Relationships Among Potassium, Calcium and Trace Elements in Tree Leaves and Associated Canopy Arthropods[1]

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ABSTRACT There is a paucity of information that describes the relationship between the suite of nutrient elements in tree foliage and associated arthropod assemblages. Foliage from chestnut oak (*Quercus prinus*), hickories (*Carya* spp.), yellow poplar (*Liriodendron tulipifera*), red maple (*Acer rubrum*), and flowering dogwood (*Cornus florida*) and associated canopy arthropods were collected in an undisturbed and a 15 yr-old successional forested watershed and analyzed for K, Ca, Mn, Fe, Cu, Zn, Rb, and Sr. Foliar Mn and Sr were found in higher concentrations in the undisturbed watershed. Foliage from hickories was generally higher in concentrations of metals (Mn, Fe, Cu, Zn) compared with other tree species. Dogwood foliage had significantly higher concentrations of Ca and significantly lower concentrations of Mn than other tree species ($P < 0.05$). Concentrations of foliar elements in herbivore-damaged and undamaged leaves did not differ significantly ($P > 0.05$). Concentrations of elements in and among arthropod feeding categories varied substantially such that no trends were apparent among tree species and between watersheds. The most apparent trend among arthropod feeding categories was the relatively large accumulation of K in chewing herbivores (primarily caterpillars). In general, there appeared to be increases in K, Fe, Cu, and Zn concentrations from primary producers to consumers. This study contributes to arthropod nutritional ecology and to defining the role of canopy arthropods in forest ecosystem nutrient cycles.

KEY WORDS herbivory, arthropods, potassium, trace elements, calcium, *Quercus, Carya, Liriodendron, Cornus, Acer,* temperate forests.

Few studies have addressed the relationships between biologically essential elements (with the exception of nitrogen) in arthropods and their host plants. Primary emphasis has been placed on elements which are required in considerable quantity (e.g., K, Ca) and are therefore more easily measured (Schowalter and Crossley 1983). Less information is available on the dynamics of trace elements or micronutrients such as Fe, Cu, Mn, Zn, Rb, and Sr which are important in metabolic processes.

In this paper I attempt to define and compare the relationships between herbivore damage and concentrations of certain foliar elements (primarily micronutrients) in two deciduous forests, one in the 15th year of uninterrupted succession

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from grass and the other undisturbed. I also examine the patterns of element concentrations in and among several arthropod functional feeding categories. The elements selected for this study were K, Ca, Mn, Fe, Cu, Zn, Rb, and Sr which are active in a variety of metabolic processes. Potassium functions in protein synthesis, cell division, and carbohydrate metabolism in both animals and plants (Smith 1980). Calcium is utilized in an intercellular cement in plants and is an osmotic regulator in animals (Thomas 1969). Manganese and iron are involved in chlorophyll production in plants and, along with copper and zinc, function as enzyme cofactors in plants and animals (Hewitt 1983). Rubidium and strontium are metabolic analogues of potassium and calcium, respectively.

Study Site

Samples were collected in 1981 from two forested watersheds at the Coweeta Hydrologic Laboratory, U.S. Forest Service, Otto, NC. Plant communities range from cove hardwoods in mesic coves at lower elevations to oak and oak-pine communities on mesic slopes and xeric ridges, respectively (Day et al. 1987).

Both watersheds face northeast, average 53% slope, and range in elevation from approximately 700 m to between 900 m and 1000 m (Swank and Crossley 1987). Watershed 6 (WS6) (9 ha) has been the subject of two large-scale treatments. The first involved cutting streamside vegetation (Dunford and Fletcher 1947) and the second consisted of clearing the catchment and planting it in fescue grass *(Festuca arundinacea* Schreb) (Hibbert 1969). During the second treatment, 6.7 metric tons of crushed dolomitic limestone and 2.2 metric tons of 2-12-12 NPK fertilizer were applied per hectare. Since 1968 the watershed has followed an otherwise uninterrupted secondary succession. At the time of this study, WS6 was dominated by black locust (*Robinia pseudoacacia* L.), yellow poplar (*Liriodendron tulipifera* L.) and associated understory species including blackberries (*Rubus* spp.) and fescue remnants.

