Diurnal Variations in Tension, Osmolarity, and the Composition of Nitrogen and Carbon Assimilates in Xylem Fluid of *Prunus persica*, *Vitis* Hybrid, and *Pyrus communis*

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Abstract. Diurnal variations in the chemical composition of xylem fluid have been established for many plant species exhibiting positive root pressure; similar patterns have not been well documented in transpiring plants. Diurnal changes in plant water status and xylem fluid chemistry were investigated for 'Flordaking' peach (*Prunus persica* (L.) Batsch), 'Suwannee' grape (*Vitis* hybrid), and 'Flordahome' pear (*Pyrus communis* L.). Xylem tension was maximum at 1200 or 1600 HR and declined to <0.5 MPa before dawn. Xylem fluid osmolarity ranged from 10 to 27 mM and was not correlated with diurnal patterns of xylem tension. The combined concentration of amino acids and organic acids accounted for up to 70%, 45%, 55%, and 23% of total osmolarity for irrigated *P. persica*, nonirrigated *P. persica*, *Vitis*, and *P. communis*, respectively. The concentration of total organic compounds in xylem fluid was numerically greatest at 0800 or 0900 HR. For irrigated *P. persica* the osmolarity of xylem fluid was reduced by 45% from 0800 to 1200 HR, 1 h after irrigation, compared to only a 12% reduction from 0800 to 1200 HR for nonirrigated trees. Asparagine, aspartic acid, glutamine, and glutamic acid were mainly responsible for diurnal changes in the concentration of total amino acids and organic N for *P. persica*; the diurnal variation in organic N for *Vitis* was due to glutamine. Arginine, rather than the amides, was the primary source of organic N in xylem fluid of *P. communis*, and there was no consistent diurnal change in the concentration of amino acids or organic N. The predominant organic acids in all species examined were citric and malic acids. No consistent diurnal trend occurred in the concentration of organic acids or sugars in xylem fluid.

Plants with positive root pressure manifest diurnal changes in the concentrations of inorganic ions (Andersen and Brodbeck, 1989a; Masuda, 1989; Wallace et al., 1966) and primary organic compounds (Andersen and Brodbeck, 1989a; Stoev et al., 1959; van Die, 1959) in xylem fluid. Positive root pressure is responsible for a small proportion of the volume flux in xylem vessels of terrestrial plants (Scholander et al., 1965); for many woody species, positive root pressure only occurs just before budbreak.

Most terrestrial plant species manifest large diurnal variations in plant water status. For transpiring plants, xylem tensions are typically maximum during midday and minimum at night. Despite much information concerning diurnal changes in plant water relations, there have been surprisingly few studies that have addressed concomitant changes in xylem fluid chemistry. Characterization of diurnal rhythms in the chemical profile of xylem fluid are relevant to studies concerning nutrient partitioning and source-sink relationships. The only woody species for which a diurnal cycle in the concentration of primary organic compounds in xylem fluid has been documented under typical day-night variations in plant water status has been *Lagerstroemia indica* (Andersen et al., 1993). A distinct circadian rhythm in the concentration of amino acids with a maximum during the daylight hours was endogenous, not mediated by changes in plant water status, persisted in constant darkness and was terminated under conditions of continuous light (Andersen et al., 1993). Changes in concentrations of glutamine were mainly responsible for the diurnal changes in xylem fluid chemistry in *L. indica*.

In this study, we measured the diurnal changes in xylem tension, xylem fluid osmolarity, and the concentrations of amino acids, organic acids, and sugars in xylem fluid of *Prunus persica*, *Vitis* hybrid, and *Pyrus communis* to examine the extent to which xylem fluid chemistry varies diurnally in plants that exhibit transpiration. These species, representing different families, were selected to ensure a wide range in xylem chemistry. The amide glutamine is the major amino acid in xylem fluid of *Vitis* spp. (Andersen et al., 1989a-c) as in *L. indica* (Andersen et al., 1993), whereas, in *P. persica*, concentrations of asparagine and glutamine predominate (Brodbeck et al., 1990). Arginine is the major amino acid in the xylem fluid of *P. communis* (P.C. Andersen, unpublished data). In addition, we investigated whether plant water status, as influenced by daily irrigation, has an influence on the diurnal pattern of xylem fluid chemistry in *P. persica*.

