

# Drought-deciduous behavior reduces nutrient losses from temperate deciduous trees under severe drought

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**Abstract** Nutrient resorption from senescing leaves is an important mechanism of nutrient conservation in temperate deciduous forests. Resorption, however, may be curtailed by climatic events that cause rapid leaf death, such as severe drought, which has been projected to double by the year 2100 in the eastern United States. During a record drought in the southeastern US, we studied 18 common temperate winter-deciduous trees and shrubs to understand how extreme drought affects nutrient resorption of the macronutrients N, P, K, and Ca. Four species exhibited drought-induced leaf senescence and maintained higher leaf water potentials than the remaining 14 species (here called drought-evergreen species). This strategy prevented extensive leaf desiccation during the drought and successfully averted large nutrient losses caused by leaf desiccation. These four drought-deciduous species were also able to resorb N, P, and K from drought-senesced leaves, whereas drought-evergreen species did not resorb any nutrients from leaves lost to desiccation during the drought. For *Oxydendrum arboreum*, the species most severely affected by the drought, our results indicate that trees lost 50% more N and P due to desiccation than would have been lost from fall senescence alone. For all drought-deciduous species, resorption of N and P in fall-senesced leaves was highly proficient, whereas resorption was incomplete for drought-evergreen species. The lower

seasonal nutrient losses of drought-deciduous species may give them a competitive advantage over drought-evergreen species in the years following the drought, thereby impacting species composition in temperate deciduous forests in the future.

**Keywords** Nutrient resorption · Leaf senescence · Temperate forest · Desiccation · Nitrogen

## Introduction

Nutrient resorption from senescing leaves is an important mechanism of nutrient conservation in temperate deciduous forests (Chapin 1980; Killingbeck 1984). On average, around 50% of leaf nitrogen (N) and phosphorus (P) is recycled via resorption during fall senescence (Aerts 1996), and although resorption of other nutrients is less efficient, it may still be important in the nutrient budgets of forest ecosystems (Duchesne et al. 2001). Nutrients that are resorbed and stored internally, rather than lost with leaf fall, are thus a readily available pool of nutrients for the plant. Furthermore, it has been shown experimentally that artificial prevention of nutrient resorption in species with high resorption efficiencies can adversely affect plant fitness (Eckstein et al. 1998; May and Killingbeck 1992).

The proportion of a nutrient withdrawn from leaves (i.e., resorption efficiency) varies widely among species (Aerts 1996; Killingbeck 1996). Even within species, resorption efficiency can be highly variable and is influenced by a number of variables, including soil fertility (Côté et al. 2002), time span of senescence (Del Arco et al. 1991), summer temperature (Nordell and Karlsson 1995), and growing season precipitation (Minoletti and Boerner 1994).

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Drought has previously been shown to decrease the resorption efficiency of N and P in some plants (Hocking 1982; Killingbeck et al. 1990), suggesting that drought-induced leaf senescence results in a net loss of nutrients from a plant. This may not be the case, however, if senescence averts even greater losses resulting from desiccation and death of leaves. A number of woody plant species regularly shed their leaves during drought to reduce transpiring surfaces, regulate plant water potential, and conserve water (Larcher 2003). Failure to regulate leaf area during severe drought can lead to sufficiently low water potentials to cause death of foliage (Engelbrecht and Kursar 2003; Slot and Poorter 2007), possibly resulting in the loss of the entire nutrient capital of the leaf.

While drought-induced leaf senescence has been regarded as an important mechanism for preventing nutrient losses (Munné-Bosch and Alegre 2004), this has not been well quantified. To do so, it is critical to distinguish between drought-induced leaf senescence, where nutrient resorption may occur, and desiccation as a result of lethal water deficits, where resorption may not be possible. Species vary greatly in their reliance upon leaf senescence during drought. For example, in regions with strongly seasonal precipitation, there is a clear distinction between drought-deciduous and drought-evergreen species (Murphy and Lugo 1986). In at least some cases, drought-evergreen species may completely lack the capacity to reduce leaf area in response to water deficit via plant-regulated senescence, and therefore retain leaves until desiccation occurs.

In temperate deciduous forests, where extreme drought is infrequent, it is less certain whether woody plants exhibit a similar diversity in drought-related phenology, though experimental evidence suggests that they do (Pallardy and Loewenstein 2004). To characterize this diversity and to determine the implications for averting leaf desiccation and nutrient loss, we undertook a study in two temperate deciduous forest sites experiencing extreme drought. Our objective was to understand how extreme drought affects nutrient resorption of the macronutrients N, P, K, and Ca in 18 species of temperate deciduous trees and shrubs. We quantified the consequences of the extreme drought on the nutrient capital of each species, which should depend upon (1) the proportion of foliage lost to desiccation versus drought-induced leaf senescence, (2) the amount of nutrient resorption from drought-senesced leaves, and (3) the amount of nutrient resorption (if any) from desiccated leaves. We hypothesized that drought would decrease nutrient resorption in all species, but species with drought-deciduous behavior would have relatively lower nutrient losses due to reduced leaf desiccation and greater nutrient resorption in drought-senesced leaves.