Watershed 18 (WS18) (12.5 ha) has been undisturbed since 1927 and serves as a reference for comparison with other treatment watersheds (Swank and Crossley 1987). Vegetation is dominated by oaks (primarily chestnut oak, *Quercus prinus* L.) (42.7% total basal area) followed by red maple (*Acer rubrum* L.) (9.3%), hickories (*Carya tomentosa, C. glabra)* (8.5%), yellow poplar (7.0%), and flowering dogwood (*Cornus florida* L.) (3.5%) (Day and Monk 1974). Watershed 18 and WS6 are separated by a 61 ha undisturbed watershed.

Materials and Methods

Three transects were established across WS6 each beginning from a randomly selected point on a lateral boundary. Transects were established in WS18 at similar elevations and compass orientations as those in WS6. A single randomly selected transect was sampled during each of ten biweekly sample periods from May through September 1981. Foliage was collected from chestnut oak, hickories, yellow poplar, red maple, and flowering dogwood. Rope-climbing techniques, modified from those described by Perry and Williams (1981) and Whitacre (1981), were used to reach the canopies of several large trees in the undisturbed watershed (Risley 1984). Small branches, their leaves, and associated arthropods were captured with a collapsable-mouth nylon bag (Crossley et al. 1976) mounted on the hoop of a 3.5 m butterfly net pole and fitted with a 50 l plastic garbage bag liner. Branches were enclosed quickly and pruned free with an extendable limb pruner. Sample bags were tied shut, removed to a nearby lab facility and refrigerated. In this manner 5 samples per tree species (hickories included as one species) in both watersheds were collected each sample period. A total of 500 samples were taken.

In the laboratory, leaves were picked from branches and separated into piles of herbivore-damaged and undamaged (< 1% photosynthetic area removed). Associated arthropods were sorted into three feeding groups: sucking herbivores (SH), chewing herbivores (CH), and predators (P). At Coweeta, biomass of arthropod herbivores in the forest canopy is dominated by insects in the orders of Coleoptera, Hemiptera, Homoptera, Lepidoptera, and Orthoptera. Biomass of predatory arthropods is dominated by arachnids (Araneae and Phalangida) and insects (some Hemiptera). Animals which did not fit into the above feeding categories (e.g., fungivores or detritivores) were not included in elemental analyses. Leaves and arthropods were lyophilized to constant weight (24 h) and ground to a homogeneous powder using a porcelain mortar and pestle in preparation for x-ray fluorescence spectrometry (XRF).

I analyzed foliage samples of 200 mg, arthropod samples of 100 mg, 50 mg, or 10 mg, and standards (National Bureau of Standards Orchard Leaves 1977) of equal weights and consistency for K, Ca, Mn, Fe, Cu, Zn, Rb, and Sr. A ^{109}Cd source was used to excite a secondary target, silver, which in turn irradiated each sample with monoenergetic x-rays. Elements in irradiated samples emitted x-rays which were sampled by a lithium-drifted silicon detector (E G & G Ortec®, Oak Ridge, TN). Detector signals were amplified, sorted, and counted in a multichannel analyzer at a resolution of 50 eV per channel. Since elements emit x-rays of discrete and characteristic energies (D'Auria and Bennett 1975) their identification was straightfoward. Areas under spectral peaks of the above elements were calculated after a counting time of 30 minutes and compared to those of the corresponding standard.

Results and Discussion

Foliar Analysis. Considerable intra- and inter-watershed variability are associated with foliar elements among the sampled tree species (Table 1). Although XRF is not a commonly reported method of tissue analysis, it is analytically sound, and results are consistent with previously reported foliar element concentrations obtained from this analysis technique (Gist and Risley 1982, Satake 1980).