Materials and Methods

Plant material. Experiments were conducted at the Univ. of Florida, North Florida Agricultural Research Center, Monticello, Fla. Separate blocks of irrigated and nonirrigated 'Flordaking' peach, irrigated 'Suwannee' grape, and nonirrigated 'Flordahome' pear were examined. Each block consisted of 30 to 200 plants of bearing age that had fruited earlier in the spring or summer. Soil type was a Dothan loamy sand (Plinthic paleudults) containing about 1% organic matter. Standard cultural practices were used and 2-m in-row weed-free strips were maintained with herbicides. Plants in irrigated plots received drip irrigation (about 8 liters) daily, from 1100 to 1200 HR. Plants were fertilized during February and June with 337 kg·ha⁻¹ 10N4.3P-8.3K with micronutrients. Total N was in the form of NH₄⁺ (85%) and NO₃⁻ (15%).

Extraction of xylem fluid. One or two terminal shoots about 25 to 35 cm long were excised from each plant and placed in a pressure chamber apparatus (Scholander et al., 1965). Tissue exterior to the

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xylem was removed from the 2 to 4 cm stem section protruding from the chamber to minimize contamination of xylem fluid by extraxylellary tissue. After recording xylem tension (i.e., the pressure at which fluid was observed at the cut surface of the stem), the pressure was increased 0.5 MPa more than the balance pressure for 90 sec (Andersen et al., 1993, 1995; Berger et al., 1994). The first two drops of fluid were discarded to minimize contamination from cut cells. Xylem fluid was collected in 1.5-ml Eppendorf tubes, then sealed and frozen at -20°C . Xylem fluid was collected at 0800, 1200, 1600, 2000, and 2400 HR on 13 July 1988 for *P. persica* and at 600, 0900, 1200, 1600, and 2100 HR on 14 July 1988 for *Vitis* hybrid and *P. communis*.

Chemical analyses. Xylem fluid was thawed to room temperature, and total osmolarity was determined with a vapor pressure osmometer (model 5500; Wescor, Logan, Utah). An osmometer technically measures osmolality ($\text{mmol}\cdot\text{kg}^{-1}$); however, since osmolality and osmolarity are virtually identical for dilute solutions, we will use osmolarity to facilitate comparisons to the concentrations of organic compounds.

Samples were centrifuged at $1200\times g$ through 10,000 MW filters (Millipore Corp., Bedford, Mass.). Supernatant was divided into subsamples for hydrolysis and analysis of amino acids and for analysis of organic acids and sugars (Andersen et al., 1993). Small sample volumes (400 to 1000 μl) precluded accurate quantification of inorganic ions.

Fig. 1. Diurnal variations in xylem fluid tension, the osmolarity of xylem fluid, the concentrations of total organic N, and the ratio of organic N to organic C in xylem fluid of irrigated and nonirrigated *Prunus persica* 'Flordaking'. Values are means $\pm$ SE, $n = 4$.

The analyses of amino acids, organic acids, and sugars have been described in detail (Andersen et al., 1993). In brief, amino acids were derivatized with phenylisothiocyanate and quantified on a high-performance liquid chromatography (HPLC) gradient system with a ultraviolet (UV) detector and a Pico Tag column (Waters Division, Millipore Corp., Milliford, Mass.). Organic acid analyses were performed on a Waters HPLC system equipped with a variable-wavelength UV detector (model 166; Beckman Corp., San Roman, Calif.) and an polymeric cation exchange column (Ion-300; Interaction Corp., San Jose, Calif.). Sugars were quantified on a Waters HPLC system with a pulse amperometric detector equipped with a gold electrode and an Ion-Pat ion exchange column (Dionex Corp., Sunnyvale, Calif.).

Subsets of nonhydrolyzed samples were used 1) for the quantification of amides to their respective acids since hydrolysis resulted in delamination and 2) to facilitate peak separation of succinic acid and an unknown compound with the use of a diode array detector (model 168; Beckman) equipped with an Ion-300 polymeric cation exchange column.

Organic N and C were calculated from the concentration of each amino acid, organic acid, and sugar quantified. The concentration of total organic compounds is defined as the combined concentration of amino acids, organic acids, and sugars.

