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THE USE OF GAMMA SPECTROMETRY TO MEASURE WITHIN-PLANT NUTRIENT ALLOCATION OF A TANK BROMELIAD, GUZMANIA LINGULATA

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ABSTRACT. Using recently developed techniques of gamma spectrometry, we investigated patterns of nutrient uptake and translocation within the tank bromeliad *Guzmania lingulata.* Uptake from foliar impoundments vs. soil was traced using four gamma-emitting radionuclides (Se-75, Cs-137, Zn-65, Mn-54). Foliage appeared to be the primary site of nutrient acquisition. In general, inflorescences were stronger nutrient sinks than leaves; labeled nutrients were detectable within days after addition to foliar tanks.

Although below-ground root systems are considered the primary organs used by terrestrial plants to acquire inorganic mineral nutrients, shoots of some plants are also capable of nutrient uptake. Foliar absorption is critical for many epiphytes, and is sometimes effected by specialized epidermal structures (Benzing & Burt, 1970; Benzing et al., 1976; DeSanto et al., 1976). Atmospheric bromeliads of the subfamily Tillandsioideae possess a specialized endomentium, which consists of peltate trichomes, each of which is composed of a stalk of living cells and capped with a shield of dead cells. Trichomes that cover the entire shoot on non-impounding atmospheric species absorb moisture and dissolved salts from films of water on the leaf surfaces. Studies with radioactive traces have confirmed that even relative immobile minerals such as calcium can be absorbed and translocated within shoots (Burt-Utley & Utley, 1975).

Shoots of non-atmospheric tank bromeliads which possess root systems and which grow in more mesic microhabitats have more sparsely distributed trichomes than shoots of atmospheric bromeliads (Benzing, 1980). The extent to which rooted tank epiphytes rely upon uptake from tanks vs. root systems has not been determined. We compared nutrient uptake and translocation following uptake by shoots and roots of the flowering tank bromeliad *Guzmania lingulata.* We asked the following questions: How rapidly are tracers absorbed and translocated following uptake by shoots vs. roots? How do leaves compare to inflorescences as nutrient sinks?

We used recently developed techniques of gamma spectrometry (Primack & Levy, 1988) with potted tank bromeliads. These methods were used rather than the more commonly used beta-emitting tracers for three reasons: 1) The distinctive and characteristic wavelengths of each radioisotope allow for simultaneous monitoring of two or more mineral elements. In contrast, only one beta-emitting tracer may be used at a time because of the overlap of their broad peaks of energy emission. By administering different gamma-emitting nuclides to different sites and then monitoring the arrival of each nuclide to leaves and stems, the source of uptake could be identified. 2) In contrast to destructive sampling required for beta-emitting radionuclides, the same plant (or plant part) can be measured repeatedly, since no tissue is removed or damaged; dynamics of uptake by intact plants can be documented. 3) The technique is fast and safe. We could take many measurements in a short time and directly compare nuclide levels for each of our replicates during each sampling interval. The disadvantages of this technique (as with other tracer studies using soil-grown plants) are: 1) the similarity in uptake and translocation of isotopes to non-isotopic mineral forms can only be assumed, and 2) the amount of nuclides adsorbed to soil particles cannot be quantified, so comparisons of uptake from different sources are qualitative.

MATERIALS AND METHODS

Experiments were conducted at the Boston University Radionuclide Laboratory. Four experimental plants of the bromeliad *Guzmania lingulata* (L.) Mez (subfamily Tillandsioideae) were purchased from a local nursery. This taxon

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is shade-tolerant and native to the understory of humid neotropical forests (Benzing, 1980). Experimental plants were grown in a local nursery in 5-liter pots of standard potting soil mix and had extensive root systems that permeated the soil in all areas of the pots. The experimental plants presumably possess more extensive root systems than plants grown under natural canopy conditions, which would bias results in favor of root uptake. Shoots consisted of 10-15 rosulate leaves which held water without leakage. Each specimen had produced a single terminal flowering spike (approximately 50 cm tall) (FIGURE 1).

