

SODIUM DYNAMICS IN FOREST ECOSYSTEMS AND THE ANIMAL STARVATION HYPOTHESIS

Sodium may be a critical limiting element for certain vertebrate herbivore populations (Aumann and Emlen 1965; Botkin et al. 1973). Arms et al. (1974, p. 1) hypothesized that the "relative exclusion of sodium from the tissues of most plants may help them against grazing by making it difficult for the grazers to obtain as much of this ion as they need." Whittaker et al. (1979, p. 215) compared sodium dynamics with those of other elements and reported, "Consistent with the animal starvation hypothesis, the concentration of Na in leaves, as above ground tissues most subject to animal consumption, had the lowest ratio to sapwood of all elements studied]." Contrary to this "animal starvation hypothesis," we contend that forest trees do not exhibit any aboveground allocation strategy for this element and that sodium concentrations in forest trees are at least one to two orders of magnitude above those levels found in soil percolates. As a null hypothesis we state that sodium levels in plants do not affect levels of herbivory; however, alternatives include not only the animal starvation hypothesis but also the opposite hypothesis, i.e., sodium levels observed in plants stimulate consumption.

SODIUM DYNAMICS IN FORESTS

Patterns and variability of sodium concentrations in soil and biota of a southern deciduous forest are reported in table 1. These data were collected between 1969 and 1974 from watershed 18 at the Coweeta Hydrologic Laboratory, North Carolina. Detailed descriptions of this oak-hickory forest, methods, and seasonality of sodium and other elemental concentrations are reported in Johnson and Swank (1973), Day and Monk (1974, 1977), Best and Monk (1975) and Swank and Henderson (1976). Sodium concentrations in bulk precipitation average less than 0.2 ppm and concentrations of sodium increase in litter and soil percolates to over 1 ppm. Extractable sodium in soil averages 6.4 ppm dry weight (B. L. Henderson, personal communication). Sodium concentrations in aboveground wood, stems, and bark are increased about 10 to 100 times those in soil. Bark concentrations may occasionally be 1,000 times those of soil percolates, probably a result of stemflow and throughflow accumulation of sodium and subsequent evaporation of water containing high amounts of sodium on bark tissues. Average leaf concentrations are generally much lower than those observed in woody tissues, although concentrations are occasionally quite high; again, a possible result of throughflow evaporation or dryfall accumulation on foliage tissues (Day and Monk 1977). Canopy arthropod herbivores exhibit sodium concentrations about 20–100 times those of foliage, and canopy arthropod predators further concentrate sodium to levels about 2–10 times those found in herbivores.

Data on long-term aboveground accumulation and flux of sodium in forests are limited. The most complete long-term data are from a northern deciduous forest at

TABLE 2

SODIUM AND POTASSIUM DYNAMICS IN A NORTHERN HARDWOOD FOREST*

PARAMETER	SODIUM		POTASSIUM	
	kg ha ⁻¹ yr ⁻¹	% of total	kg ha ⁻¹ yr ⁻¹	% of total
Total aboveground uptake	.4542	100.0	53.13	100.0
Immobilization in wood (including heartwood)	.0316	7.0	4.25	8.0
Insect consumption (leaves only)	.0046	1.0	2.10	4.0
Leaf fall				
Total woody litter	.0330	7.2	2.10	4.0
Leaves and reproductives	.0750	16.5	14.60	27.5
Leaching losses	.3100	68.3	30.08	56.5
Losses of insect consumption, leaf litter, and leaching losses	.3896	85.5	46.78	88.0

Data from Whittaker et al. (1979, p. 211).