Statistics. Xylem fluid was collected from four plants of each species or treatment at the times specified above. Means and standard errors of the means were computed for xylem tension, xylem fluid osmolarity, and the concentration of total and individual amino acids, organic acids, sugars, total organic compounds, organic N, and the ratio of organic N to organic C. Although data for the individual amino acids, organic acids, and sugars were collected and analyzed for all the time periods described above, data are presented only for 0800 and 2400 HR for *P. persica* and 0900 and 2100 HR for *Vitis* and *P. communis*, the time periods for which greatest differences were observed.

Results

Xylem tension was maximum during midday (1200 or 1600 HR) and or 1600 HR) and minimum before dawn (Fig. 1, Table 1). Maximum xylem tensions of 2.1, 2.7, 1.5, and 1.2 MPa were recorded for irrigated *P. persica*, nonirrigated *P. persica*, irrigated *Vitis*, and nonirrigated *P. communis* trees. Predawn xylem tension ranged from 0.2 to 0.5 MPa.

Xylem fluid osmolarity varied from 10 to 27 mM among species and times of day (Fig. 1, Table 1). Although xylem fluid osmolarity was maximum during the morning, no consistent correlation existed between xylem tension and osmolarity. The osmolarity of xylem fluid was maximum (19 mM) for *P. persica* at 0800 HR and declined to 10 mM at night. Xylem fluid osmolarity was maximum at 0900 or 1200 HR for *Vitis* and *P. communis* and declined toward predawn with two exceptions (i.e., 1600 HR for *Vitis* and 2100 HR for *P. communis*). The combined sum concentration of amino acids and organic acids accounted for up to 70%, 45%, 55%, and 23% of total osmolarity of xylem fluid from irrigated *P. persica*, nonirrigated *P. persica*, *Vitis*, and *P. communis*, respectively (Fig. 2, Table 1).

The concentration of total amino acids and organic N in xylem fluid was numerically highest at 0800 or 0900 HR for all species (Figs. 1 and 2, Table 1), although diurnal differences were minimal for *P. communis*. The concentrations of amino acids were particularly high (11.4 mM) for irrigated *P. persica* at 0800 HR. A fairly consistent decrease in the concentration of amino acids occurred from 0800 or 0900 HR until 2000 or 2100 HR occurred for nonirrigated *P. persica* and *Vitis* hybrid.

Table 1. Diurnal variations in xylem fluid tension, the osmolality of xylem fluid, and concentrations of total amino acids, organic acids, sugars, total Organic compounds quantified, total organic N and the ratio of organic N to organic C (N : C) in xylem fluid of *Vitis* hybrid 'Suwannee' and *Pyrus communis* 'Flordahome'.

Species or variable	Time (HR)				
	0600	0900	1200	1600	2100
<i>Vitis</i> hybrid					
Xylem tension (MPa)	0.61 ± 0.04 ^z	0.93 ± 0.09	1.48 ± 0.15	1.50 ± 0.08	0.44 ± 0.03
Osmolarity (mM)	17.0 ± 0.4	21.8 ± 4.7	23.5 ± 0.80	16.0 ± 0.50	18.8 ± 0.90
Amino acids (mM)	2.50 ± 0.35	2.98 ± 0.48	2.49 ± 0.29	2.61 ± 0.50	1.12 ± 0.07
Organic acids (mM)	3.47 ± 0.62	5.93 ± 0.67	4.87 ± 0.27	6.08 ± 1.54	5.43 ± 0.38
Sugars (mM)	0.17 ± 0.05	0.54 ± 0.15	0.55 ± 0.16	0.20 ± 0.06	0.39 ± 0.12
Total organics (mM)	6.15 ± 0.44	9.56 ± 0.96	7.91 ± 0.47	8.89 ± 2.10	6.94 ± 0.49
Organic N (mM)	4.64 ± 0.73	5.62 ± 0.89	4.67 ± 0.59	4.84 ± 0.98	2.06 ± 0.15
N : C	0.17 ± 0.03	0.13 ± 0.02	0.13 ± 0.01	0.13 ± 0.01	0.07 ± 0.01
<i>Pyrus communis</i>					
Xylem tension (MPa)	0.21 ± 0.04	0.73 ± 0.09	1.18 ± 0.07	0.70 ± 0.12	0.61 ± 0.10
Osmolarity (mM)	12.3 ± 1.0	27.3 ± 3.2	20.3 ± 1.8	20.8 ± 3.4	26.5 ± 3.0
Amino acids (mM)	1.22 ± 0.11	1.92 ± 0.26	1.88 ± 0.36	1.74 ± 0.29	1.86 ± 0.35
Organic acids (mM)	1.62 ± 0.28	2.76 ± 0.23	1.60 ± 0.19	2.25 ± 0.58	1.71 ± 0.01
Sugars (mM)	0.18 ± 0.04	0.37 ± 0.09	0.21 ± 0.06	0.37 ± 0.03	0.27 ± 0.09
Total organics (mM)	2.97 ± 0.37	4.99 ± 0.23	3.65 ± 0.53	4.29 ± 0.83	3.78 ± 0.27
Organic N (mM)	2.74 ± 0.16	3.91 ± 0.71	3.61 ± 0.71	3.31 ± 0.57	3.75 ± 0.90
N : C	0.19 ± 0.07	0.17 ± 0.02	0.21 ± 0.02	0.16 ± 0.02	0.21 ± 0.04

