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A comparison of mineral uptake and translocation by above-ground and below-ground root systems of *Salix syringiana*

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Abstract

Nutrient uptake and translocation by above-ground adventitious roots and below-ground roots of woody *Salix syringiana* saplings were studied with gamma spectrometry. Each of four radionuclides (^{75}Se, ^{138}Cs, ^{54}Mn, and ^{65}Zn) administered to adventitious and belowground roots were detected in stems and leaves within one month. Nuclides tended to be immobilized in the leaves and branches closest to the adventitious roots that absorbed them, while nuclides absorbed from below-ground sources were distributed more evenly throughout the plant. The capacity of adventitious roots to acquire nutrients from above-ground sources suggests they function as a potential 'auxiliary' pathway of nutrient uptake and might enhance plant nutrient status where below-ground root uptake is hindered by adverse soil conditions.

Introduction

Most work on adventitious roots (AR) has been on their anatomy and development and their role in plant water relations (*e.g.*, Fjell, 1985; Hook *et al.*, 1970; Kling and Meyer, 1983; Nanda *et al.*, 1974; Sena Gomes and Kozlowski, 1980a). The predominance of species that readily produce AR in habitats which are subject to frequent flooding or other adverse soil conditions suggests that they increase tolerance to flooding (Gill, 1975; Wample and Reid, 1978). Recent experimental work corroborates that the production of AR increases flooding tolerance by increasing soil aeration, oxidizing the rhizosphere, reducing water stress, and transforming toxins to less harmful products (Clemens *et al.*, 1978; Gilman *et al.*, 1982; Hook and Kormanik, 1971; Hook *et al.*, 1970; Pereira and Kozlowski, 1977; Sena Gomes and Kozlowski, 1980b; Tsukahara and Kozlowski, 1985).

One type of above-ground AR ('canopy roots') is found beneath mats of epiphytes and crown humus (dead organic matter that accumulates beneath them) (Nadkarni, 1981). These roots are produced by many species of trees in temperate and tropical wet forests (Fink, 1983; Gill, 1969; Gill and Tomlinson, 1969; Herbert, 1958; Jenik, 1973; Lanner, 1966; Lyford, 1969; Nadkarni, 1981; Nadkarni, 1983). The importance of these AR in nutrient acquisition has been inferred only from indirect evidence: 1) occurrence on trees growing on infertile and/or chronically water-saturated soils; 2) presence on canopy branches and trunks only where there are substantial amounts of crown humus; 3) morphological similarity to below-ground roots (BR) (abundant root hairs, unsuberized root tips), and 4) association of some canopy roots with mycorrhizal and nitrogen-fixing symbionts (Nadkarni, 1981). A first step in determining the selective advantage of these roots and in ascertaining their importance at the plant community level is to directly measure the capacity of these roots to absorb nutrients.

The present study dealt with absorption and translocation of radioactive tracers by AR and BR roots. We used techniques of gamma spectrometry modified from Kirkham *et al.* (1967) with soil-rooted woody saplings. These methods were used rather than the more commonly used beta-emitting nuclides 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 root locations 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, and for isotope studies in which exudates from decapitated stems are analyzed (*e.g.* Ferguson and Bollard, 1971), the same plant (or plant part) can be measured repeatedly, since no tissue is removed or damaged. The within-plant circulation of nuclides absorbed from different sources could be compared; 3) The technique is fast (3 to 5 min per reading) and safe (only very small amounts of each radionuclide are used). We could take many measurements in a short time and thus directly compare all nuclide levels for each of our replicates during each sampling interval.

Most experimental work on mineral uptake and within-plant circulation has been done with hydroponically grown plants (Biddulph, 1955; Broeshart and Nethsinghe, 1972; Epstein, 1972). Growing roots in soils as in the present experiments more closely approximates field conditions. It was not possible to quantify the amounts of tracers adsorbed to the surfaces of soil particles and roots, and so our comparisons are only qualitative. This approach was used to: 1) determine if AR absorb water and minerals from solutions in a soil matrix, 2) identify translocation paths of mineral nutrients absorbed by above-ground and below-ground organs, and 3) determine whether minerals absorbed from above- and below-ground sources are immobilized in different tissues.