## Methods

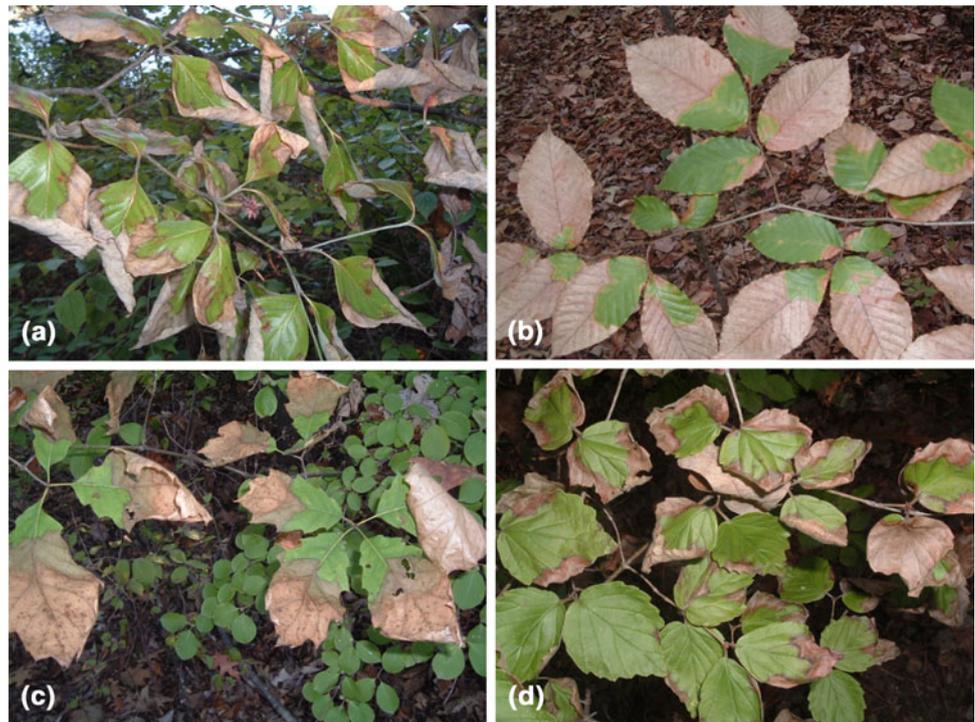
### Study sites and conditions

Our study was conducted in central North Carolina, USA in the late summer of 2007, where much of the region was experiencing record drought conditions as a result of low precipitation and high temperature. August 2007, the month preceding the study period, was the driest on record (since 1895) for the state of NC (49 mm vs. mean of 135 mm), and it was the second hottest on record (26.9 vs. 24.5°C). By the end of October 2007, however, drought conditions had effectively ended, following several days during which 142 mm of rainfall were recorded.

We chose two study sites in mixed hardwood forests in Wake County, NC that exhibited widespread wilting, leaf senescence, and desiccation of foliage (Fig. 1). The sampling area at Hemlock Bluffs Nature Preserve (HB; 35.7225°N, 78.7895°W, 124 m asl) was located 10 km from the study site at Fred G. Bond Metro Park (BP; 35.7791°N, 78.8289°W, 113 m asl). The HB study site was on Pacolet sandy loam (Typic Kanhapludults, Ultisol) located on a west-facing slope between two drainages (13–24% slope). The BP study site, located on an east-facing slope near Bond Lake (13–20% slope), was on White Store sandy loam (Vertic Hapludalf, Alfisol) derived from Triassic materials. Both sites had sandy loam surface soils underlain by clay-rich soil layers, with shallow paralithic bedrock at depths of 80–100 cm. At BP, the paralithic layer is composed of sandstone, but at HB it is argillite. The most abundant tree species at HB were *Liquidambar styraciflua*, *Carya glabra*, *Acer rubrum*, *Fagus grandifolia*, and *Oxydendron arboreum*, whereas the most abundant trees at BP were *Quercus alba*, *Carya alba*, *Fraxinus americana*, *A. rubrum*, and *Acer floridanum*. Sampling areas were kept small (HB: approximately 2,100 m<sup>2</sup>; BP: approximately 1,250 m<sup>2</sup>) to minimize microsite differences in the environment and accurately characterize differences in species response to drought conditions. When pooling all species together, there was no evidence of a difference in mean foliar nutrient concentration between sites (healthy leaves,  $P = 0.22$ ; fall-senesced leaves,  $P = 0.17$ ).