^zValues are means ± SE, n = 4.

The concentration of total amino acids was much greater than total organic acids in *P. persica* (Fig. 2), yet concentrations of organic acids were generally greater than or equal to that of amino acids in *Vitis* and *P. communis* (Table 1). All species examined lacked a consistent diurnal change in the concentration of organic acids in xylem fluid. The concentration of sugars was very low, and typically contributed to only 1% to 2% of total osmolality (Table 1). The trend in the concentration of total organic compounds for *P. persica* and *Vitis* resembled changes in amino acid concentration, with a maximum observed at 0800 or 0900 HR, respectively. For *P. communis*, the concentration of organic acids contributed heavily to the trend in total organic compounds. The ratio of organic N to organic C in organic compounds varied from about 0.07 in *P. communis* at 2100 HR to 0.36 in *P. persica* at 0800 HR.

The predominant organic compounds in xylem fluid were asparagine, aspartic acid, glutamine, glutamic acid, arginine (*P. communis* only), citric acid, and malic acid (Tables 2 and 3). Although the high concentration of total amino acids recorded at 0800 HR in xylem fluid of irrigated *P. persica* was mainly a function of the amides and their respective acids, many amino acids varied asynchronously in concentration through the day (Table 2; data not shown pertaining to time periods other than for 0800 and 2400 HR). For example, the amides plus their respective acids represented 90% and 55% of the amino acid profile at 0800 HR and 70% to 75% of the amino acid profile at 2400 HR for irrigated and nonirrigated *P. persica*, respectively. Only alanine, leucine (which belongs to the alanine family of amino acids), and methionine (a sulfur amino acid) were higher in concentration at 2400 HR compared to 0800 HR.

Malic acid was the predominant organic acid at all time periods and accounted for over 50% of the total organic acids quantified. The diurnal changes in the concentration of most organic acids were usually opposite for irrigated (higher at 0800 HR) and nonirrigated (higher at 2400 HR) *P. persica*.

The concentration of glutamine in *Vitis* xylem fluid represented up to 90% of total amino acids (Table 3). Glutamine was responsible for most of the diurnal cycling of total amino acids, although

Fig. 2. Diurnal variations in the concentrations of total amino acids, organic acids, sugars, and organic compounds quantified in xylem fluid of irrigated and nonirrigated *Prunus persica* 'Flordaking'. Values are means ± SE, n = 4.

fluid not accounted for by primary organic compounds was likely in the form of inorganic ions.

The pronounced peak in the concentration of glutamine-glutamic acid or asparagine-aspartic acid for irrigated and nonirrigated *P. persica* was responsible for the maximum concentration of total amino acids, organic N, total organic compounds, and the N : C ratio at 0800 HR (Figs. 1 and 2, Table 2). The concentration of glutamine also varied diurnally in xylem fluid of *Vitis*, whereas in *P. communis*, in which amides did not predominate, a diurnal trend in amino acids did not occur (Tables 1 and 3). The high N to C ratio represented in primary compounds of xylem fluid from irrigated *P. persica* at 0800 HR was significantly higher than that of pure protein (Gnaiger and Bitterlich 1984) due to the high concentration of the amides. The amides are the predominant nitrogenous compound in xylem fluid of many woody species (Andersen and Brodbeck, 1989a, 1989b, 1991; Andersen et al., 1989, 1993; Clark et al., 1986; Glad et al., 1992) and are readily converted to many other amino acids (Lacey and Wilmore, 1990; Pate, 1980). Andersen et al. (1993) also documented that glutamine mainly accounted for the circadian rhythm in the concentration of amino acids (and organic N) in xylem fluid of *L. indica*. This rhythm persisted and was accentuated after 3 days of constant darkness.