Materials and methods

Experiments were carried out in the Plant Laboratory of Boston University, Boston, Massachusetts, from June 16 to July 18, 1985. Willow saplings (*Salix syringiana*) were chosen because they readily produce AR (Carlson, 1950) and their congenerics have naturally occurring canopy root systems where epiphytes and canopy organic matter are abundant (Nadkarni 1983). Four saplings (1.5 m ± 0.2 m in height, 6.0–7.5 cm in stem diameter, with 5–8 branch systems each) were grown singly in 16-liter pots of standard potting soil mix under greenhouse conditions and maintained throughout the experiments under a 12-hr photoperiod beginning at 7 AM.

Production of AR was first stimulated on twig crotches of the experimental saplings using the standard technique of air-layering (Hartmann and Kester 1975). On each sapling, two branch systems of equal size that bifurcated from the main stem close to the soil were selected so that one pair of higher order twigs was separated from the other pair (Fig. 1). On each plant, 'wads' of sphagnum moss (approximately 250 cc in volume) were wrapped around the twig junctions of each of these branches. The wads were moistened and wrapped loosely in plastic sheeting. Extensive production of adventitious roots was evident within 30 days. These had characteristic branching rootlets, unsuberized root tips, and root hairs. The soil in each pot was permeated with extensive BR that app-

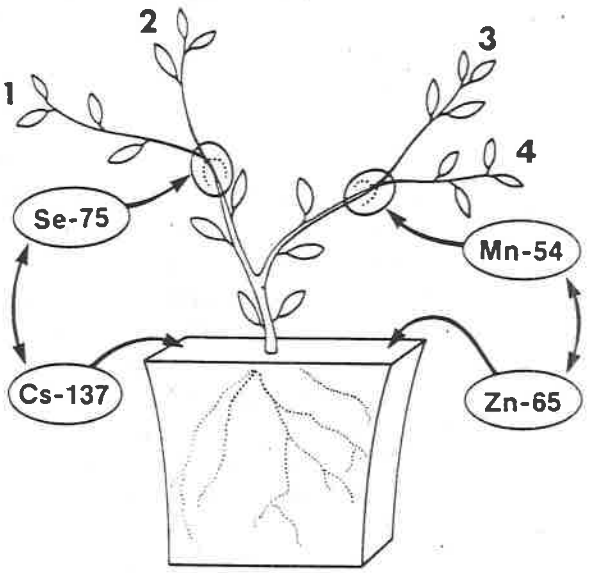

Fig. 1. Schematic of one combination of nuclides administered to experimental plants. Each nuclide was administered to the wad of one above-ground root system of two replicate plants, and to belowground roots of two other plants. For each nuclide, target twigs were designated 'above, near' and 'above, far' (for ^{75}Se, twigs 1 and 2 are 'above, near' and twigs 3 and 4 are 'above, far'). In two other replicate plants, ^{75}Se and ^{54}Mn were administered to the below-ground roots, and the two above-ground root wads received either ^{65}Zn or ^{137}Cs.

eared to be morphologically similar to the aboveground roots.

Four gamma-emitting radionuclides were used to trace mineral uptake and translocation: ^{75}Se, ^{137}Cs, ^{54}Mn, and ^{65}Zn. These nuclides were selected because they emit gamma rays at spectral peaks greater than 300 KeV and have sufficiently long half-lives to be detected in plants for the duration of the month-long experiments. Each has an abrupt spectral peak which is readily distinguished from the spectral peaks of the other nuclides. 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). ^{137}Ce 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 (Epstein, 1972; Witherspoon, 1964). Manganese and zinc are micronutrients and their isotopic forms are also expected to be taken up by plant roots (Robertson, 1957; Tiller, 1979).

Each above-ground sphagnum wad and associated AR was labelled with a single nuclide so that uptake from AR of individual branches could be differentiated. Each wad of two replicate plants were administered doses of a single radionuclide (^{75}Se or ^{54}Mn); the potting soil of those two plants were administered doses of two different nuclides (^{137}Cs and ^{65}Zn) (Fig. 1). Nuclides were delivered to two other replicate plants in the opposite combination (^{137}Cs or ^{65}Zn to the above-ground wads, ^{75}Se and ^{54}Mn to potting soil), so there were two replicate saplings for each combination of nuclides. 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.