SODIUM CONCENTRATIONS AND HERBIVORY

Our null hypothesis states that sodium levels in forest trees do not affect levels of herbivory. This hypothesis has not been adequately tested for either vertebrates or invertebrates. Available data suggest that vertebrates may be sodium limited (Aumann and Emlen 1965; Botkin et al. 1973), and that mammals will search out sources of sodium in the environment (e.g., Weeks and Kirkpatrick 1988). However, selective grazing on plants relatively high in sodium content has not been demonstrated. The nutritional properties most often associated with food selection by vertebrates are high nitrogen or phosphorus content (Lay 1956; Klein 1970). Radwan (1974) reported that the literature is inconsistent with regard to which elements are selected. We suspect that selective feeding by vertebrates or invertebrates on plants because of a particular property such as nitrogen content will result in other and perhaps spurious correlations with the particular mineral nutrition of that plant species. Cook et al. (1978) correlated nutrient concentrations in white spruce needles with levels of defoliation by sawflies. They reported positive correlations with nitrogen, phosphorus, potassium, magnesium, and copper content of foliage, but found no correlation with sodium content. Our work at Weetabaw has also failed to produce any correlations between numbers, biomass, and consumption by canopy arthropods and sodium content of foliage (D. A. Bossley and C. S. Gist, unpublished data). Work on insect nutrition has not reported sodium limitations. Dadd (1973) noted that sodium requirements for insects are very low and are often provided by "unavoidable dietary impurities." Insects may obtain adequate amounts of sodium in spite of low concentrations in their diet because of high assimilation efficiency for this element. Reichle and Bossley (1966) estimated about 90% assimilation of sodium by domestic crickets. Assimilation of sodium by sucking herbivores and spiders approaches 100% (C. S. Gist, personal communication). Herbivores may also supplement their diets by consuming materials relatively high in sodium content, as exemplified by puddling behavior of butterflies (Arms et al. 1974). Naturally occurring puddles or areas of

eral accumulation on the forest floor are rare at Coweeta and probably rare in most forest ecosystems. However, sodium from bulk precipitation, throughfall, and stemflow may be occasionally concentrated on foliage and wood, as indicated by the high sodium concentrations reported in table 1. Sodium supplements may be obtained by feeding on epiphytic lichens or on fungi (Cromack et al. 1977).

DISCUSSION

Sodium inputs to forested ecosystems from bulk precipitation and weathering of parent materials are large when compared with the standing crops of sodium in abiotic components of these ecosystems. Turnover of sodium is very rapid, and ecosystems do not conserve this element (e.g., Johnson and Swank 1973; Likens et al. 1977; Whittaker et al. 1979). Sodium is perhaps the most magnified element in plant-herbivore-predator food chains (Reichle and Crossley 1966; Cornaby and Crossley 1973). However, we find no evidence that sodium levels in trees affect levels of herbivory or that trees allocate this element to any specific tissue. Sodium, an element that has little or no function in higher land plants, is unavoidably obtained by root uptake and subsequently magnified, perhaps as a consequence of selective uptake of other, required elements. Sodium concentrations in above-ground plant tissues are 10–100 times those observed in soil percolates, and levels may occasionally be much higher, perhaps the result of stemflow, throughfall, or litter accumulation on plant tissues. Perhaps because roots discriminate against sodium, sodium concentrations and amounts in terrestrial plants appear to be primarily influenced by abiotic factors such as inputs from bulk precipitation and weathering of parent materials, and by leaching rates from plant tissues. While sodium demand by herbivores is large and sodium limitations may occur in certain invertebrate populations, no data suggest that sodium is limiting to canopy arthropods, the major grazers of forest systems.

Low sodium concentrations in foliage could stimulate rather than reduce consumption by herbivores. Assimilation of sodium by chewing insects is believed to be very high (ca. 90%; Reichle and Crossley 1966), while energy assimilation is only about 25%–35% (Wiegert and Evans 1967). Faced with a chronic shortage of sodium, invertebrate and perhaps certain vertebrate herbivores may have relatively low energy assimilation efficiencies and increased consumption rates in order to obtain a sufficient amount of sodium. A similar hypothesis has been proposed for lemmings, which have been reported to periodically experience reduced availability of nitrogen, calcium, and phosphorus (Barkley et al. 1980). Silvertown et al.'s (1974) hypothesis implies that grazing per se has a negative impact on plants and is therefore to be avoided. That assumption has been questioned by a number of investigators (e.g., Mattson and Addy 1975; Owen 1978; Simberloff et al. 1978). Let us assume that grazing is "bad" and that sodium is indeed limiting to consumers. The observed pattern of sodium concentrations in woody tissue such as bark and twigs is higher than that observed in foliage. Provided assimilation efficiencies for all tissues are equal, wood feeding would be favored over foliage feeding. Making one final assumption that wood feeding is more deleterious than foliage feeding to the long-term survivorship and reproductive potential of plants,

conclude that the retention of sodium in supportive tissue is maladaptive. Lichens, which contain equal or greater levels of sodium than bark tissues (Whitford et al. 1979), would also be selected by herbivores. Sodium exclusion in lichens (either by design or physical leaching) while maintaining sodium in supportive structures or roots is not a good idea if consumers are sodium starved. However, we doubt that the pattern of sodium concentrations observed in forest species affects the level of herbivory by invertebrate consumers. Vertebrate herbivores are rarely found in forest canopies, and whether this last observation is a result of sodium limitation has yet to be demonstrated.

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