Four gamma-emitting radionuclides were used to follow absorption and mobility in intact plants: Se-75, Cs-137, Mn-54, and Zn-65. Selenium was provided as selenic acid; the other nuclides were chloride salts. Individual plants received less than 10^{-9} moles of each element, a negligible quantity considering the volume of water and soil in each pot. These nuclides have distinct energy levels exceeding 300 keV and are sufficiently stable for use in the month-long experiments. Each nuclide has been used in other studies of plant nutrition. Selenium-75 has been considered a sulfur analogue; it can be incorporated into certain amino acids and proteins (NRC Comm., 1976). Cesium-137 has been used as a potassium analogue, since it is bound by the same binding sites in plant root cells and its movements in xylem are the same (Witherspoon, 1964; Epstein, 1972). Manganese and zinc are micronutrients and their isotopic forms are also expected to be taken up by plant roots (Robertson, 1957; Tiller, 1979).

One microcurie of each nuclide, diluted in 0.5 ml of distilled water, was delivered by syringe to the tanks and to the soil. The radioactive fluids were applied directly to the water in the rosette pools. We were careful to deliver the solutions to portions of the potting soil that contained fine roots. For the duration of the experiments, plants were given sufficient water to keep the potting medium moist but not enough to cause leakage from the bottom of the pots. Plants were maintained throughout the experiments under a 12-hr photoperiod with fluorescent and incandescent lights beginning at 7 A.M.

The plants received the four radionuclides from two sources. Two plants (B1 and B2) had Se-75 and Mn-54 radionuclides administered to their above-ground rosette pools and Cs-137 and Zn-65 applied to the soil in the location of below-ground roots (FIGURE 1). Another pair of plants (B3 and B4) received the opposite complement of radionuclides; Se-75 and Mn-54 were added to the soil and Cs-137 and Zn-65 added to the rosette pool. The sample size was limited by the time needed to measure all plant parts of all replicates within a short enough time interval so that the dynamics of nuclide uptake and translocation could be directly compared.

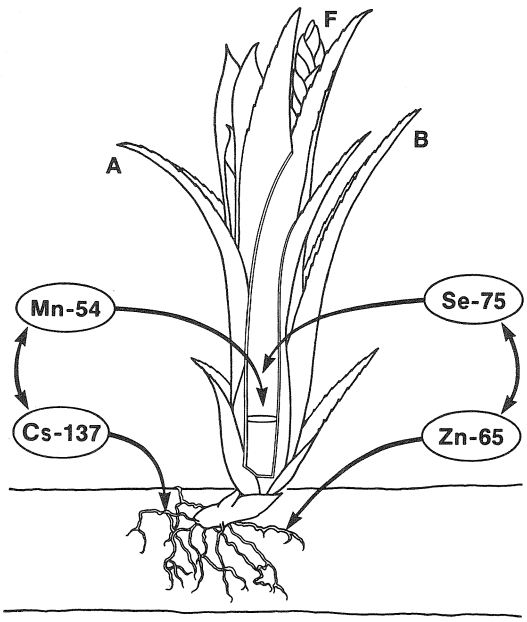

FIGURE 1. Schematic of experimental design for bromeliads B1 and B2. Nuclides were delivered either to the rosette pool or to the rhizosphere of soil roots. Target organs were leaves A, B and inflorescence, F.

The presence, identity, and amount of nuclides present were determined by spectral analysis with a NaI crystal (Tracor Northern TN-7200) enclosed in a lead chamber with an adjustable aperture, connected to a 1024 pulse-height analyzer (Chapman and Ayrey, 1981; Levy et al., 1982; Primack and Levy, 1988; Stegmann et al., 1988). For each reading, the target organ (leaf or inflorescence) was placed in front of the aperture against the crystal face. The lead shielding prevented detectable radiation reaching the crystal except from the plant part under scrutiny. Each sample was counted for 100–300 sec according to the amount of the nuclide present. Background readings were made and subtracted for each reading. The amounts of radioactivity reaching target organs were monitored once each day for each plant part during the first week, and once each week for the next three weeks. Nuclides present were identified by peak position and quantified by peak height. The amounts of radionuclides arriving at the target organs were calculated as a percentage of the total radionuclides administered.

RESULTS AND DISCUSSION

All four radionuclides were absorbed from rosette pools and translocated to shoots (TABLE 1).