Between the two sites, we chose to monitor 18 common temperate deciduous forest species. For this study, we designated a species as “drought-deciduous” if it exhibited widespread leaf senescence, although no trees became completely leafless as a result of the drought. In contrast, a species was considered “drought-evergreen” if we did not observe leaf senescence in response to drought. Only four of our study species were drought-deciduous: *A. rubrum*, *L. styraciflua*, *Liriodendron tulipifera*, and *Nyssa sylvatica*. By early September 2007, these species had lost many

**Fig. 1** Examples of leaf desiccation in **a** *Cornus florida*, **b** *Fagus grandifolia*, **c** *Quercus rubra*, **d** *Viburnum rafinesquianum*



leaves, typically retaining only the youngest leaves on each branch. Unlike leaf death due to desiccation, this senescence was characterized by a loss of chlorophyll followed by leaf abscission, and was therefore visually similar to autumnal leaf loss, which did not occur until mid- to late October in the non-drought year 2008. In *Prunus serotina* and *F. americana*, we observed a smaller amount of leaf senescence during the drought, but the response in these species was not as uniform as with the previous species, and thus these two species were classified as drought-evergreen.

#### Leaf desiccation and water potential

We placed several transects across each of the sampling sites to quantify species responses to drought in the tree and shrub community. Along the transect, two observers provided independent visual estimates of the percentage of desiccated leaf area for individual plants of the target species ( $n = 1\text{--}27$ , mean = 15) that were >1 m tall. For species underrepresented in the transects, we sampled additional individuals from outside the transects.

We measured predawn water potential ( $\Psi_w$ ) of leaves for 3–6 individuals per species at the study sites during the height of the drought (7–12 September 2007). Each cut leaf was put in a sealable plastic bag containing a small piece of wet paper towel, placed in a cold, dark, insulated cooler, and returned to the laboratory for measurement. Water potentials were measured within 2 h with a pressure

chamber (Model 1000, PMS Instruments, Corvallis, OR, USA).

#### Foliar nutrient concentration

To assess the consequences of leaf desiccation for plant nutrient budgets, we compared nutrient concentrations of (1) healthy, mature leaves, (2) desiccated leaves, (3) leaves that had senesced during the drought, and (4) leaves that senesced during the normal period of autumn leaf fall. For the first three classes of leaves, samples were collected on 7–8 September 2007, during the period of most extreme drought. Here, we considered a leaf to be desiccated if it dried while still attached to the plant, and we did not include leaves from individuals in which the whole plant appeared dead (i.e., every leaf was desiccated and terminal branches were dehydrated). In many cases, leaves on a plant would be only partially desiccated, with the petiole and part of the leaf blade remaining alive (Fig. 1). In these cases, only the dead portions of the leaves were collected for analysis, but care was taken to ensure that samples included midrib and leaf blades in proportions similar to that of a whole leaf. In contrast, a leaf was considered to be senesced if it underwent a change in color similar in appearance to autumnal leaf senescence, despite occurring many weeks earlier than usual. On 7–17 November 2007, five weeks after the first collection period and after drought conditions had ended, we collected recently senesced leaves for each species during natural fall senescence.

Senesced leaves were chosen by either gently shaking a branch to promote leaf fall or collecting recently fallen leaves from directly below an individual. In the latter case, we limited collection to leaves that were obviously recently senesced, based on color and level of hydration.

For each leaf class, we collected 3–5 leaves per individual and three individuals per species. Each species was sampled at only one site, except for *Viburnum rafinesquianum*, which was sampled at both sites. Leaves were dried in an oven at 70°C for 48 h, and leaves were pooled by individual and ground in a Wiley mill. Analysis for N, P, K, and Ca content was performed by the Analytical Services Laboratory of the NCSU Soil Science Department (Raleigh, NC, USA).

Nutrient resorption efficiency is most accurately calculated as the change in nutrient concentration between green and senesced leaves while accounting for changes in total leaf mass during senescence, such that a nitrogen resorption efficiency of 50% indicates that 50% of the nitrogen in leaves was withdrawn before abscission (van Heerwaarden et al. 2003). An alternative measure of resorption is resorption proficiency, which is simply the concentration of an element in senesced leaves (Killingbeck 1996). One advantage of measuring resorption as proficiency is that the variability associated with green leaf nutrient content is removed as a source of error (Killingbeck 2004). With this measure, a low value of resorption proficiency indicates high nutrient resorption by the plant. Killingbeck (1996) determined the maximal potential withdrawal of nutrients from senescing leaves by compiling data from 89 species of woody perennials, concluding that in deciduous species, resorption proficiencies of below 0.7% for N and below 0.05% for P are complete. In this study, we used resorption proficiency to compare resorption among species. Proficiency is most accurately expressed on a concentration basis (mass of nutrient per mass of leaf, Killingbeck 2004) and avoids any underestimation of resorption due to mass resorption during senescence (Oland 1963; van Heerwaarden et al. 2003).

