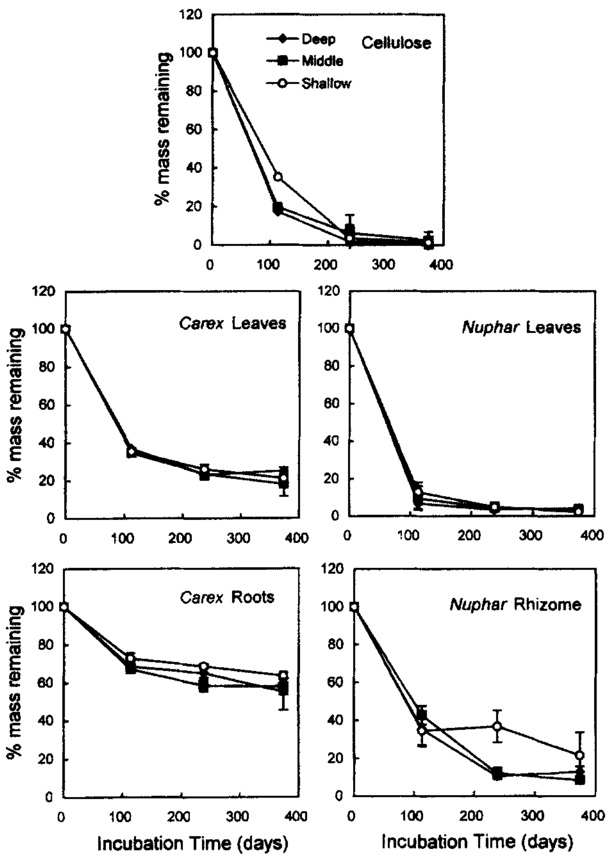

Figure 2. Percent remaining dry mass during a one-yr litter bag study with cellulose, *Carex* leaves and roots, and *Nuphar* leaves and rhizomes, at three water depths in a subalpine marsh: deep (100 cm), middle (60 cm), shallow (0 - 5cm).

of active microbial decomposition. The remaining refractory compounds are then degraded very slowly in the final stage (Swift et al., 1979). In the current study, the mass loss by 113 d had included the first stage, with the second stage continuing to the end of incubation for the *Carex* roots. Compared with the pattern of decomposition in other plant materials, leaching apparently was relatively unimportant in the process of weight loss from the *Carex* roots. This may have been caused by its larger proportion of non-leachable material, as was found by Hemminga et al. (1988) for *Spartina* root decomposition. Cellulose and *Nuphar* materials reached the third stage of decomposition in 238 d (Fig. 2).

Cellulose

Cellulose (filter paper) is a standard material used for measuring decay rates, even though its decomposition is determined by only environmental factors. The decomposition rates (k) for cellulose ranged from 2.669 to 11.236 yr^{-1} (6.49 - 0.01% of the remaining mass) over 374 d (Table 1). These decomposition rates are much faster than those found by Thormann and Bayley (1997). In their study, 15 to 95% of the mass remained after 365 d in fens, bogs, and marshes in the northern United States and southern Canada. Likewise, Kim and Rejmánková (1999) found that 25 to 96% of the mass remained after 90 d for subalpine marshes in the same area as was used in the current study. This difference can be explained by the location of the litter bag in the top 10 cm of the soil column in this study versus being located in the water column for the other studies.

Water depth did not significantly affect decomposition rates, although annual decomposition rates were highest for the deep locations and lowest in the middle zones (Tables 1 and 2). Thormann and Bayley (1997) showed that cellulose decomposition was best related to SRP in fens and marshes, while Verhoeven et al. (1996) suggested that decomposition was positively correlated with the richness of both interstitial water nutrients and soil P. However, nutrient-rich wetlands do not always show higher decomposition rates

Table 1. Annual decomposition rates, k (yr^{-1}, mean ± SE, (n)), calculated from a single negative exponential model at the end of the study (374 d).