Concentrations of foliar Fe and Cu were not significantly different within tree species between watersheds while Mn and Sr were significantly higher in the undisturbed watershed (Table 1). Among tree species, spectra of foliar elements from hickories and flowering dogwood were least similar between watersheds while those from red maple and chestnut oak most similar. Concentrations of foliar elements were generally higher for trees growing in the undisturbed watershed. Exceptions to this were Zn and Ca in yellow poplar, and Ca in dogwood. Assuming that physical conditions in WS18 and pre-treatment conditions in nearby WS6 were similar, probably the single greatest influence on concentrations of foliar elements was the alteration of soil pH by liming associated with the forest-to-grass

Table 1. Concentrations of elements in foliage from selected tree species in the successional (WS6) and undisturbed (WS18) watersheds. Concentrations are expressed as mean (µg/g) dry weight with standard errors of means in parentheses (n = 20). Means in a row followed by the same letter are not significantly different (P = 0.05; Ryan-Einot-Gabriel-Welsch multiple range test) (SAS 1985). T-tests (P = 0.05; n = 20; ns = not significant; * = significant) were utilized for watershed comparisons of elements within tree species.

Element	WS	*Quercus prinus*		*Carya* spp.		*Liriodendron tulipifera*		*Acer rubrum*		*Cornus florida*	
K	6	7428	(257.2)^{b}	6969	(328.1)^{b}	8853	(472.6)^{a}	6630	(348.2)^{b}	7683	(235.5)^{b}
		ns		*		ns		ns		*	
	18	8117	(286.3)^{bc}	9059	(497.0)^{ab}	9972	(746.1)^{a}	6777	(290.4)^{c}	9764	(314.0)^{ab}
Ca	6	7515	(234.6)^{c}	10313	(445.7)^{b}	10860	(542.4)^{b}	7089	(354.2)^{c}	16325	(461.2)^{a}
		ns		ns		*		ns		*	
	18	7431	(172.2)^{bc}	10374	(657.6)^{ab}	9491	(306.1)^{a}	7134	(264.8)^{c}	12848	(737.7)^{ab}
Mn	6	102	(4.5)^{b}	156	(7.8)^{a}	92	(2.1)^{b}	93	(3.2)^{b}	71	(0.1)^{c}
		*		*		*		*		*	
	18	307	(14.1)^{a}	344	(18.3)^{a}	148	(10.8)^{c}	202	(16.4)^{b}	77	(2.2)^{d}
Fe	6	130	(3.7)^{a}	135	(3.4)^{a}	132	(6.7)^{a}	127	(5.9)^{a}	130	(5.5)^{a}
		ns		ns		ns		ns		ns	
	18	134	(3.3)^{ab}	143	(6.1)^{a}	130	(5.2)^{ab}	120	(2.8)^{b}	131	(5.1)^{ab}
Cu	6	11	(0.2)^{ab}	12	(0.2)^{a}	11	(0.2)^{ab}	11	(0.1)^{b}	11	(0.1)^{b}
		ns		ns		ns		ns		ns	
	18	11	(0.1)^{b}	12	(0.2)^{a}	11	(0.2)^{b}	11	(0.1)^{b}	11	(0.1)^{b}
Zn	6	21	(0.5)^{b}	26	(1.0)^{a}	21	(0.6)^{b}	21	(0.7)^{b}	19	(0.4)^{b}
		ns		*		*		ns		ns	
	18	20	(0.4)^{b}	34	(1.2)^{a}	19	(0.4)^{b}	20	(0.3)^{b}	19	(0.4)^{b}
Rb	6	13	(0.8)^{a}	11	(0.7)^{ab}	12	(0.7)^{a}	9	(0.5)^{b}	9	(0.3)^{b}
		*		*		ns		*		*	
	18	22	(1.2)^{a}	19	(1.6)^{a}	14	(1.2)^{b}	11	(0.6)^{b}	13	(0.7)^{b}
Sr	6	14	(0.5)^{c}	38	(3.6)^{b}	35	(2.8)^{b}	17	(1.2)^{c}	52	(2.7)^{a}
		*		*		*		*		*	
	18	28	(1.1)^{c}	89	(8.7)^{ab}	74	(4.4)^{b}	38	(2.1)^{c}	96	(4.9)^{a}