One microcurie of each nuclide, diluted in 0.5 ml of distilled water, was delivered by syringe to the rhizospheres of AR and BR. The radioactive solutions were carefully administered to portions of the potting soil medium and the sphagnum wads that were permeated with fine roots. The dose of nuclides administered was less than 10^{-9} moles for each mineral, a negligible quantity considering the volume of water and soil in each pot. Selenium was administered as selenic acid; the other nuclides as chloride salts. For the duration of the experiments, plants were given sufficient water to keep the potting medium moist, but not enough to induce drainage from the bottom of the pots.

The two terminal branches directly above each wad and accompanying AR were designated 'target twigs'. Each twig was 12 to 15 cm long, with 10 to 15 leaves, and located so measurements of nuclide activity of each twig could be made individually, *i.e.*, with minimal background counts from other twigs or the pot. Four target twigs were measured on each sapling; two were on branches adjacent to that root wad ('above, near'), and two were on a separate branch system ('above, far') (Fig. 1).

The scintillation counter consisted of one NaI crystal detector with an associated photomultiplier and 1024 channel pulse-height analyzer (Tracor Northern TN-7200), regulated power supply, and associated electronic equipment. This instrument

Table 1. Amounts of nuclides arriving at target twigs, expressed as a percentage of total amount of nuclide delivered to below- and aboveground roots after 15 and 29 days. For each nuclide administered to aboveground wads, 4 target twigs were measured on each individual; 2 were on branches adjacent to that root wad ('above, near'), and 2 were on a separate branch system ('above, far'). There were two replicate saplings for each combination of nuclides

Replicate	Nuclide location	^{75}Se		^{137}Cs		^{54}Mn		^{65}Zn	
		Day 15	Day 29	Day 15	Day 29	Day 15	Day 29	Day 15	Day 29
1	Above, near	2.24	2.33	0.43	0.68	-0-	0.09	-0-	-0-
2	Above, near	2.11	4.46	0.13	0.32	0.19	0.86	-0-	-0-
1	Above, far	-0-	-0-	-0-	-0-	-0-	-0-	-0-	-0-
2	Above, far	-0-	-0-	-0-	-0-	-0-	-0-	-0-	0.3
1	Soil	1.09	2.44	-0-	0.52	-0-	-0-	-0-	-0-
1	Soil	0.53	0.46	0.02	0.11	-0-	-0-	-0-	-0-
2	Soil	0.79	1.78	0.05	0.13	0.39	-0-	-0-	0.04
2	Soil	0.65	2.61	0.22	0.68	-0-	-0-	0.45	0.15

has been used for a variety of applications that require the capability of picocurie sensitivity (Ayrey, and Chapman, 1981; Levy *et al.*, 1976, 1982; Primack and Levy, 1988; Stegman *et al.*, 1988). Nuclide uptake and transport were monitored with the NaI crystal, which was enclosed in a 5-cm-thick box of lead bricks, the front of which could be opened to create an aperture of adjustable width. The lead shielding prevented detectable rdiation reaching the crystal except from the plant part under scrutiny. At each time of reading of activity, the target twig was placed in front of the aperture against the crystal face. The plant was then removed, and a background reading was made for the same amount of time as used for the sample. Data are given as readings for the sample minus that for background.

The amounts of radioactivity reaching target organs was monitored once each day for each plant part during the first week, and once each week for the next three weeks. During the first week of the experiments, the amount of activity of each target twig was measured for 300 seconds, but as radionuclide levels increased, an interval of 100 seconds was sufficient for measuring the amount of activity present. Counts per minute were corrected for half-life decomposition. The amounts of radionuclides arriving at the target twigs were calculated as a percentage of total radionuclides administered.

On day 23 of the experiment, nuclide activity of twig segments 10 cm above and 10 cm below each above-ground wad were taken. This was to ascertain the direction nuclides moved within the plant as an indication of the translocation pathways (xylem versus phloem) of nuclides absorbed by AR and BR.