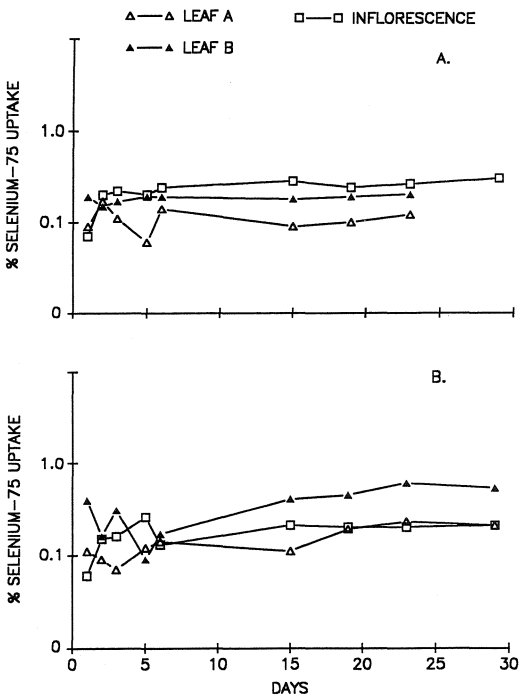

FIGURE 2. Dynamics of uptake and translocation of Se-75 in two experimental plants (2a = B1; 2b = B2) arriving at leaves A and B (triangles) and inflorescence (square), expressed as a percentage of total nuclide delivered in the rosette pool. None of the Se-75 was detected in shoots when this nuclide was administered to the soil.

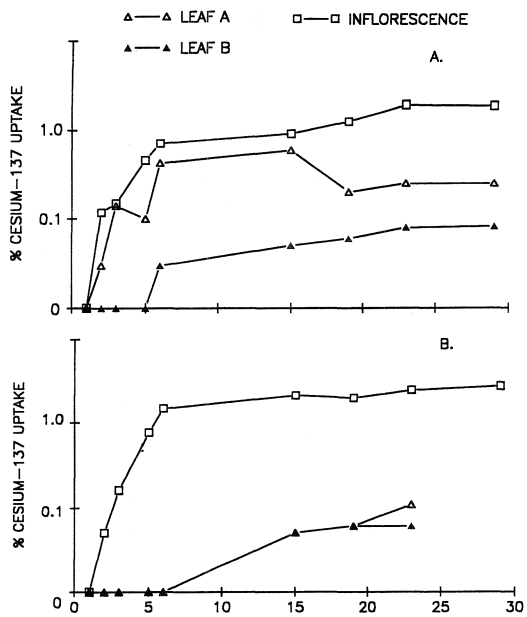

FIGURE 3. Dynamics of uptake and translocation of Cs-137 in two experimental plants (3a = B3; 3b = B4) arriving at leaves A and B (triangles) and inflorescence (square), expressed as a percentage of total nuclide delivered in the rosette pool. None of the Cs-137 was detected in shoots when this nuclide was administered to the soil.

Selenium-75 and Cs-137 were absorbed and transferred from the tank to shoots to a greater extent than were Mn-54 and Zn-65. The dynamics of uptake varied with each nuclide, but showed a general pattern of rapid uptake during the first week followed by a plateau (FIGURES 2, 3).

Tanks greatly surpassed roots as sites of absorption. Three of the four nuclides administered in tank fluids were detected in leaves and inflorescences while those administered to the soil showed no movement into above-ground plant parts (TABLE 1). Manganese-54 was detected in above-ground plant parts when delivered to the soil in one of the plants (B3), which indicates that at least a portion of the root system was functional. The failure to detect activity of the other three nuclides administered to the soil indicates either that functional roots were absent in other areas of the pot or those nuclides were adsorbed on soil surfaces or immobilized by microflora.

Once nutrients were absorbed from tanks, inflorescences appeared to be stronger nutrient sinks than the leaves for three of the four nuclides (Cs-137, Mn-54 and Zn-65), but leaves and inflorescences were equally strong sinks for Se-75 (TABLE 1). Comparatively little is known about the ways that epiphytic plants allocate mineral nutrients among different parts of plants. Benzing (1981) pointed out that an "adaptive strategy" for successfully exploiting the epiphytic biotope is to allocate a large proportion of nutrients to reproductive parts. Atmospheric bromeliads have been reported to have generally low vegetative nutrient contents and a high proportion of nutrients allocated to seeds (Benzing & Davidson, 1979).