conversion in WS6. Soil pH in WS6 increased considerably soon after treatment (to pH 6.0) (Norris 1969) and had changed very little by 1981 (pH 5.7 - 5.8) (Montagnini et al. 1986). Soils in an undisturbed watershed, located between WS6 and WS18, exhibited lower pH values (pH 4.7) (Montagnini et al. 1986) charcteristic of undisturbed soils in the area (Swank and Crossley 1987). Root uptake of Mn is inhibited by alkaline conditions (McHargue 1945) thus the more acid soils in WS18 have favored greater Mn uptake and subsequently greater Mn concentrations in plants. The same may hold true for other foliar elemental concentrations in WS18. For example, higher foliar concentrations of Ca in dogwood and yellow poplar in WS6 may indicate increased availability on the treated watershed. Because pre-treatment data on foliar elemental concentrations are not available for WS6 and these watershed comparisons have limited statistical meaning (see Hurlbert 1984), caution should be employed in interpreting the above results as treatment effects.

Comparisons of foliar elemental concentrations among trees in each watershed were made using multiple range tests (Table 1). Hickories were characterized by relatively high foliar metal concentrations (Mn, Fe, Cu, Zn) which is consistent with the tendency for *Carya* spp. to accumulate metals (Robinson and Edington 1945). This characteristic has been useful in assessing concentrations of metals in the surrounding environment (Ragsdale and Berish 1987). Dogwood is known to accumulate Ca (Day and McGinty 1975, Thomas 1969) and foliar concentrations of this element were significantly higher in dogwood than in other tree species in both watersheds (Table 1). In addition, dogwood had significantly lower foliar concentrations of Mn than other tree species in both watersheds (Table 1). As expected, concentrations of foliar Sr tracked those of Ca, whereas concentrations of Rb were more similar among tree species than its analogue, K.

Perhaps the most interesting result came from attempting to use the 9 individual elements to distinguish between herbivore-damaged and undamaged leaves (not illustrated). There were no singificant ($P > 0.05$) differences between foliar element concentrations of damaged and undamaged leaves for any of the examined elements (model I single classification ANOVA, $n = 10$) (Sokal and Rohlf 1969). A similar comparsion of foliage mineral status in heavily-defoliated and lightly-defoliated trees was made by Cook et al. (1978). They reported significantly higher concentrations of N, P, K, Mg, and Cu, and significantly lower Ca in heavily-defoliated leaves. Wallace and O'Hop (1985) found that K concentrations were lower in yellow water lily (*Nuphar luteum* (L.)) (Nymphaeaceae) leaves damaged by the waterlily leaf beetle, *Pyrrhalta nymphaeae* (L.), (Coleoptera: Chrysomelidae). Potassium concentrations in red maple foliage were higher in insecticide-treated trees compared with untreated trees at Coweeta (Seastedt et al. 1983). The studies by Wallace and O'Hop (1985) and Seastedt et al. (1983) illustrate that K is readily leached from damaged (leaky) leaves (see Tukey 1970). My data fail to confirm these trends. All damaged leaves, without regard to amount of damage, were included in the "damage" category. Because most leaves had less than 10% area removed by herbivores, the level of herbivore damage may have been too low to cause significant leaching or other damage-induced changes in elemental concentrations.

Arthropod Analyses. Concentrations of nutrient elements, based on whole body analyses, are given in Table 2 for arthropods associated with samples of foliage. There was sufficient material for only one determination within feeding categories among tree species and between watersheds. I found that despite the

Table 2. Concentrations of elements in canopy arthropods associated with selected tree species in the successional (WS6) and undisturbed (WS18) watersheds. Concentrations are expressed as µg/g dry weight and each value represents an analysis of a composite of individuals collected during one growing season. WS = watershed, SH = sucking herbivores, CH = chewing herbivores, P = predators.