#### Statistical analyses

Linear regression was used to test for a correlation between leaf  $\Psi_w$  and leaf desiccation. Separate matched-pairs Student's *t* tests were used to analyze differences in the mean foliar nutrient concentrations between the following leaf groups: healthy versus drought-senesced, healthy versus fall-senesced, and drought-senesced versus fall-senesced leaves. For these analyses, values were paired by species. Additional Student's *t* tests (unpaired) were performed to test for differences between leaf groups within each species. Analysis of variance (ANOVA) was used to test

for differences in resorption proficiency of N and P between drought-deciduous and drought-evergreen species. Mean increase in nutrient loss of N and P due to leaf desiccation was determined for each species according to the following formula:

$$NL = \left( \frac{(a - a')}{a'} \right) b$$

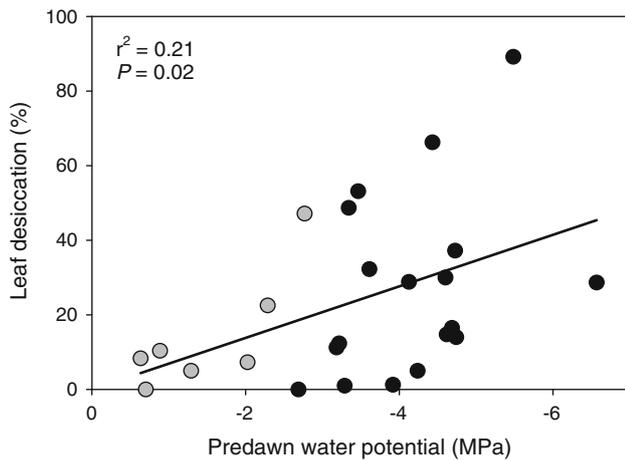
where *a* is the mean nutrient concentration of desiccated leaves, *a'* is the mean nutrient concentration of fall-senesced leaves, and *b* is the mean percentage of desiccated leaf area. Differences in mean seasonal nutrient loss were compared between drought-deciduous and drought-evergreen species with ANOVA. All data were tested for normality with the Shapiro and Wilk's test ( $P \leq 0.05$ ), and data were ln-transformed to fit a normal distribution when necessary. Analyses were performed with JMP 7.0 (SAS Inst., Cary, NC, USA).

#### Results

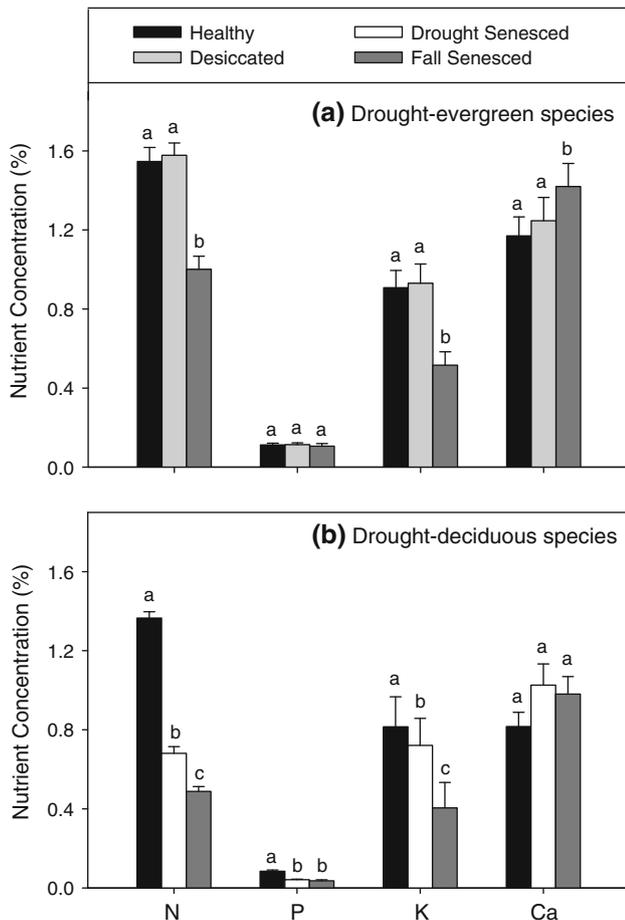
The study area exhibited signs of acute water deficit in early September 2007, following six months of little rainfall and high temperatures. The leaves of many species had desiccated while still attached to the plant (Fig. 1), although this response was highly variable among species. Within the same two sites, mean predawn water potential ( $\Psi_w$ ) varied considerably among species, ranging from –6.6 MPa in *V. rafinesquianum* to –0.6 MPa in *N. sylvatica* (Fig. 2). Mean  $\Psi_w$  ranged from –0.6 to –2.8 MPa among drought-deciduous species, while the range for drought-evergreen species was –2.7 to –6.6 MPa. There was a significant correlation ( $R^2 = 0.21$ ,  $P = 0.02$ ) among species between predawn water potential and percent leaf desiccation (Fig. 2), and species with lower  $\Psi_w$  had higher percentages of leaf desiccation.

