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Conservation of element concentration in xylem sap of red spruce

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Abstract We investigated the chemistry of xylem sap as a marker of red spruce metabolism and soil chemistry at three locations in northern New England. A Scholander pressure chamber was used to extract xylem sap from roots and branches cut from mature trees in early June and September. Root sap contained significantly greater concentrations of K, Ca, Mg, Mn, and Al than branch sap. Sap collected in June contained a significantly greater concentration of Mn than sap collected in September. Sap concentration was related to forest location for N and Mn. Variations in concentrations of N and K were significantly related to the interaction of tree organ and month of collection. Variations in concentrations of P, Cu, Zn, and Fe were not attributable to tree organ, month of collection, or forest location. Patterns of element concentration in xylem sap compared to previously published data on soil solution chemistry indicated a high degree of homeostatic control of xylem sap chemistry. This control likely represents a significant allocation of resources within the tree energy budget.

Keywords Root uptake · Homeostasis · Sap chemistry · Allometry

Introduction

Xylem sap is one component of the linkage between the soil environment and tree physiology. The chemistry of xylem sap integrates soil element availability, discrimination in root uptake, and internal element cycling. Previous research used xylem sap chemistry as a marker of element availability in soils of untreated forest stands (Osonubi et al. 1988; Stark and Spitzner 1985; Stark et al. 1989) and in response to fertilization (Carter and Larsen 1965). More recent research has linked xylem sap

chemistry of *Picea abies* Karst. to internal cycling of elements as well as to soil availability (Dambrine et al. 1995).

Interest in xylem sap chemistry has increased due its potential application as a marker of tree and forest condition under different chemical environments. Acidic deposition has likely altered the chemical environment in sensitive soils of red spruce (*Picea rubens* Sarg.) (Lawrence et al. 1995). Perturbations of soil chemistry due to acidic deposition include the mobilization of base cations (Shortle and Bondietti 1992), reduced uptake of essential base cations of Ca and Mg due to Al antagonism (Schröder et al. 1988; Smith et al. 1995), and depletion of essential base cations from the tree rooting zone (Lawrence et al. 1995). Physiological stress in apparently healthy, nonsymptomatic spruce was linked to adverse soil chemistry associated with these perturbations (Shortle et al. 1997, 2000).

In some respects, xylem sap appears to be a seemingly continuous conduit for the flow of elements from the soil throughout the tree. Although the flow path appears obvious, the relative dependence of xylem sap chemistry on soil chemistry and tree metabolism is unclear. On the cellular scale, element uptake may be considered as passive (moving along a decreasing electrochemical gradient) or active (moving against a decreasing electrochemical gradient) through the expenditure of metabolic energy (Salisbury and Ross 1992). On the organismal scale, such distinctions neglect the metabolic costs required to maintain the electrochemical gradients as well as to operate the tree system for element uptake and translocation. For example, N uptake from the soil environment into the tree symplast requires the direct expenditure of metabolic energy (Marschner 1995). A less direct energy expenditure is the required diversion of potentially energy-yielding C skeletons to form amino acids with N (Marschner 1995) or organic complexes with Ca and Mg (Schell 1997). Similarly, the carbohydrate supplied to the fungal partner of mycorrhizal roots represents an energy expenditure to facilitate P uptake (Salisbury and Ross 1992). Although indirect, no less an energy expenditure

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Table 1 Soil characteristics at locations sampled for analysis of xylem sap of red spruce^a

Location	Loss-on-ignition (%)	Total (g kg ⁻¹)		Exchangeable (cmol _c kg ⁻¹)					Cation exchange capacity (%)
		C	N	Ca	Mg	K	Al	H	
Oa soil horizon									
Mt Abraham	59	360	18.5	2.1	0.8	0.7	11.9	8.2	23
Crawford Notch	84	476	16.6	6.8	2.1	1.0	7.5	14.8	33
Howland	84	476	10.9	11.4	2.6	1.7	4.8	13.1	34
B soil horizon									
Mt Abraham	16	75	4.0	0.4	0.1	0.1	6.4	3.0	10
Crawford Notch	16	77	2.8	0.3	0.1	0.1	8.0	1.1	10
Howland	10	47	1.5	0.2	0.1	0.1	4.1	0.5	5

^a Table derived from previously published data (David and Lawrence 1996). For ease of comparison, some of the tabular values are reported with less precision than in the original publication

is represented through the increase in fine root turnover necessitated by the antagonistic binding of Al and blockage of Ca and Mg uptake in acidic soil environments (Shortle et al. 2000).