Tree Species	WS	Feeding Category	K	Ca	Mn	Fe	Cu	Zn	Rb	Sr
Quercus prinus	6	SH	10360	6077	90	289	12	26	12	31
		Ch	14865	6343	102	183	14	41	15	20
		P	9430	5402	88	190	14	38	14	18
	18	SH	8756	5745	86	255	12	25	11	29
		CH	12186	5722	116	201	14	40	17	23
		P	11365	6363	96	176	14	46	13	16
Carya spp.	6	SH	9378	5247	87	203	14	34	13	18
		CH	10446	5370	89	159	12	34	12	19
		P	10466	5956	89	166	13	39	10	14
	18	SH	9253	6026	89	270	12	26	12	29
		CH	12168	6488	107	205	12	34	10	18
		P	10838	6468	94	362	13	31	13	31
Liriodendron tulipifera	6	SH	10596	5667	88	160	12	25	8	13
		CH	14677	7990	106	199	15	41	18	41
		P	10250	6063	88	165	14	40	10	15
	18	SH	10047	6071	92	267	12	28	11	30
		CH	14946	5993	98	177	13	41	17	20
		P	10399	6273	92	289	13	34	12	31
Acer rubrum	6	SH	9057	5990	87	253	12	25	11	30
		CH	13930	5844	84	269	13	35	11	18
		P	9242	5796	87	145	13	33	8	13
	18	SH	—*	—*	90	295	12	27	12	34
		CH	11813	5986	103	148	12	31	9	16
		P	9187	5940	90	258	12	27	11	28
Cornus florida	6	SH	10360	6277	90	265	12	30	11	30
		CH	15379	6696	85	192	13	31	12	22
		P	9491	6089	87	264	12	29	11	29
	18	SH	9577	6182	113	263	13	27	14	30
		CH	11311	5972	104	159	12	30	10	16
		P	10322	6201	94	163	12	33	10	15

* Data lost.

many large bags of branches and leaves collected, canopy arthropods were uncommon. This has been observed elsewhere in forests and in the eastern U.S. (Schultz 1983). Utilization of XRF permitted the analysis of multi elemental concentrations from single samples among arthropod feeding categories where more commonly used techniques (e.g., atomic absorption spectrometry) would have required a sample run for each element.

For any given element, concentrations in and among the arthropod feeding categories varied substantially such that no trends were apparent among tree species and between watersheds. Concentrations of elements in arthropods do not appear to track those of the corresponding tree species on which they were collected. Independence of elemental spectra in foliage compared with associated arthropods was documented by Bowden et al. (1984). Elemental spectra within feeding groups among tree species do not mirror the large differences visible in taxonomic representation associated with those feeding groups (Table 3). For example, caterpillars contributed 94% of the biomass to the CH group in WS6 dogwood while caterpillars contributed 18% of the biomass to CH in WS6 red maple and in WS6 yellow poplar. However, although Ca was higher on dogwood, most of the elemental spectra of CH from those three tree species in WS6 did not exhibit any trends associated with the differences in taxonomic structure.

To further illustrate the complexities of interpretation, there are at least two types of elemental accrual in organisms: accumulation and concentration. An accumulator species takes on relatively high concentrations of elements which are in excess in its source. Lepidoptera larvae have been reported to accumulate K (50 mg/g ash free dry matter) (Duvigneaud and Denaeyer-DeSmet 1975). Concentrator species accrue high concentrations of elements which are not in excess in the source. According to McLean and Bennett (1978) insects can act as concentrators by binding certain elements to lipids and proteins, thus preventing their excretion. Variability in the dynamics of nutrient processing by arthropods probably adds to the lack of similarity between elemental spectra of foliage and arthropods.

The most apparent trend among the arthropod feeding groups involved K. This element occurred generally in higher concentrations in CH than in either SH or P in all cases except WS6 hickory. The same trend was noted by Schowalter and Crossley (1983) and Schowalter et al. (1981) who examined canopy arthropods from clear-cut and undisturbed watersheds at Coweeta. Van Hook (1970) found no significant ($P > 0.05$) difference between herbivore K and predator K in an east Tennessee grassland ecosystem, but when I compared his SH to CH there was an increase in K in his data similar to that illustrated in Table 2.