	Filter Paper	*Carex* Leaves	*Carex* Roots	*Nuphar* Leaves	*Nuphar* Rhizome
Deep	9.800 ± 1.435 (3)	1.434 ± 0.294 (3)	0.619 ± 0.121 (3)	3.127 ± 0.159 (4)	1.999 ± 0.113 (3)
Middle	4.413 ± 0.641 (4)	1.672 ± 0.069 (4)	0.572 ± 0.034 (3)	3.201 ± 0.028 (3)	2.410 ± 0.066 (4)
Shallow	6.749 ± 1.568 (4)	1.527 ± 0.101 (4)	0.441 ± 0.018 (3)	3.699 ± 0.119 (2)	1.618 ± 0.289 (4)

Table 2. Two-way ANOVA for time and water depth effects on cellulose, *Carex*, and *Nuphar* decomposition rates. Results from StatView; degrees of freedom of water depth is 2, that of time is 3; figures are *P* values.

Factor	Cellulose	*Carex* leaves	*Carex* roots	*Nuphar* Leaves	*Nuphar* rhizome
Water Depth	0.09	0.543	0.004	0.236	0.017
Time	<0.001	<0.001	<0.001	<0.001	<0.001
Water Depth X Time	0.020	0.797	0.146	0.066	0.011

(Bayley et al., 1985; Rochefort et al., 1990; Bridgham and Richardson, 1992), as was also demonstrated in the current study.

Carex

After 374 d, the decomposition rates (k) for *Carex* leaves and roots ranged from 0.888 to 1.895 yr^{-1} and from 0.420 to 0.837 yr^{-1} (40.2 to 14.3% and 65.0 to 42.4% mass remaining), respectively. In other studies, the mass remaining for decomposing *Carex* spp. was 17 to 65% in the Spring fens of Sweden (Ohlson, 1987); 41 to 50% for boreal fens and 46 to 51% for marshes in Alberta, Canada (Thormann and Bayley, 1997); 55% in the bogs and 55 to 69% in the fens of central Alberta, Canada (Szumigalski and Bayley, 1996); and 50% in Iowa, USA, marshes (Davis and van der Valk, 1978). In comparison, the decay rates for *Carex* materials were very high in the subalpine Pope Marsh. Again, the location of the litter bags may have been a factor here. Average decomposition rates (k) for Carex roots were 0.619, 0.572, and 0.441 in deep, middle, and shallow locations, respectively (Table 1). The belowground root rates were lower than those for aboveground leaf materials, which may have been due to lower initial nutrient levels and higher amounts of structural materials in the root litters (Hackney and de la Cruz 1980).

Nuphar

The decomposition rates (k) for *Nuphar* leaves and rhizomes ranged from 2.852 to 3.819 yr^{-1} and from 0.967 to 2.532 yr^{-1} (5.4 to 2.0% and 37.1 to 7.5%), respectively. This leaf decay rate (k) at Pope Marsh was within the ranges found in other studies: i.e., 3.6 to 4.4 yr^{-1} for *Nuphar lutea* and *Nymphaea alba* in the Netherlands (Kok et al., 1990); and ~10% remaining material for spatterdock (*Nuphar* sp.) after 200 d (Fogel and Tuross, 1999). Howard-Williams et al. (1983) proposed that an elevated N content (up to 7.1%) might be responsible for the high decomposition rate for fresh samples of *Nasturtium officinale* (only 4% of the original remaining after 27 d). Wrubleski et al. (1997) also suggested that collecting only live material could have led to the high leaching rates in the early stage of decomposition. This high rate can be partially explained by the relatively low level of structural carbohydrates in the green tissues and by the rapid loss of relatively large protoplasmic components (Brock et al., 1985). Although the *Nuphar* rhizome has a large amount of carbohydrates such as starch, its decomposition rates were lower than for the leaves (Table 1). This may have been due to the relatively low N and P concentrations available for microorganisms as well as a much lower level of phosphatase activity than in the leaves (Kim, unpublished data).

Effect of Water Depth on Dry Mass Decomposition

A two-way ANOVA test demonstrated the effect of water depth on decay rates (Table 2). Depth significantly affected decomposition of both *Carex* roots and *Nuphar* rhizomes. This factor can also influence light intensity, diurnal changes in temperature, and levels of dissolved oxygen. Decay rates for *Carex* roots and *Nuphar* rhizomes were greatest in the deep and middle locations, respectively. This result was the opposite of that expected, where shallow zones generally have higher decay rates.