There was no evidence of nutrient resorption from leaves that had died from desiccation. Mean nutrient concentrations of healthy and desiccated leaves were not different for N (1.55 vs. 1.58%, paired  $t_{13} = 0.66$ ,  $P = 0.52$ ), P (0.11 vs. 0.11%, paired  $t_{13} = 0.47$ ,  $P = 0.65$ ), K (0.91 vs. 0.93%,  $t_{13} = 0.69$ ,  $P = 0.50$ ), or Ca (1.17 vs. 1.25%,  $t_{13} = 1.63$ ,  $P = 0.13$ , Fig. 3a). Similarly, when analyzed for each species separately, no species exhibited a significant difference in concentrations of N, P, K, or Ca between healthy and desiccated leaves (Table 1).

In contrast, concentrations were significantly lower in leaves that had senesced during the drought, relative to healthy leaves, in N (0.68 vs. 1.37%, paired  $t_3 = 15.03$ ,  $P = 0.0006$ ), P (0.04 vs. 0.08%, paired  $t_3 = 9.44$ ,  $P = 0.003$ ), and K (0.72 vs. 0.82%, paired  $t_3 = 04.69$ ,  $P = 0.02$ ), but not



**Fig. 2** Linear regression between mean predawn water potential (MPa) and mean leaf desiccation (%) for drought-deciduous species (shaded circles) and drought-evergreen (black circles). Each point represents the mean for one species at a site



**Fig. 3 a** Mean nutrient concentrations (N, P, K, Ca %) of healthy, desiccated, and fall-senesced leaves of 14 species. **b** Mean nutrient concentrations (N, P, K, Ca %) of healthy, drought-senesced, and fall-senesced leaves of four drought-deciduous species. Bars not connected by the same letter are statistically different

Ca (1.03 vs. 0.82% paired  $t_3 = 3.25$ ,  $P = 0.05$ , Fig. 3b). When tested for each species separately, concentrations of N and P were always significantly lower in drought-senesced leaves than in healthy leaves, while for K and Ca, the differences were not significant for any species (Table 2).

Although there was considerable nutrient resorption from drought-senesced leaves, this process was not as proficient as in fall-senesced leaves. Drought-senesced leaves, when compared to fall-senesced leaves, had higher concentrations of N (0.68 vs. 0.49%, paired  $t_3 = 5.37$ ,  $P = 0.02$ ) and K (0.72 vs. 0.40%, paired  $t_3 = 10.30$ ,  $P = 0.002$ ), but not of P (0.04 vs. 0.04%, paired  $t_3 = 0.88$ ,  $P = 0.44$ ) or Ca (1.03 vs. 0.98%, paired  $t_3 = 0.44$ ,  $P = 0.69$ , Fig. 3b).

Nutrient resorption during fall senescence was highly variable among species. Mean concentrations were significantly lower in fall-senesced leaves, relative to healthy leaves, of N (0.49 vs. 1.37%, paired  $t_3 = 17.77$ ,  $P = 0.0004$ ), P (0.04 vs. 0.08%,  $t_3 = 5.72$ ,  $P = 0.01$ ), and K (0.40 vs. 0.82%,  $t_{13} = 10.93$ ,  $P = 0.002$ ), but not Ca (0.98 vs. 0.82%,  $t_{13} = 1.56$ ,  $P = 0.22$ ) for the drought-deciduous species (Fig. 3b). Among drought-evergreen species, mean concentrations were significantly lower in fall-senesced versus healthy leaves for N (1.00 vs. 1.55%,  $t_{13} = 6.05$ ,  $P < 0.0001$ ) and K (0.52 vs. 0.91%,  $t_{13} = 9.08$ ,  $P < 0.0001$ ), but not P (0.11 vs. 0.11%,  $t_{13} = 1.06$ ,  $P = 0.31$ ) or Ca (1.42 vs. 1.17%,  $t_{13} = 3.11$ ,  $P = 0.009$ , Fig. 3a). When analyzed individually, most species had lower concentrations of N, P, and K in fall-senesced versus healthy leaves, although this difference was not always significant (Tables 1, 2). Concentrations of Ca were not significantly lower in fall-senesced versus healthy leaves for any species (Tables 1, 2).

Resorption proficiencies of below 0.7% for N and below 0.05% for P are considered complete for fall-senesced leaves of deciduous species (Killingbeck 1996). During fall senescence after the extreme drought, complete N resorption was found in the four drought-deciduous species and one drought-evergreen species, whereas complete P resorption was found in the four drought-deciduous and two drought-evergreen species (Tables 1, 2). Overall, the drought-deciduous species were more proficient at nutrient resorption, as evidenced by significantly lower resorption proficiencies for N (0.49 vs. 0.99%,  $F = 17.03$ ,  $P = 0.0008$ ) and P (0.036 vs. 0.106%,  $F = 8.17$ ,  $P = 0.01$ ) than drought-evergreen species (Tables 1, 2). Mean nutrient loss due to desiccation was high for both N and P in *O. arboreum* and *Viburnum acerifolium* (Fig. 4). These species lost 57.3 and 42.9%, respectively, of the N and 52.9 and 48.3% of the P that would normally be resorbed during the fall.