The objectives of the current research were to evaluate xylem sap chemistry as a comparative marker for the energy required to maintain mature red spruce at three locations in the northeastern United States.

Materials and methods

The field research areas were located in coniferous or mixed-wood forests of northern New England at Mt. Abraham (44°06'N×72°56'W, 1020 m elevation) in Vermont, Crawford Notch (44°12'N×71°23'W, 800 m elevation) in New Hampshire, and Howland (45°13'N×68°43'W, 60 m elevation) in Maine. Chemical analyses of the soil (Table 1) and soil solution have been previously published (David and Lawrence 1996). Sample collections of xylem sap were timed to minimize phenological variation among the various forest locations. Red spruce trees selected for sampling were dominant or codominant in the canopy, 25–50 cm DBH, and appeared healthy. Roots and branches were collected in the early morning at each location in June and September of 1989 and 1990. Woody roots were hand-dug and clipped from the root system. Branches from the exposed, upper canopy were cut with a pole pruner. For each collection, one root and two branches were cut from each of ten red spruce, and immediately placed in black plastic bags prior to sap extraction. Sap was extracted within 4 h of root and branch collection.

Sap was extracted using a Scholander pressure chamber from the proximal ends of branches and roots 60–90 cm in length and 1.0–1.5 cm in diameter at the cut in a procedure modified from Stark and Spitzner (1985). Bark, phloem, and the vascular cambial zone were stripped from the cut end of the branch for a length of 6 cm. The cut end was inserted through a tight-fitting rubber stopper. The root or branch was placed in the pressure chamber and the stopper was fitted into the chamber lid. The cut end was cleaned with acetone and partially inserted into a short length of plastic tubing. The upper portion of the tubing above the cut end served as a reservoir of extracted sap. Sap was extracted at a chamber pressure of 2.4–2.8 MPa to produce an overpressure of approximately 0.5 MPa. Sap was removed from the reservoir tubing using a syringe. One-milliliter aliquots of sap were added to 2 ml of 0.1 N nitric acid and to 2 ml of concentrated sulfuric acid. Nitric acid samples were analyzed for P, K, Ca, Mg, Mn, Fe, Cu, Zn, and Al by inductively coupled plasma spectroscopy. Sulfuric acid samples were processed by microKjeldahl digestion and analyzed for total N concentration.

Overall variability in element concentration in xylem sap was calculated as the ±confidence interval expressed as a percentage of the mean concentration. The confidence interval was calculated as the product of the SEM multiplied by 2.069, the critical value for two-tailed t $\alpha=0.05$, 23 df .

Log-transformed element concentrations in xylem sap were analyzed in a three-way ANOVA ($n=24$) using the computer program SYSTAT 7.0 (SPSS, Chicago, Ill.). The three treatment factors (and levels for each factor) were forest location (Mount Abraham, Crawford Notch, and Howland), organ (root, branch), and month of collection (June, September). The 2 years of collections were treated as replicate observations for each combination of treatment factors. The ANOVA tested the effects of the three main treatment factors, the three two-way interactions, and the one three-way interaction (total $df=23$, treatment $df=11$, error $df=12$). To protect the significance level from inflation due to multiple comparisons, the desired effective significance level of 0.05 was divided by 7 (the number of comparisons involving the main treatment factors and their interactions) to yield the nominal tested significance level of 0.007 (Neter et al. 1985). When indicated by ANOVA, treatment means were separated after adjustment for multiple comparisons using the Bonferroni technique (Neter et al. 1985).

Element concentrations in root xylem sap were compared with element concentrations in the soil solution from the Oa and upper B horizons, as reported by David and Lawrence (1996). Soil solutions were obtained by expulsion from soil samples using positive air pressure (Lawrence and David 1996). Enrichment ratios for each location were calculated as the mean element concentration (untransformed) in root sap divided by the concentration in the soil solution. [The enrichment ratio was termed the "transpiration stream concentration factor" by Russell and Shorrocks (1959).] The range of mean element concentration in root sap and soil solution across all three locations was expressed by the range factor, calculated by dividing the highest concentration by the lowest concentration of each element for the root sap and in the soil solution.