The mechanisms responsible for the diurnal pattern of organic

N concentrations in xylem fluid are not known. However, the diurnal trend was not mediated by plant water status since changes in chemistry were not correlated with xylem tension in any of the plant species thus far tested. Also, this trend occurred for irrigated and nonirrigated *P. persica* (Fig. 1, Table 2). A marked (i.e., 45%) decline in osmolarity and total amino acids in xylem fluid of *P. persica* occurred at 1200 HR, 1 h after irrigation, whereas a more gradual reduction occurred for nonirrigated *P. persica*. Although the significance of irrigation (and irrigation timing) on N flux in xylem vessels and N partitioning distribution in plant tissues have not yet been adequately explored, these data indicate that an irrigation episode may drastically reduce osmolarity and the concentration of organic N in xylem fluid.

Changes in organic N may be due to differences in the rate of uptake and assimilation of N by roots. Nitrogen derived from soil NO_3^- or NH_4^+ is initially incorporated into the amide-N of glutamine and later appears in other amino acids (Kate, 1980; Pate, 1980). The circadian rhythm in organic N may be due to the recycling of N between xylem and phloem or to the differential transfer into or out of xylem vessels (Clausen and Apel, 1991; Cooper and Clarkson, 1989; Simpson et al., 1982; van Bel, 1990). However, the 1- to 1.5-h interval between dawn and the 0800 HR collection period is not consistent with current day's photoassimilate being

Table 3. Diurnal variations in the concentration of amino acids, organic acids, and sugars in the xylem fluid of *Vitis* hybrid 'Suwannee' and *Pyrus communis* 'Florahome'.

Chemical compound	Concn (μM)			
	<i>Vitis</i>		<i>P. communis</i>	
	0900 HR	2100 HR	0900 HR	2100 HR
Amino acid				
ASN ²	15 $\pm$ 3 ^y	8 $\pm$ 1	355 $\pm$ 59	387 $\pm$ 116
ASP	60 $\pm$ 11	30 $\pm$ 5	290 $\pm$ 48	167 $\pm$ 50
GLU	119 $\pm$ 19	37 $\pm$ 3	248 $\pm$ 18	308 $\pm$ 63
GLN	2267 $\pm$ 366	708 $\pm$ 61	70 $\pm$ 5	34 $\pm$ 7
SER	37 $\pm$ 6	15 $\pm$ 6	46 $\pm$ 6	52 $\pm$ 9
GLY	155 $\pm$ 49	98 $\pm$ 22	125 $\pm$ 35	109 $\pm$ 29
HIS	1 $\pm$ 1	0 $\pm$ 0	2 $\pm$ 1	3 $\pm$ 0
ARG	85 $\pm$ 25	74 $\pm$ 7	500 $\pm$ 172	485 $\pm$ 199
ALA	59 $\pm$ 16	28 $\pm$ 5	53 $\pm$ 4	78 $\pm$ 24
THR	25 $\pm$ 5	8 $\pm$ 1	56 $\pm$ 10	47 $\pm$ 10
PRO	39 $\pm$ 5	29 $\pm$ 2	36 $\pm$ 3	40 $\pm$ 6
TYR	8 $\pm$ 3	2 $\pm$ 1	16 $\pm$ 7	8 $\pm$ 2
VAL	26 $\pm$ 9	16 $\pm$ 1	34 $\pm$ 3	24 $\pm$ 6
CYS	16 $\pm$ 7	7 $\pm$ 5	2 $\pm$ 1	26 $\pm$ 15
MET	12 $\pm$ 4	6 $\pm$ 3	9 $\pm$ 5	6 $\pm$ 3
ILE	19 $\pm$ 5	18 $\pm$ 2	29 $\pm$ 5	31 $\pm$ 4
LEU	12 $\pm$ 3	11 $\pm$ 1	18 $\pm$ 1	16 $\pm$ 3
PHE	11 $\pm$ 2	12 $\pm$ 3	15 $\pm$ 9	12 $\pm$ 5
LYS	12 $\pm$ 5	9 $\pm$ 0	18 $\pm$ 4	21 $\pm$ 6
Organic acid				
OX	19 $\pm$ 5	21 $\pm$ 10	111 $\pm$ 24	88 $\pm$ 2
CIT	326 $\pm$ 63	224 $\pm$ 76	230 $\pm$ 90	269 $\pm$ 10
MAI	718 $\pm$ 146	1104 $\pm$ 172	2189 $\pm$ 282	1170 $\pm$ 27
SUC	413 $\pm$ 121	389 $\pm$ 61	208 $\pm$ 39	149 $\pm$ 5
FUM	39 $\pm$ 6	32 $\pm$ 7	26 $\pm$ 2	32 $\pm$ 4
Sugar				
SUCR	158 $\pm$ 58	93 $\pm$ 33	128 $\pm$ 39	75 $\pm$ 24
FRUC	158 $\pm$ 41	154 $\pm$ 55	135 $\pm$ 30	119 $\pm$ 43
GLUC	228 $\pm$ 66	147 $\pm$ 75	103 $\pm$ 25	75 $\pm$ 31