**Table 1** Mean nutrient concentration (N, P, K, Ca %) of healthy (H), desiccated (D), and fall-senesced (FS) leaves in 14 species ( $n = 3$ ) from two heavily droughted sites

Species	Nutrient	Healthy	Desiccated	Fall-senesced		P values		
						H vs. D	H vs. FS	D vs. FS
<i>Acer floridanum</i>	N	1.42	1.49	0.65	●	ns	***	***
	P	0.17	0.19	0.16	○	ns	ns	ns
	K	0.63	0.72	0.17		ns	***	***
	Ca	1.35	1.32	1.58		ns	ns	ns
<i>Carya alba</i>	N	1.44	1.47	0.87	○	ns	***	**
	P	0.10	0.10	0.10	○	ns	ns	ns
	K	0.73	0.81	0.29		ns	*	*
	Ca	1.68	1.91	1.87		ns	ns	ns
<i>Carya glabra</i>	N	1.66	1.84	0.70	○	ns	**	**
	P	0.10	0.11	0.06	○	ns	*	*
	K	0.71	0.73	0.34		ns	**	**
	Ca	1.55	1.72	1.59		ns	ns	ns
<i>Cornus florida</i>	N	1.34	1.39	1.11	○	ns	ns	ns
	P	0.09	0.09	0.07	○	ns	*	*
	K	0.94	1.03	0.60		ns	ns	ns
	Ca	1.62	1.39	2.12		ns	ns	ns
<i>Fagus grandifolia</i>	N	1.61	1.71	1.23	○	ns	*	*
	P	0.08	0.09	0.06	○	ns	*	*
	K	0.94	0.67	0.21		ns	***	*
	Ca	0.67	0.42	0.68		ns	ns	ns
<i>Fraxinus americana</i>	N	1.87	1.73	1.02	○	ns	*	*
	P	0.17	0.17	0.18	○	ns	ns	ns
	K	1.04	1.08	0.55		ns	***	***
	Ca	1.37	1.54	1.81		ns	ns	ns
<i>Oxydendrum arboreum</i>	N	1.68	1.73	0.79	○	ns	***	***
	P	0.09	0.09	0.04	●	ns	**	**
	K	0.88	0.77	0.44		ns	*	ns
	Ca	0.83	1.06	1.01		ns	ns	ns
<i>Prunus serotina</i>	N	1.79	1.58	1.08	○	ns	ns	ns
	P	0.18	0.12	0.13	○	ns		
	K	0.90	0.78	0.58		ns		
	Ca	1.48	1.87	1.49		ns		
<i>Quercus alba</i>	N	1.92	2.02	1.23	○	ns	**	**
	P	0.11	0.11	0.14	○	ns	**	*
	K	0.60	0.62	0.47		ns	ns	ns
	Ca	1.10	1.20	0.96		ns	ns	ns
<i>Quercus rubra</i>	N	1.67	1.88	1.45	○	ns	ns	ns
	P	0.11	0.12	0.12	○	ns	ns	ns
	K	0.66	0.83	0.50		ns	ns	*
	Ca	0.88	0.87	1.04		ns	ns	*
<i>Vaccinium fuscatum</i>	N	1.18	1.24	0.83	○	ns	**	**
	P	0.06	0.06			ns		
	K	0.47	0.41			ns		
	Ca	0.59	0.65			ns		

**Table 1** continued

Species	Nutrient	Healthy	Desiccated	Fall-senesced		P values		
						H vs. D	H vs. FS	D vs. FS
<i>Viburnum acerifolium</i>	N	1.49	1.50	0.71	○	ns	***	***
	P	0.09	0.09	0.04	●	ns	**	**
	K	1.50	1.54	0.93		ns	ns	ns
	Ca	0.99	0.98	1.12		ns	ns	ns
<i>Viburnum nudum</i>	N	1.26	1.45	1.08	○	ns	ns	*
	P	0.12	0.13	0.10	○	ns	ns	ns
	K	1.58	1.71	0.97		ns	ns	*
<i>Viburnum rafinesquianum</i>	Ca	1.49	1.62	1.61		ns	ns	ns
	N	1.20	1.24	1.11	○	ns	ns	ns
	P	0.10	0.11	0.16	○	ns	*	*
	K	1.20	1.53	0.64		ns	*	ns
	Ca	1.17	1.15	1.57		ns	ns	*

Resorption proficiencies of below 0.7% for N and below 0.05% for P in FS leaves are considered complete (Killingbeck 1996) and are denoted by a filled circle; incomplete resorption proficiencies are denoted by an open circle. Values left blank did not have sufficient samples for analysis. Significant differences between leaf types are denoted by stars: \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ .

**Table 2** Mean nutrient concentration (N, P, K, Ca %) of healthy (H), drought-senesced (DS), and fall-senesced (FS) leaves in four drought-deciduous species ( $n = 3$ ) from two heavily droughted sites

Species	Nutrient	Healthy	Drought-senesced	Fall-senesced		P values		
						H vs. DS	H vs. FS	DS vs. FS
<i>Acer rubrum</i>	N	1.31	0.74	0.49	●	***	***	***
	P	0.09	0.05	0.02	●	***	***	***
	K	0.65	0.55	0.21		ns	**	*
	Ca	0.62	0.74	0.84		ns	ns	ns
<i>Liquidambar styraciflua</i>	N	1.45	0.68	0.43	●	***	***	**
	P	0.10	0.04	0.04	●	***	**	ns
	K	0.50	0.46	0.16		ns	*	*
	Ca	0.94	1.22	0.87		ns	ns	ns
<i>Liriodendron tulipifera</i>	N	1.37	0.71	0.55	●			
	P	0.07	0.04	0.03	●			
	K	1.18	1.07	0.68				
	Ca	0.81	1.16	1.23				
<i>Nyssa sylvatica</i>	N	1.33	0.59	0.48	●	***	***	ns
	P	0.08	0.04	0.05	○	**	*	ns
	K	0.93	0.80	0.56		ns	ns	**
	Ca	0.90	0.97	0.98		ns	ns	ns

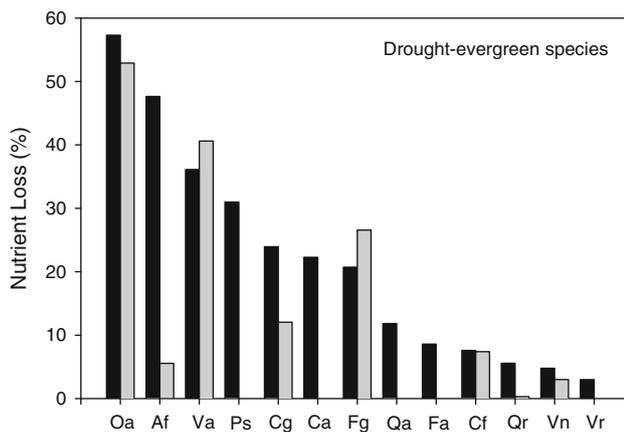
Resorption proficiencies of below 0.7% for N and below 0.05% for P in DS and FS leaves are considered complete (Killingbeck 1996) and are denoted by a filled circle; incomplete resorption proficiencies are denoted by an open circle. Values left blank did not have sufficient sample sizes for analysis.

Significant differences between leaf types are denoted by stars: \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ .

**Discussion**

By early September 2007, the woody plant communities of the temperate deciduous forest in NC were under severe drought, as caused by record low precipitation combined

with near-record high temperatures over the previous six months. There was considerable variation in the effects of the drought on local tree and shrub species. The leaves of many species became desiccated while still attached to the plant (Fig. 1), but some species exhibited leaf



**Fig. 4** Mean increase in nutrient loss (%) of N (black bars) and P (shaded bars) due to desiccated leaves in drought-evergreen species during an extreme drought. Species codes: Af, *Acer floridanum*; Ca, *Carya alba*; Cf, *Cornus florida*; Cg, *Carya glabra*; Fa, *Fraxinus americana*; Fg, *Fagus grandifolia*; Oa, *Oxydendron arboreum*; Ps, *Prunus serotina*; Qa, *Quercus alba*; Qr, *Quercus rubra*; Va, *Viburnum acerifolium*; Vn, *Viburnum nudum*; Vr, *Viburnum rafinesquianum*

senescence in response to the drought. To our knowledge, this is the first study to examine the consequences of these differing responses for nutrient budgets of temperate deciduous tree species.

The drought-deciduous species had higher predawn water potentials and lower levels of leaf desiccation than drought-evergreen species (Fig. 2), suggesting that the reduction in leaf area contributed to the prevention of lethal levels of foliar water potential. Mean  $\Psi_w$  for these species ranged from  $-2.8$  to  $-0.6$  MPa, while the mean range of  $\Psi_w$  for drought-evergreen species was from  $-6.6$  to  $-2.7$  MPa (Fig. 2). These differences in  $\Psi_w$  result from species responses to extreme drought, where drought-deciduous species with higher  $\Psi_w$  have stomata that are more sensitive to leaf water potential (Augé and Moore 2002; Croker et al. 1998). Contrary to expectations, these species also had lower percentages of cavitated vessels, most likely due to the partial drought-deciduous behavior (Hoffmann, unpublished data). Augé et al. (1998) found similar results for the differential dehydration tolerance of the leaves of these temperate deciduous tree species under a simulated drought. In this study, species with lower leaf water potentials tended to have a higher percentage of total leaf desiccation (Fig. 2).