Results

Element concentrations in xylem sap were determined for roots and branches of red spruce in June and September of 1989 and 1990 (Table 2). Elements listed in order of overall abundance in xylem sap were: N, K>Ca>P, Mg>Mn>Fe, Cu, Zn, Al (Table 2). Variability expressed as the percent confidence interval ($P<0.05$) for each overall mean element concentration ranged from K ($\pm 14\%$) to

Table 2 Mean concentration (μM , untransformed) of elements in xylem sap of red spruce collected from roots and branches in June and September of 1989 and 1990

Location	Organ	Month	N		P		K		Ca		Mg	
			1989	1990	1989	1990	1989	1990	1989	1990	1989	1990
Howland	Root	June	1,164	795	83	139	1,440	2,080	446	470	150	253
Howland	Root	September	945	2,043	158	216	1,490	2,470	241	860	93	247
Howland	Branch	June	1,243	1,194	197	211	1,830	2,220	357	351	86	116
Howland	Branch	September	757	1,350	115	190	1,070	1,130	135	157	48	49
Crawford	Root	June	1,850	2,322	69	172	1,740	1,910	574	657	130	212
Crawford	Root	September	3,186	3,364	262	277	2,700	2,900	860	523	222	207
Crawford	Branch	June	2,570	2,713	102	281	1,510	1,490	307	182	96	68
Crawford	Branch	September	886	1,014	103	168	1,090	840	123	104	46	29
Abraham	Root	June	2,521	3,758	168	340	1,740	1,780	636	476	191	217
Abraham	Root	September	2,729	2,586	313	313	2,570	2,260	611	411	207	148
Abraham	Branch	June	3,664	4,647	181	315	1,310	1,560	214	234	62	84
Abraham	Branch	September	1,450	2,029	166	374	1,020	1,060	122	172	43	64
Overall mean; % confidence interval ^a			2,116; 22		205; 18		1,717; 14		384; 25		128; 24	
Location	Organ	Month	Mn		Fe		Cu		Zn		Al	
			1989	1990	1989	1990	1989	1990	1989	1990	1989	1990
Howland	Root	June	53	44	0.9	0.9	5.8	4.6	6.7	1.5	8.9	9.2
Howland	Root	September	20	57	1.6	2.1	10.8	7.9	4	9.2	8.9	18.5
Howland	Branch	June	46	44	2	1.6	5.2	2.8	5.2	7	7	10.7
Howland	Branch	September	19	16	0.5	2	10.7	6.1	2.1	8.6	4.4	8.9
Crawford	Root	June	82	113	1.1	0.7	4.9	9.6	9.5	12.4	5.6	10
Crawford	Root	September	108	78	1.8	2	15.7	4.7	11.8	26	10	11.1
Crawford	Branch	June	54	44	1.8	2.2	26	7.9	5.7	12.7	5.2	8.1
Crawford	Branch	September	22	22	0.7	0.9	4.7	2.7	3.2	2.4	4.1	3.3
Abraham	Root	June	240	132	1.4	4.8	32.3	9.9	7.6	10.4	11.1	17.8
Abraham	Root	September	172	89	1.8	1.3	7.9	6.3	9.2	6.7	10	8.5
Abraham	Branch	June	97	84	1.2	3.9	9.4	7.2	3.4	4.4	7	9.3
Abraham	Branch	September	47	60	0.7	1.2	6.8	4.7	2.6	4.6	4.1	7
Overall mean; % confidence interval ^a			73; 31		1.6; 26		8.9; 33		7.4; 30		8.7; 18	

^a The overall mean was the average concentration of each element across all replicates and blocking factors. The confidence interval was calculated as the SEM multiplied by 2.069 (the critical two-tailed *t*-statistic $\alpha=0.05$, $df=23$), expressed as a percentage of the mean

Cu ($\pm 33\%$) with a mean of $\pm 24\%$ across all elements. Concentrations of N, K, Ca, Mg, Mn, and Al in xylem sap were related to one or more of the treatment factors of forest location, tree organ, or the interaction of tree organ with month of sap extraction (Table 3). Variations in concentrations of P, Cu, Zn, and Fe were not attributable to any of the main treatment factors or their interactions.