The upper tree canopy has been considered a microhabitat chronically lacking in water and nutrients which has led to an array of adaptive features that promote high water and nutrient use efficiency (Benzing, 1981). Atmospheric bromeliads, which have been shown to rely entirely on inorganic nutrients dissolved in rain and mist rather than mineralized from soil, represent the extreme of the anatomical and physiological adaptations to the epiphytic biotope (Benzing & Renfrow, 1980). Our experiments suggest epiphytes which occupy less extreme conditions, the mesic understory of humid tropical forests, may be at least partially independent of root uptake from mineral substrates. In situations where inorganic nutrients are unavailable to epiphyte roots

TABLE 1. Amounts of nuclides arriving at leaves and inflorescences for experimental bromeliad plants expressed as a percentage of the total amount of nuclide delivered to roots and rosette pools after 29 days. In plants B1 and B2, Se-75 and Mn-54 were added to the rosette pool while Cs-137 and Zn-65 were added to the roots. The reverse treatments were used in plants B3 and B4. Uptake percentages are underlined where a nuclide was added to the rosette pool.

Plant number	Structure monitored	Se-75	Cs-137	Mn-54	Zn-65
B1	Leaf A	0.11	0	0	0
	Leaf B	0.20	0	0	0
	Inflor.	0.30	0	0.28	0
B2	Leaf A	0.21	0	0	0
	Leaf B	0.53	0	0.16	0
	Inflor.	0.21	0	0.32	0
B3	Leaf A	0	0.25	0	0
	Leaf B	0	0.08	0	0
	Inflor.	0	1.88	0.14	0.12
B4	Leaf A	0	0.10	0	0
	Leaf B	0	0.07	0	0
	Inflor.	0	2.83	0	0.13

(due to irregular inputs or immobilization of minerals on substrate surfaces or in the microflora), tank bromeliads with well-developed root systems have rapid access to nutrients captured and stored in their tank fluids.

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LITERATURE CITED

BENZING, D. H. 1980. The biology of the bromeliads. Mad River Press, Inc., Eureka, California. 305 pp.

———. 1981. Mineral nutrition of epiphytes: an appraisal of adaptive features. Selbyana 5: 219–223.

——— AND K. M. BURT. 1970. Foliar permeability among twenty species of the Bromeliaceae. Bull. Torrey Bot. Club 97: 269–279.

——— AND E. A. DAVIDSON. 1979. Oligotrophic *Tillandsia circinnata* Schlect (Bromeliaceae): an assessment of its patterns of mineral allocation and reproduction. Amer. J. Bot. 66: 386–397.

———, K. HENDERSON, B. KESSEL, AND J. SULAK. 1976. The absorptive capacities of bromeliad trichomes. Amer. J. Bot. 63: 1009–1014.

——— AND A. RENFROW. 1980. The nutritional dynamics of *Tillandsia circinnata* in southern Florida and the origin of the "air plant" strategy. Bot. Gaz. 141: 165–172.

BURT-UTLEY, K. AND J. UTLEY III. 1975. Calcium^{45} translocation in *Tillandsia balbisiana* Schult. (Bromeliaceae). Brenesia 5: 51–65.

CHAPMAN, J. AND G. AYREY. 1981. The use of radioactive isotopes in the life sciences. George Allen & Unwin Ltd., London, England. 299 pp.

DESANTO, A. V., A. ALFANI, AND P. DELUCA. 1976. Water vapour uptake from the atmosphere by some *Tillandsia* species. Ann. Bot. (London) 40: 391–394.

EPSTEIN, E. 1972. Mineral nutrition of plants: principles and perspectives. John Wiley and Sons, New York. 412 pp.

LEVY, C., D. YOUNGSTROM, AND C. MALETSKOS. 1982. Radioecology on a nuclear power station site using recapturable wild birds and whole-body spectroscopic analysis. Pp. 329–343 *in* Environmental migration of long-lived radionuclides. Int. Atomic Energy Agency, Vienna, Austria.

NATIONAL RESEARCH COUNCIL. 1976. Selenium committee on the medical and biological effects of environmental pollutants. National Academy of Sciences, Washington, D.C.

PRIMACK, R. AND C. LEVY. 1988. Measuring maternal fitness in plants using gamma spectrometry. Ecology 69: 796–800.

ROBERTSON, J. 1957. Theory and use of tracers in determining transfer rates in biological systems. Physiol. Rev. 37: 133–154.

STEGMANN, E., R. PRIMACK, AND G. ELLMORE. 1988. Exploitation of terrapin eggs by roots of *Ammophila breviligulata* (Gramineae). Can. J. Bot. 66: 714–718.

TILLER, K. 1979. Applications of isotopes to micronutrient studies. Pp. 359–370 *in* International symposium on the use of isotopes and radiation on soil–plant relationships. Colombo, Sri Lanka.

WITHERSPOON, J. 1964. Cycling of cesium-134 in white oak trees. Ecol. Monogr. 34: 403–420.