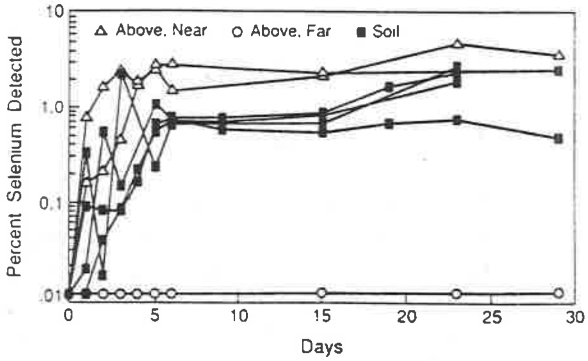

Fig. 2. Amounts of ^{75}Se arriving at target twigs, expressed as a percentage of total nuclide delivered. Twig designations follow Fig. 1. ^{75}Se was administered to the soil in two plants and to the above-ground roots in two plants. No ^{75}Se was detected in either 'above, far' twig when ^{75}Se was administered to the above-ground wad, so the two lines of zero values are indistinguishable.

Results

By the 15th day of the experiment, each of the nuclides was detected in at least one target twig, indicating that minerals absorbed by both AR and BR were translocated and incorporated into plant tissues (Table 1). The patterns of uptake and translocation differed for the four radionuclides. Selenium-75 was detected in target twigs first and in the largest amounts, followed by ^{137}Cs. ^{65}Zi and ^{54}Mn were detected in smaller amounts and their patterns of activity were not consistent *e.g.* ^{54}Mn was present in one replicate on day 15, but was not detected on day 29. Patterns of the former two nuclides will be discussed in detail.

^{75}Se was detected in target twigs within 24 hours. Uptake from both above- and below-ground sources increased rapidly for five days, and then reached a plateau (Fig. 2). ^{137}Ce was also absorbed rapidly during the first week and translocated to twigs from both AR and BR, but accumulated more gradually than did ^{75}Se (Fig. 3). Assuming that similar amounts of nuclides were immobilized on AR and BR surfaces and soil media, the rates of uptake and translocation of these nuclides were comparable for above- and below-ground sources.

The site of immobilization of minerals depended on the source of uptake. For ^{75}Se and ^{137}Cs, tracers administered to AR were trnsported to and imm-

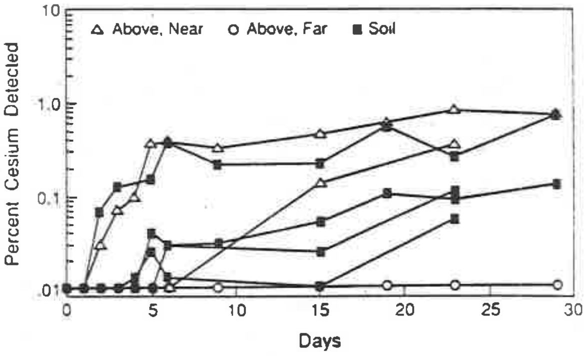

Fig. 3. Amounts of ^{137}Cs arriving at target twigs, expressed as a percentage of total nuclide delivered. Twig designations follow Fig. 1. As in Fig. 2, no ^{137}Cs was detected in the 'above, far' twigs so that the two lines of zero values are indistinguishable.

obilized in the branches nearest to them. These two nuclides were detected only in twigs adjacent to the wad to which they were administered ('near' twigs). No nuclides were detected in the target twigs of the 'far' branch system of the same plants (Table 1). In contrast, plants which absorbed ^{75}Se and ^{137}Cs through the BR system had comparable amounts of activity in all of the target twigs, indicating that nuclides are more evenly distributed throughout the plant when absorbed from below-ground sources (Fig. 2 and 3).