Root sap contained significantly higher concentrations of K, Ca, Mg, Mn, and Al than branch sap (Tables 3, 4). Sap collected in June contained significantly higher concentrations of Mn than sap collected in September (Tables 3, 4). Location significantly affected the sap concentrations of N (Mt. Abraham, Crawford Notch>Howland) and Mn (Mt. Abraham>Crawford Notch>Howland) (Table 4). The interaction of tree organ with the month of sap extraction significantly affected the concentration of N (June branch, September root>September branch, with June root sap being intermediate in N concentration and not significantly different from either group) and K (September root>June root, June branch>September branch) (Table 4).

Enrichment ratios were highly variable, both among elements at a given location and among locations for a

given element (Table 5). For both the Oa and upper B soil horizons, enrichment ratios of N followed the order of Howland>Crawford Notch>Mt. Abraham. Enrichment ratios of Ca, Mg, and K were usually in the reverse sequence. Al was largely excluded from the root sap at all three locations. Between locations, element concentrations in the soil solution (Table 5) ranged from a factor of 2 (Al) to a factor of 11 (N, Ca). In root sap, element concentrations were highly conserved with N having the greatest range factor of 2.3.

Discussion

We infer that the narrow range of element concentrations indicated a high degree of metabolic control of the mineral constituents of xylem sap. Across the three forest locations, the high range factors in the soil solution [derived from David and Lawrence (1996)], the low range factors in the root sap, and the wide range of root sap enrichment ratios suggested substantial physiological investment in homeostatic control of root sap chemistry. Specific homeostatic levels are likely to vary with re-

Table 3 ANOVA of the log-transformed element concentrations in xylem sap of red spruce as affected by forest location (Mount Abraham, Crawford Notch, Howland), organ (root, branch), or month (June, September)

Source	df	F	P>F ^a	Source	df	F	P>F
N				Mn			
Location	2	26.46	<0.001	Location	2	25.64	<0.001
Organ	1	4.04	0.068	Organ	1	33.40	<0.001
Month	1	5.37	0.039	Month	1	15.98	0.002
Location×organ	1	2.12	0.163	Location×organ	1	2.55	0.086
Location×month	1	3.00	0.088	Location×month	1	0.31	0.560
Organ×month	1	20.64	0.001	Organ×month	1	3.85	0.778
Location×organ×month	2	1.96	0.086	Location×organ×month	2	0.46	0.769
Error	12			Error	12		
P				Fe			
Location	2	3.69	0.056	Location	2	0.86	0.449
Organ	1	<0.01	0.932	Organ	1	0.20	0.666
Month	1	1.34	0.269	Month	1	1.42	0.257
Location×organ	1	0.43	0.659	Location×organ	1	0.38	0.694
Location×month	1	0.15	0.864	Location×month	1	1.70	0.223
Organ×month	1	4.83	0.048	Organ×month	1	5.79	0.033
Location×organ×month	2	0.648	0.541	Location×organ×month	2	0.92	0.425
Error	12			Error	12		
K				Cu			
Location	2	0.16	0.850	Location	2	0.90	0.432
Organ	1	52.70	<0.001	Organ	1	1.47	0.248
Month	1	1.98	0.185	Month	1	0.90	0.362
Location×organ	1	4.31	0.039	Location×organ	1	0.44	0.657
Location×month	1	1.72	0.221	Location×month	1	4.04	0.046
Organ×month	1	35.07	<0.001	Organ×month	1	0.48	0.503
Location×organ×month	2	0.34	0.721	Location×organ×month	2	2.58	0.117
Error	12			Error	12		
Ca				Zn			
Location	2	0.06	0.941	Location	2	2.49	0.125
Organ	1	60.94	<0.001	Organ	1	7.64	0.017
Month	1	6.62	0.024	Month	1	0.17	0.690
Location×organ	1	2.08	0.167	Location×organ	1	2.88	0.095
Location×month	1	0.16	0.853	Location×month	1	0.33	0.726
Organ×month	1	6.49	0.026	Organ×month	1	3.74	0.077
Location×organ×month	2	0.41	0.672	Location×organ×month	2	1.27	0.315
Error	12			Error	12		
Mg				Al			
Location	2	0.14	0.873	Location	2	2.12	0.163
Organ	1	75.15	<0.001	Organ	1	15.18	0.002
Month	1	6.82	0.023	Month	1	1.58	0.233
Location×organ	1	0.62	0.553	Location×organ	1	0.22	0.803
Location×month	1	0.40	0.681	Location×month	1	1.04	0.384
Organ×month	1	4.94	0.046	Organ×month	1	3.79	0.075
Location×organ×month	2	1.05	0.380	Location×organ×month	2	1.16	0.346
Error	12			Error	12		

^a The desired significance level of $P < 0.05$ was protected from inflation due to multiple comparisons by testing at the nominal $P < 0.007$

spect to tree maturation and phenology (Glavac et al. 1990; Kazda and Weilgony 1988; Stark and Spitzner 1985).