The decomposition of other plant materials, however, was not significantly affected by water depth. Therefore, one cannot make a general statement about the effect of depth on decay rates, although the frequency of inundation is an important factor in the rate of decay processes in a salt marsh (Hemminga et al., 1988). Overall, the results of the current study do support the conclusions of Wrubleski et al. (1997), who showed that flooding depth had little effect on dry mass decomposition rates for the belowground litter of emergent macrophytes (*Typha glauca, Phragmites australis, Scolochloa festucacea, Scirpus lacustris*) in a northern prairie marsh.

Changes in Elemental Contents during the Decomposition Process, and the Relationship between Litter Type, Water Depth, and Element Losses

Table 3 shows the changes in N, C, P, Na, K, Ca, and Mg contents over time. During the study period, N content increased for *Carex*, converging to 1.07%. Levels of N in *Nuphar* leaves decreased, while *Nuphar* rhizomes showed an increase in N from 1.19 to 2.07%, and oscillating at this level. Most vascular plant litter increases in N content over time (Kim and Chang, 1989; Szumigalski and Bayley, 1996). Although N content in *Carex* was not high but did increase, the amount of N in *Nuphar* leaves originally was high, but then decreased.

P content in *Carex* decreased over the first 113 d, then was maintained at a level of 600 to 750 mg/kg. The level of phosphorus in *Nuphar* was more than twice that of *Carex*, but continuously decreased over

Table 3. Mean (± SE) contents of seven elements for *Carex* and *Nuphar* plant materials from decomposition bags in a subalpine marsh over 374 d in 1997. n = 9.

	Time (d)	Remaining Mass (%)	N (%)	C (%)	P (mg/kg)	Na (mg/kg)	K (mg/kg)	Ca (mg/kg)	Mg (mg/kg)
Carex	Initial	100.0	0.70 ±0.06	42.57±0.99	1473±146	1222± 78	14579±1540	2478±105	1212±63
Leaves	113	35.4±0.7	0.89±0.03	45.49±0.64	645± 24	614± 25	435± 36	2344± 58	613±17
	238	24.8±1.3	0.97±0.07	43.48±1.20	685± 37	562± 26	578± 126	3121±590	1022±74
	374	21.1±2.7	1.07±0.05	44.01±0.92	752± 54	572± 57	524± 70	2782±211	725±45
Carex	Initial	100.0	0.80±0.02	43.80±0.44	977±100	2947±389	10166±986	2620± 32	1451±31
Roots	113	69.0±1.3	0.81±0.03	46.33±0.51	601± 9	383± 12	382± 15	3355±111	844±34
	238	64.2±1.7	0.94±0.06	47.18±0.24	657± 31	515± 49	367± 42	3896±192	995±45
	374	58.5±2.5	1.07±0.12	47.45±0.56	738± 61	664± 28	441± 70	4797±552	765±49
Nuphar	Initial	100.0	3.18±0.04	43.07±0.13	3947± 41	1291± 65	23192±629	5076±161	1375±27
Leaves	113	10.0±1.1	3.54±0.42	44.60±1.75	1594±289	768± 28	411± 26	7778±302	982±61
	238	4.1±0.3	2.53±0.48	42.06±1.05	1244±250	788± 40	578± 57	5765±388	1325±98
	374	3.4±0.3	1.83±0.15	49.65±0.51	679± 74	1037± 54	429± 11	6314±371	994±58
Nuphar	Initial	100.0	1.19±0.16	41.76±0.01	2980±575	1371±155	21582±419	2957±143	1186±46
Rhizome	113	38.8±2.5	2.07±0.11	44.19±0.43	950± 33	477± 28	542± 28	11009±789	863±61
	238	24.9±4.7	1.97±0.10	43.54±0.62	820± 52	700± 23	498± 25	9822±676	1131±59
	374	16.9±3.5	2.09±0.08	45.41±0.77	667± 53	706± 62	521± 40	10017±939	954±39

Table 4. Three-way ANOVAs for litter type, water depth, and time effects on mass, N, C,P, Na, K, Ca, and Mg losses. Results from SPSS program for PC (version 10); d.f.: degrees of freedom; all other figures are *P* values.