Generally, there appeared to be increases in K, Mn (dogwood only), Fe, Cu, and Zn concentrations from producers to consumers. Decreases were noted for Ca and Mn (except dogwood). Patterns were not consistent for Rb and Sr. Reichle et al. (1970) showed increases for Ca and K from producers to consumers in an east Tennessee forest dominated by yellow poplar. Satake (1980) reported than Zn was accumulaed up a food chain from host plant (*Alnus hirsuta*) to insect herbivore "*Agerastica coerulea*" to a spider "*Nephila clavata*" which preyed upon the herbivore. That pattern was not apparent in my results.

There is a paucity of information on relationships between host plant foliage and associated arthropods with respect to some macronutrients and especially trace elements (e.g., metals) despite the influential role of arthropods in transfers of materials and coupling of ecosystem processes (Risley and Crossley 1988,

Table 3. Relative contributions of canopy arthropod taxa to the feeding categories in which they were placed. Proportions are based on dry weight. WS = watershed, SH = sucking herbivores, CH = chewing herbivores, P = predators.

Tree Species	WS	SH	CH	P
Quercus prinus	6	42%-Homoptera:Aphidoidea 58%-Homoptera:Fulgoroidea	79%-Lepidotera 12%-Orthoptera† 8%-Coleoptera‡	57%-Hemiptera* 20%-Araneae
	18	99%-Homoptera:Fulgoroidea	59%-Coleoptera 40%-Lepidoptera	74%-Araneae 23%-Hemiptera
Carya spp.	6	70%Homoptera:Fulgoroidea 28%-Hemiptera§	48%-Orthoptera 38%-Lepidoptera 14%-Coleoptera	49%-Araneae 29%-Hemiptera
	18	94%-Homoptera:Fulgoroidea 6%-Homoptera:Aphidoidea	65%-Lepidoptera 34%-Coleoptera	52%-Araneae 21%-Phalangida
Liriodendron tulipifera	6	74%-Homoptera:Aphidoidea 26%-Hemiptera	77%-Orthoptera 18%-Lepidoptera 5%-Coleoptera	78%-Araneae 12%-Hemiptera
	18	47%-Homoptera:Aphidoidea 53%-Hemiptera	67%-Lepidoptera 33%-Coleoptera	42%-Phalangida 24%-Araneae 23%-Hemiptera
Acer rubrum	6	87%-Homoptera:Fulgoroidea 13%-Homoptera:Aphidoidea	82%-Coleoptera 18%-Lepidoptera	91%-Araneae 4%-Hymenoptera[5]
	18	86%-Hemiptera 13%-Homoptera:Aphidoidea	64%-Coleoptera 26%-Lepidoptera 6%-Orthoptera	45%-Hemiptera 34%-Araneae 11%-Hymenoptera
Cornus florida	6	97%-Homoptera:Fulgoroidea 3%-Homoptera:Aphidoidea	94%-Lepidoptera 3%-Orthoptera	57%-Araneae 33%-Hemiptera 3%-Hymenoptera
	18	90%-Hemiptera 10%-Homoptera:Fulgoroidea	86%-Coleoptera 14%-Lepidoptera	43%-Hymenoptera 29%-Hemiptera 19%-Phalangida 6%-Araneae

* For example, Reduviidae and some Miridae and Pentatomidae.
† Primarily Tettigoniidae.
‡ Primarily Chrysomelidae.
§ For example, some Miridae and Pentatomidae.
¶ Parasitoid wasps.

Seastedt and Crossley 1984). This study provides information that can be utilized to develop canopy arthropod nutrient pools (see Schowalter and Crossley 1983) and thereby can better define the role of canopy arthropods in nutrient cycling. Further, the importance of micronutrients in herbivore nutrition (Chapman 1982), their abundance in host plant foliage, and their potentially controlling effects on rates of herbivory (see Seastedt and Crossley 1981) could provide new avenues of research.

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