The large differences among locations in enrichment ratios for a specific element strongly contrast with the low range factors in root sap. In the Oa soil horizon, for example, Ca enrichment ratios varied from 4 to 41 versus a range factor of 1.3 and K enrichment varied from 11 to 84 versus a range factor of 1.2. These contrasts show the plasticity of tree response to varying soil element concentrations to maintain homeostatic levels in xylem sap.

N and K were the elements found in greatest concentrations in xylem sap. A significantly reduced N concentration in branch sap in September may indicate removal from the sap and seasonal storage of N in roots and stemwood. Concentrations of K in the root sap were highly conserved with a range factor of 1.2 compared with a range factor of 7 in the soil solution. The greatest concentration of K was in September root sap, perhaps reflecting a seasonal decrease in loading of the symplast. Removal of K, Ca, Mg, Mn and Al along the sapstream from roots to branches indicated net uptake into the symplast, bind-

Table 4 Significant effects of location, organ, and month of collection on mean element concentrations in red spruce xylem sap^a

Element	Comparison	Mean concentration ($\mu\text{M} \pm \text{SE}$) ^b
N	Location	Howland, 1,186 \pm 114 (a); Crawford Notch, 2,238 \pm 327 (b); Mt. Abraham, 2,923 \pm 366 (b)
	Organ \times month	Branch \times September, 1,248 \pm 190 (a); root \times June, 2,068 \pm 432 (ab); root \times September, 2,476 \pm 360 (b); branch \times June, 2,672 \pm 552 (c)
K	Organ	Branch, 1,344 \pm 114 (a); root 2,090 \pm 140 (b)
	Organ \times month	Branch \times September, 1,035 \pm 42 (a); branch \times June, 1,653 \pm 132 (b); root \times June, 1,782 \pm 87 (b); root \times September, 2,398 \pm 202 (c)
Ca	Organ	Branch, 205 \pm 26 (a); root 564 \pm 52 (b)
Mg	Organ	Branch, 66 \pm 7.3 (a); root 190 \pm 14 (b)
Mn	Location	Howland, 37 \pm 6.0 (a); Crawford Notch 65 \pm 12 (b); Mt. Abraham 115 \pm 23 (c)
	Organ	Branch, 46 \pm 7.3 (a); root, 100 \pm 18 (b)
	Month	September, 59 \pm 14 (a); June, 86 \pm 16 (b)
Al	Organ	Branch, 6.6 \pm 0.7 (a); root 11 \pm 1.1 (b)

^a Means were separated by ANOVA of log-transformed values (Table 3) followed where appropriate by the Bonferroni procedure. Non-transformed means (and SE) are displayed in this table

^b For each comparison, mean values followed by the same letter (in parentheses) are not significantly different ($P < 0.05$, adjusted for multiple comparisons)

Table 5 Mean element concentrations (μM) and enrichment ratios^a of soil solutions^b and root sap of red spruce

Element	Mount Abraham, Vermont					Crawford Notch, New Hampshire					Howland, Maine					Across all locations		
	Soil solution		Root sap	Enrichment ratio		Soil solution		Root sap	Enrichment ratio		Soil solution		Root sap	Enrichment ratio		Range factor ^c		
	Oa	B		Oa	B	Oa	B		Oa	B	Oa	B		Oa	B	Soil solution	Root sap	
	Oa	B	Oa	B	Oa	B	Oa	B	Oa	B	Oa	B	Oa	B	Oa	B		
N ^d	24	14	2,899	121	207	12	6	2,680	223	447	5	2	1,237	247	618	5	11	2.3
Ca	13	8	534	41	67	47	22	654	14	30	143	43	504	4	12	11	5	1.3
Mg	15	4	191	13	48	28	4	193	7	48	58	5	186	3	37	3	1.3	<1.1
K	25	11	2,088	84	189	47	10	2,312	49	231	173	14	1,870	11	136	7	1.4	1.2
Al	34	28	12	0.4	0.4	21	27	9	0.4	0.3	54	21	11	0.2	0.5	2	3	1.3