²Ratios of ASN : ASP and of GLN : GLU were determined for a pooled sample at each time period.

^yValues are means $\pm$ SE, n = 4.

the C source for the enriched N-status of xylem fluid. Alternatively; given that the synthesis and subsequent conversion of amino acids to glutamine occurs before loading in xylem vessels (Clausen and Apel, 1991; Sauter and van Cleve, 1992), the enriched N-status of xylem fluid at 0800 to 0900 HR may result from the export of amino acids from preexisting pools in xylem parenchyma cells.

A circadian rhythm in nitrate reductase (NR) activity with a maximum during daylight hours often occurs in leaves (DeDeng et al., 1989; Reed et al., 1983; Ruffy et al., 1984) and roots (Queiroz et al., 1993). In leaves of *Nicotiana tabacum*, NR activity was correlated with the concentration of malate; however, the rhythm persisted in continuous light and was terminated in constant darkness (DeDeng et al., 1989). Malate concentrations in xylem fluid were not correlated with amides or organic N in *L. indica* (Andersen et al., 1993) or in the species used in the current study, and constant darkness terminated diurnal patterns for NR while continuous light terminated diurnal patterns in xylem composition (Andersen et al., 1993). Thus, we cannot attribute the diurnal pattern in xylem chemistry to changes in NR activity.

The enzymes responsible for the synthesis of glutamine from oxaloacetate and ammonia are glutamine synthetase (GS) and glutamate synthase (GOGAT). The activity of GS and GOGAT in *Sinapis alba* L. (Schmidt and Mohr, 1989) and *Pinus sylvestris* L. (Elmlinger and Mohr, 1991, 1992) was controlled by light and was mediated by phytochrome; nitrate concentrations had a minor role and NH_4^+ actually inhibited GS activity (Elmlinger and Mohr, 1991, 1992; Schmidt and Mohr, 1989). Whether the increased concentration of glutamine in xylem fluid during the morning is a result of phytochrome-mediated increases in glutamine synthesis by GS and/or GOGAT has not been determined. However, plant species thus far tested that have had amides as the primary nitrogenous compounds in xylem fluid [i.e., *L. indica* (Andersen et al., 1993); *P. persica* (Table 2); *V. rotundifolia* (Andersen and Brodbeck, 1989a); *Vitis* hybrid (Table 3)] have all manifested diurnal variations in the concentrations of amino acids and organic N. In contrast, *P. communis* did not exhibit this diurnal pattern nor did it have significant levels of either amide.

Conclusions

The diurnal fluctuation in plant water relations is characteristic of terrestrial plant species; however, diurnal variations in xylem fluid osmolarity and the concentration of organic N in xylem fluid (and likely the N flux to foliar tissue) also appears to be a widespread phenomenon. Diurnal changes in the concentration of amino acids and organic N occurred in the three species tested having the amides as the primary nitrogenous compound in xylem fluid (Tables 2 and 3) (Andersen et al., 1993). The enriched N status of xylem fluid during the morning hours is concomitant with increases in photosynthesis and other physiological activities. The importance of the diurnal variations of organic N in xylem fluid to N loading and transport to aerial plant tissue and to plant N balance remains to be determined.

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