	d.f.	Dry Mass	Total N	Total C	Total Na	Total K	Total Ca	Total Mg
Litter type	3	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Water depth	2	0.002	0.18	0.002	0.004	0.001	0.040	0.294
Time	3	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Litter type X Water depth	6	0.054	0.169	0.048	0.028	0.198	0.009	0.143
Litter type X Time	9	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Water depth X Time	6	0.070	0.171	0.166	<0.001	0.015	0.069	0.807
Litter type X Water depth X Time	18	0.014	0.348	0.021	0.011	0.350	0.006	0.054

time until it was at the same level as for *Carex* (~670 mg/kg) by the end of the incubation period. Similar results were seen with *N. lutea* and *N. alba* decomposition in the Netherlands, where initial N and P concentrations were highest, then decreased with time (Kok et al., 1990).

Carbon contents did not change significantly during the test period, whereas both Na and K contents decreased within the first 113 d and then were maintained at similar levels. These two latter elements are very labile and can easily be leached. In contrast, the levels of the more recalcitrant elements Ca and Mg did not fluctuate over time.

Mass loss of all elements, including those measured in the dry mass, was significantly related to litter type (Table 4). The four types in this study varied in their levels of N and P, a determining factor for decay rates (Verhoeven et al., 1990; Taylor et al., 1991). Although water depth significantly affected mass loss of dry weight, C, Na, K, and Ca, the two-way ANOVA revealed little effect on dry mass loss (Table 2). Time and litter type X time also had a significant effect on mass loss of all elements. The loss rate followed the order of K>Na>P>Mg>C>Ca>N in *Carex* leaves, K>Na>Mg>P>C>N>Ca in *Carex* roots, K>P>Na>Mg>N>C>Ca in *Nuphar* leaves, and K>P>Na>Mg>C>N>Ca in the *Nuphar* rhizome. Brock (1984) showed loss rates of various elements from the coarse detritus of *Nymphoides peltata* in the order of K>Na>P>Mg>C>N>Ca>Fe. Overall, loss rates were highest for K and lowest for Ca in the current study. The loss of other elements might depend on plant materials and environmental factors.

Changes in C/N Ratios over Time

The C/N ratio in plant materials changed over time (Fig. 3), with that of *Carex* decreasing continuously. The ratio for *Nuphar* rhizomes decreased within 113 d, then stabilized at ~22. Szumigalski and Bayley (1996) had shown that the C/N ratios for vascular tissues usually decreased gradually during two yr of

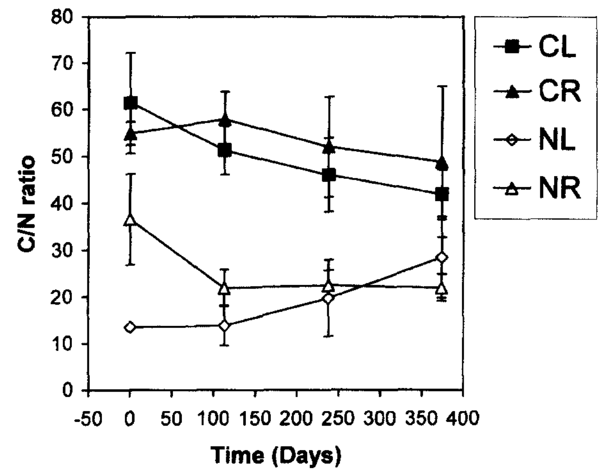

Figure 3. Change in average C/N ratios for *Carex* leaves and roots, and *Nuphar* leaves and rhizomes, over 113, 238, and 374 d of decomposition in a subalpine marsh. Average and 1 S.E. of 12 samples.

decomposition. However, the C/N ratio for *Nuphar* leaves in the current study increased continuously. Extrapolating these results would suggest that the C/N ratio converges to a common value in the long run. This is supported by the observations of Fogel and Tuross (1999), who showed that the C/N ratio of spatterdock (*Nuphar* sp.) converged from 56 to 17 during 100 d of incubation. Likewise, Thormann and Bayley (1997) found that C/N ratios for *Carex lasiocarpa* and *Typha latifolia* approached values of 15 to 21 over 456 d. This convergence of C/N ratios over time has an important implication for paleoecological interpretations of C/N ratio changes in the sediment core; the shift in ratios resulting from environmental changes, rather than from changes in the source plant materials of the sediment.

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