Detection of nuclides at a finer spatial scale revealed that nuclide movement was not exclusively unidirectional. In plants which absorbed nuclides from below-ground sources, the amounts of activity of all nuclides in stem areas 10 cm above and 10 cm below AR wads was comparable (Table 2). This indicates that there was equally strong acropetal movement in the xylem to all branches. This may or may not have been accompanied by translocation and subsequent basipetal movement in the phloem. In contrast, plants to which nutrients were administered to AR wads had ^{75}Se, ^{54}Mn (both replicates and ^{65}Zn (one replicate) in stem tissue above but not below the root wads. This pattern indicates that nuclide movement occurred only in the xylem stream; nuclides were transported acropetally and then immobilized in leaf tissues. ^{137}Ce (both replicates) and ^{65}Zn (one replicate), however, were detected in stem regions both above and below the AR wads to which they were administered (Table 2). This suggests that after being absorbed by AR, nuclides were transported in the xylem and then moved basipetally in the phloem, which corroborates with other studies that show cesium and zince to be phloem-mobile (Bukovac and Wittwer, 1957; Fischer, 1967). Undoubtedly xylem movement was much more important than phloem movement in translocation, since none of the 'far' twigs contained ^{75}Se, ^{54}Mn, or ^{137}Cs and only one 'far' target twig contained ^{65}Zn.

Discussion

Our experiments showed that AR can absorb dissolved minerals from the soil solution of an organic matter medium. Once absorbed, ions were preferentially transported to and immobilized in tissues of the branch system nearest to the site of above-ground uptake. The relative mobility of nuclides varied appreciably among nuclides and presumably among different nutrient ions. It is not surprising that due to the rather short transport distances in these saplings, the transport of minerals was clear-cut; when comparing these processes for mature plants, the distribution patterns may be more diffuse, due to the longer transport distances between below- and above-ground parts.

In these experiments, the predominant pathway of ion movement of nutrients absorbed in AR was undoubtedly via the xylem, as virtually no activity was detected in leaf tissues of the 'far' target twigs. The major factor governing the movement of water and ions through the xylem is the rate of transpiration, which is inversely proportional to distance it must travel in the xylem (Heine, 1970). The relatively small differences in distances between AR and BR, however, did not appear to have an effect on rates of arrival, as there was little difference in the time when nuclides were first detected in 'near' twigs when absorbed by AR and BR.

The most striking difference between nuclides that were absorbed by AR versus BR was the localization of nuclides absorbed by AR in leaf tissues

Table 2. Directional movement of nuclides in experimental plant stems. Measurements are amounts of nuclides detected in stem parts 10 cm above and 10 cm below above-ground AR wads, expressed as a percentage of total nuclide administered. Top portion of table are the amounts detected in the two replicates to which the nuclide was administered to the above-ground roots ('near' wad). The bottom portion of the table are the corresponding replicates which absorbed the nuclide from the soil

	^{75}Se		^{137}Cs		^{54}Mn		^{65}Zn	
	Above	Below	Above	Below	Above	Below	Above	Below
AR	0.27	-0-	0.73	0.57	0.82	-0-	0.02	-0-
AR	0.22	-0-	0.89	0.71	1.44	-0-	0.21	0.16
BR	0.30	0.43	0.06	0.22	0.30	0.26	0.04	0.09
BR	0.38	0.55	0.07	0.26	1.71	5.41	0.11	0.42

closest to the point of absorption. This indicates that within-plant nutrient circulation may be more complex than previously considered. In natural systems where substantial amounts of nutrient input and transfer occur via precipitation, nutrients which are absorbed by AR within the canopy (in stemflow and throughfall) would have a greater probability of being 'recycled' within the branch systems or crown areas from which they were generated than if they were to fall to the forest floor and be absorbed by BR.

The importance of above-ground absorbing organs such as adventitious roots, bark, and foliage in mineral nutrition of whole plants and nutrient cycles of entire plant communities has been discussed in only a few studies (Benzing and Burt, 1970; Ticknor and Tukey, 1955; Wittwer and Bukovac, 1969). The present study indicates that adventitious roots potentially increase the absorbing capacity of plants for mineral nutrients by providing access to nutrients from atmospheric and/or epiphyte-derived sources. Above-ground Ar are undoubtedly less exposed to flooding and an anaerobic environment than are BR, and so the former may provide an alternate pathway of nutrient acquisition when ground soils are saturated or otherwise unfavorable. This function would be most important in habitats which are periodically or chronically subject to adverse soil conditions and where above-ground nutrient sources are available. Trees in tropical cloud forests and temperate rainforests support considerable amounts of nutrients in the canopy (Nadkarni, 1984, 1985). Adventitious root systems may increase the efficiency of nutrient transfer from epiphytes and the dead organic matter they create to the trees which support them. Further quantitative studies on the distribution and phenology of adventitious AR and BR are needed to determine the role of the former at the plant community leve.