As hypothesized, extreme drought decreased nutrient resorption in all species with desiccated leaves, although drought-deciduous species were less affected than drought-evergreen species (Tables 1, 2; Fig. 3). There was no evidence of nutrient resorption from desiccated leaves for any species studied here (Table 1; Fig. 3a), but resorption of N, P, and K occurred during drought-induced leaf senescence (Table 2; Fig. 3b). Concentrations of N and K were even

lower in fall-senesced leaves of drought-deciduous species (Table 2; Fig. 3b), however, indicating that nutrient resorption during drought-induced leaf senescence is less efficient than nutrient resorption during fall leaf senescence. We did not attempt to measure foliar leaching in this study, but our measurements of N and P should be unaffected by this process, as these nutrients are not readily leached from tree crowns (Cole and Rapp 1981; Ryan and Bormann 1981; Parker 1983). Potassium, however, has been shown to be extensively leached from tree canopies (Hagen-Thorn et al. 2006). A total of 161.4 mm of rainfall was recorded at weather stations near the study sites for the period between the two leaf collection dates, so it is possible that the lower concentrations of K in fall-senesced leaves may be due to leaching as well as resorption. We do not suspect that loss of nutrients by leaching was very high in these plants, however, because leaching experiments have shown that Ca is also easily leached from leaves (Hagen-Thorn et al. 2006), and mean concentrations of Ca here did not decrease by the time of fall leaf senescence (Fig. 3). Resorption of the non-mobile element Ca has been found to be negligible for many forest trees (Likens et al. 1998), and modest Ca resorption rates (10, 11.5% resorption) have only been found in ecosystems where soil Ca availability is low (Duchesne et al. 2001; Ostman and Weaver 1982).

Even in a year of extreme drought, nutrient resorption of drought-deciduous species in the fall was highly proficient (Table 2). The concept of nutrient resorption proficiency, which is the minimum level to which a plant can reduce an element in senescing leaves (Killingbeck 1996), can be used to compare the success of resorption as a nutrient conservation mechanism among species. The mean nutrient resorption proficiencies for N (0.49%) and P (0.036%) in drought-deciduous species were more complete than the worldwide averages for deciduous plants (N 0.87%, P 0.067%, Killingbeck 1996), so fall nutrient resorption in this functional group is high. Killingbeck (2008) also found higher than average nutrient resorption in a drought-deciduous species (*Fouquieria splendens*, ocotillo) in the Chihuahuan Desert, although resorption was highly variable on an interannual basis. During some years, N resorption efficiency in this shrub was not significantly different from 0% (Killingbeck 1992). In temperate tree species, resorption of N and K was less efficient in drought-senesced leaves than in fall-senesced leaves (Table 2; Fig. 3b), suggesting that resorption efficiency in temperate drought-deciduous species is dependent on water availability and thus also variable among years. Perhaps high nutrient resorption efficiency is an adaptation of drought-deciduous species to compensate for the drier years, when total resorption may be low due to less efficient resorption.

For drought-evergreen species, nutrient resorption in the fall was incomplete (Table 1), and the mean resorption proficiencies of N (0.99%) and P (0.106%) were above the global means. Previous work has shown that drought can reduce resorption efficiency during fall senescence (Killingbeck et al. 1990; Minoletti and Boerner 1994), suggesting that drought may have contributed to the low resorption found here. More importantly, these species lost valuable N and P to leaf desiccation, and in some cases (*O. arboreum*, *A. floridanum*, and *V. acerifolium*) these losses were over 40% greater than the amount that would have been lost in the fall (Fig. 4). These estimates of drought-induced nutrient loss have likely underestimated actual nutrient loss, since the drought may have decreased autumn nutrient resorption below that which would occur in a normal year (e.g., Killingbeck et al. 1990; Minoletti and Boerner 1994).

It has been shown experimentally that preventing nutrient resorption leads to negative impacts on growth of woody plants, such as lower leaf area and biomass the following season (Eckstein et al. 1998) and even lower radial stem growth (May and Killingbeck 1992). Conversely, the lower seasonal nutrient losses of drought-deciduous species may give them a competitive advantage over drought-evergreen species in the years following the drought. Differential patterns of nutrient resorption between drought-deciduous and drought-evergreen species may therefore impact the species composition of temperate forests in the future.

Climate projections indicate that temperate forests will be exposed to increased growing-season potential evapotranspiration and an increased frequency of drought in the near future (Cooter et al. 2000; Sheffield and Wood 2008). In natural ecosystems, the largest impact on the nutrient capital of deciduous species will likely be during extremely dry periods, such as in this record drought, when percentages of drought-induced leaf senescence and foliar desiccation are higher. It has been shown that drought can lead to branch decline (Bréda et al. 2006) and decreased annual growth for up to six years in some tree species (Orwig and Abrams 1997), and our work suggests that drought-induced nutrient losses could contribute to these phenomenon. The drought-deciduous species in this study are predominantly mesic, so it is counterintuitive that these species are better able to avert nutrient losses than xeric species under a climate regime of more frequent drought. This study highlights the current difficulty involved in predicting the impact of climate change on forest ecosystems.

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