^a Enrichment ratios were calculated as the ratio of the mean concentration (untransformed) of each element in the root sap divided by the concentration in the organic soil solution as reported by David and Lawrence (1996)

^b Element concentrations in Oa and B horizon soil solutions as reported by David and Lawrence (1996)

^c The range factor was calculated by dividing the highest concentration in each soil solution and root sap by the lowest concentration across all three locations. High values indicated a wide range of concentrations across locations and a value approaching 1 indicated little variation in concentration across locations

^d N concentration in the soil solution was calculated as the sum of NO_3^- and NH_4^+ -N

ing to wood cell walls, or precipitation of the elements. Although beyond the scope of this investigation, the flow of Ca (and to a lesser extent Mg) in the sapstream could be affected by greater amounts of cell wall material per unit volume of xylem in slow-growing trees (McLaughlin and Wimmer 1999). Highly localized differences within the sapstream redox and electronegative environment could affect the binding and flow of Mn and N.

Variation in some of the essential elements was not significantly related to location, organ, or month sampled. Variation in P was conserved ($\pm 18\%$ of the mean value) which does suggest metabolic control of xylem sap concentrations. Concentrations of Cu, Zn, and Fe varied more widely; although essential, their levels were likely to be well in the range of physiological sufficiency.

True differences in xylem sap chemistry were not likely to have been masked at the relatively low overpressure (maximum of 0.5 mPa) applied to the sample

roots and branches (Berger et al. 1994; Osonubi et al. 1988). Enrichment ratios were not likely to have been biased by transpiration rates in that xylem sap concentrations were independent of transpiration rates (Berger et al. 1994; Kazda and Weilgony 1988) and that bulk water flow was not likely to have varied greatly across locations due to similar sample timing, tree size, canopy position, and organ water potentials.

Prenzel (1979) described element uptake by tree roots as consisting of positive and negative discrimination relative to transpirational water uptake. Both positive and negative discrimination involves the expenditure of metabolic energy. Obvious energy-requiring processes involve proton export for exchange with essential base cations or the formation and operation of membrane-bound pumps. Less obvious is the maintenance of fine roots, ion exchange sites, transport proteins, channels, and gates that facilitate ion uptake. The uptake of NO_3^- im-

mediately involves the amination of C skeletons, removing organic acids from energy-yielding respiration. The release of organic acids into the sapstream and the formation of organic complexes with Ca and Mg may be a mechanism to control concentrations in xylem sap (Schell 1997). Metabolic energy is also required to maintain the pH gradient that precipitates Al out of xylem sap through precipitation in the root cortex as well as to produce new fine root tips to act as filters for Al and Fe.

The high enrichment ratios for Ca, Mg, and K at Mt. Abraham suggest that the trees at that location are expending a greater amount of energy for element uptake than at Howland and perhaps Crawford Notch. The high Al:Ca molar ratio of 2.5 in the soil solution at Mt. Abraham compared with a ratio of 0.4 at Crawford Notch and Howland also suggest that maintenance of uptake of potentially blocked Ca and Mg may require additional energy expenditure through the added production of fine roots. The abundant N in the Mt. Abraham soil solution may initially result in a reduced energy requirement for N uptake, yet lead to an increased allocation of energy in the form of organic acids for subsequent amination.

The concept of homeostatic control through tree biology provides a powerful explanation for the apparent lack of relationship between soil chemistry and tree elemental composition. The energy demand to maintain homeostasis of xylem sap composition is likely to be an important allometric component in tree survival. This energy requirement for homeostasis is likely to be integral for tree resource budgets as has been outlined for energy requirements for tree growth and defense (Herms and Mattson 1992; Loehle 1988). Arguably, trees with reduced energy availability due to pest and pathogen attack and other adverse environmental conditions are likely to allocate a larger proportion of compromised resources to maintain homeostasis at the cost of decreased growth and reduced implementation of inducible defenses.

Far from being a continuous aquifer with the soil solution, the chemistry of xylem sap reflects a dynamic homeostasis that results in comparatively conserved concentrations of mineral elements. While xylem sap analysis has only limited utility as a marker for soil chemistry, the comparison of xylem sap chemistry with soil chemistry can yield information on the likely metabolic burden placed on trees in varying chemical environments.

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