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References

Benzing D H and Burt K M 1970 Foliar permeability among twenty species of the Bromeliacea. Bull. Torrey Bot. Club 97, 269–279.

Biddulph O 1955 Studies of mineral nutrition by use of tracers. Bot. Rev. 21, 251–295.

Broeshart H and Nethsinghe D A 1972 Studies of the pattern of root activity of tree crops using isotope techniques. *In* Symposium on Isotopes and Radiation in Soil-Plant Relationships Including Forestry, I.A.E.A., Vienna.

Bukovac M and Wittwer S 1957 Absorption and mobility of foliar-applied nutrients. Plant Physiol. 32, 428–435.

Carlson M 1950 Nodal adventitious roots in willow stems of different ages. Am. J. Bot. 17, 555–561.

Chapman J and Ayrey G 1981 The Use of Radioactive Isotopes in the Life Sciences. George Allen and Unwin Ltd., London, U.K.

Clemens J, Kirk A and Mills P 1978 The resistance to waterlogging of three *Eucalyptus* species. Oecologia (Berl.) 34:125–131.

Epstein E 1972 Mineral Nutrition of Plants: Principles and Perspectives. John Wiley and Sons. New York, USA.

Fergusion I B and E G Bollard 1976 The movement of calcium in woody stems. Ann. Bot. 40, 1057–1065.

Fjell I 1985 Morphogenesis of the root cap in adventitious roots of *Salix viminalis*. Nord. J. Bot. 5, 555–574.

Fink S 1983 The occurrence of adventitious and preventitious buds within the bark of some temperate and tropical trees. Am. J. Bot. 70, 532–542.

Fischer H 1967 Phloem transport and Stoffaufnahme. Z. Pflanzenernaehr. Dueng. Bodenkd. 118, 100–111.

Gill A 1969 The ecology of an elfin forest in Puerto Rico. 6. Aerial roots. J. Arn. Arb. 50, 197–209.

Gill C 1975 The ecological significance of adventitious rooting as a response to flooding in woody species, with special reference to *Alnus glutinosa* (L.) Gaertn. Flora 164, 85–97.

Gill A and Tomlinson P 1969 Aerial roots: An array of forms and functions. *In* The Development of Woody Plants. Eds. J Torrey and D Clarkson. Chapter 12. Academic Press, London.

Gilman E, Leone I and Flower F 1982 Influence of soil gas contamination on tree root growth. Plant and Soil 65, 3–10.

Hartmann H and Kester D 1975 Plant Propagation: Principles and Practices. Prentice-Hall, Englewood Cliffs, 377 pp.

Heine R W 1970 Absorption of phosphate and potassium ions in poplar stems. J. Exp. Bot. 21, 497–503.

Herbert D 1958 Natural air-layering in humus-collecting epiphytes. Queensland Nat. 16, 22–23.

Hook D D and Kormanik P 1971 Induced flood tolerance in swamp tupelo (*Nyssa sylvatica* var. *biflora* (Walt)Sarg.). J. Exp. Bot. 22, 78–89.

Hook D D, Langdon O G, Stubbs J and Brown C L 1970 Effect of water regimes on the survival, growth, and morphology of Tupelo seedlings. For. Sci. 16, 304–311.

Jenik J 1973 Root systems of tropical trees. 8. Stilt roots and allied adaptations. Preslia 45, 250–264.

Kirkham D, Rolston D E and Fritton D D 1967 Gamma-radiation detection of water content in two-dimensional evaporation experiments. *In* Proceedings of Isotope and Radiation Techniques in Soil Physics and Irrigation Studies, pp 3–14. Istanbul.

Kling G and M Meyer 1983 Effects of phenolic compounds and IAA on adventitious root initiation in cuttings of *Phaseolus aureus*, *Acer saccharinum* and *Acer griseum*. Hortscience 18, 352–354.

Lanner R 1966 Adventitious roots of *Eucalyptus robusta* in Hawaii. Pacific Science 20, 379–381.

Levy C, Youngstrom D and Maletskos C 1976 Whole-body gamma-spectroscopic assessment of environmental radionuclides in recapturable wild birds. *In* Radioecology and Energy Resources. Ed. C Cushing, Jr. pp 113–122. Dowden, Hutchinson, and Ross, Stroudsburg.

Levy C, Youngstrom K and Maletskos C 1982 Radioecology on a nuclear power station site using recapturable wild birds and whole-body gamma-spectroscopic analysis. *In* Environmental migration of long-lived radionuclides. pp 329–343. International Atomic Energy Agency, Vienna.

Lyford W 1969 The ecology of an elfin forest in Puerto Rico. 7. Soil, root, and earthworm relationships. J. Arn. Arb. 50, 210–224.

Moorby J 1964 The foliar uptake and translocation of caesium. J. Exp. Bot. 15, 457–469.

Nadkarni N 1981 Canopy roots: Convergent evolution in rainforest nutrient cycles. Science 213, 1023–1024.

Nadkarni N 1983 The effects of epiphytes on nutrient cycles within temperate and tropical rainforest tree canopies. Ph.D. Dissertation. University of Washington, Seattle.

Nadkarni N 1984 Epiphyte biomass and nutrient capital of a neotropical elfin forest. Biotropica 16, 249–256.

Nadkarni N 1985 Biomass and mineral capital of epiphytes in an *Acer macrophyllum* community of a temperate moist coniferous forest, Olympic Peninsula, Washington State. Can. J. Bot. 62, 2223–2228.

Nanda K, Bhattacharya N and Kochhar V 1974 Biochemical basis of adventitious root formation on etiolated stem segments. N.Z.J. For. Sci. 10, 347–358.

National Research Council 1976 Selenium Committee on the medical and biological effects of environmental pollutants. National Academy of Sciences, Washington, D.C.

Pereira J and T Kozlowski 1977 Variations among woody angiosperms in response to flooding. Physiol. Plant 41, 184–192.

Primack R and Levy C 1988 A method to label seeds and seedlings using gamma-emitting radionuclides. Ecology 69, 796–800.

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

Sena Gomes A R and Kozlowski T T 1980a Responses of *Melaleuca quinquenervia* seedlings to flooding. Physiol. Plant. 49, 373–377.

Sena Gomes A R and Kozlowski T T 1980b Growth responses and adaptations of *Fraxinus pennsylvanica* seedlings to flooding. Plant Physiol. 66, 267–271.

Stegman E W, Primack R and Ellmore G 1988 Absorption of nutrient exudates from terrapin eggs by roots of *Ammophila breviligulata* (Graminea). Can. J. Bot. 66, 714–718.

Ticknor R and Tukey H B Jr. 1955 Evidence for the entry of mineral nutrients through the bark of fruit trees. Proceedings of the American Society of Horticultural Science. 69, 13–16.

Tiller K G 1979 Applications of isotopes to micronutrient studies. *In* International Symposium on the Use of Isotopes and Radiation on Soil-Plant Relationships. pp 359–370, Colombo.

Tsukahara H and Kozlowski T T 1985 Importance of adventitious roots to growth of flooded *Platanus occidentalis* seedlings. Plant and Soil 88, 123–132.

Wample R L and Reid D M 1978 Control of adventitious root production and hypocotyl hypertrophy of sunflower (*Helianthus annuus*) in response to flooding. Physiol. Plant 44, 351–358.

Witherspoon J 1964 Cycling of Cesium-134 in white oak trees. Ecol. Monogr. 34, 403–420.

Wittwer S and Bukovac M 1969 The uptake of nutrients through leaf surfaces. *In* Handbuch der Pflanzenernährung und Düngung Vol. 1 Ed. H Linser. pp 235–261. Springer, Vienna.