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Intraclonal nitrogen allocation in the bunchgrass *Schizachyrium scoparium* Hubb.: an assessment of the physiological individual

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Abstract. The size of the physiological individual within the bunchgrass *Schizachyrium scoparium* Hubb. was investigated by evaluating the pattern and magnitude of ^{15}N allocation within and between individual ramet hierarchies (sequences of connected ramet generations). Nitrogen-15 was acropetally allocated throughout the three generation hierarchies within 24 h regardless of the ramet generation or organ labelled. Both primary and secondary ramet generations allocated nitrogen to juvenile, tertiary ramets. Basipetal nitrogen allocation, from secondary to ontogenetically older primary ramets, was observed, but accounted for less than 1% of the ^{15}N mass in the ramet hierarchies at the end of the 5-day experiment. Foliarly labelled ramets exported less nitrogen intraclonally than did root labelled ramets indicating that a greater proportion of the nitrogen was rapidly incorporated into metabolic compounds. A majority (>93%) of the ^{15}N introduced into the ramet hierarchies remained within the labelled hierarchies as opposed to being allocated to associated hierarchies within individual clones. Clones of this bunchgrass consist of an assemblage of autonomous physiological individuals, composed of a minimum of three connected ramet generations, as opposed to a system of completely integrated ramet hierarchies. The propensity for acropetal resource allocation appears to be the predominant factor limiting resource allocation between ramet hierarchies within young clones possessing complete vascular continuity.

Key-words: Acropetal allocation, caespitose growth form, clonal biology, ^{15}N, physiological integration, resource allocation

Introduction

The bunchgrass or caespitose growth form consists of an assemblage of genetically identical ramets growing in close proximity. The potential for physiological integration between and among ramets is established by the vascular connections formed when juvenile ramets are initiated from axillary buds of parental ramets. Acropetal resource allocation within ramet hierarchies (sequences of connected ramet generations) has been documented in several clonal graminoids with isotopic tracers (Anderson-Taylor & Marshall, 1983; Welker *et al.*, 1985; Welker, Briske & Weaver, 1987). Although these data clearly demonstrate the capacity for physiological integration within the clone, the number of connected ramet generations participating in the acquisition, allocation and utilization of resources to form the physiological individual has received relatively little attention (Watson & Casper, 1984; but see Jonsdottir & Callaghan, 1988).

The capacity for resource allocation between and among ramet hierarchies is a prerequisite for complete clonal integration and may be an important constraint regulating the size of the physiological individual. However, interhierarchical resource allocation requires basipetal resource allocation through older intervening ramet generations including the common progenitor of the clone. Basipetal resource allocation has been observed in several clonal species, but the ecological significance of this allocation pattern is obscured by the minimal quantities of resource allocation and the apparent inconsistency of the process (Clifford, Marshall & Sagar, 1973; Lauer & Simmons, 1988; Magda, Warembourg & Labeyrie, 1988; Jonsdottir & Callaghan, 1989).

The pattern of resource allocation may also influence the rate and extent of intraclonal allocation. Nutrients may be absorbed and recycled between the root and shoot system of individual ramets (Simpson, Lambers & Dalling, 1982), absorbed, assimilated and eventually remobilized to connected ramet generations (Jonasson & Chapin, 1985; Thorne & Wood, 1987) or absorbed and

allocated to connected ramets without being assimilated by the ramet which acquired the nutrient from the environment (Marshall & Sagar, 1968; Welker *et al.*, 1985, 1987). The predominant allocation route is presumably determined by the relative sink strengths among ramet generations and organs (i.e. roots, leaves, culms and inflorescences) within the clone and resource availability in the immediate environment (Pitelka & Ashmun, 1985; Lang & Thorpe, 1986).

This investigation was conducted to evaluate the size of the physiological individual within intact clones of *Schizachyrium scoparium* Hubb. by identifying the pattern and magnitude of nitrogen allocation within and between ramet hierarchies. Root and foliar absorbed nitrogen were evaluated to contrast the importance of soil-absorbed and remobilized nitrogen, respectively, on the potential size of the physiological individual. *S. scoparium* possesses an architecture representative of the perennial bunchgrass growth form and is distributed throughout the eastern two-thirds of the USA (Gould, 1975).

Materials and methods

Perennating crown tissue of *S. scoparium* var. *frequens* was collected from a *S. scoparium*/*Paspalum plicatulum* grassland of east central Texas on the Texas A&M University Native Plant and Animal Conservancy, College Station, Texas, USA. Individual crowns (basal 2 cm of a ramet) were planted in 10 × 100 cm cylindrical polyvinylchloride growth containers filled with sandy loam soil from the site of plant collection. The top 10 cm of each container was filled with vermiculite to facilitate subsequent access to developing adventitious root systems.

Clones were grown in a controlled environment chamber with an 11-h photoperiod (to prevent floral induction), quantum flux density of 400 μmol m^{-2} s^{-1} at the top of the canopy and a complementary thermal period of 30/25 °C. Containers were initially saturated, allowed to drain and maintained at field capacity throughout the experiment by regular watering. One hundred millilitres of 1/4 strength Peter's nutrient solution (N-P-K) was added to each container weekly during the propagation period. Ramet ontogeny was documented by weekly inspection and marking with colour-coded wire. Ramets were defined as the sum of all subunitary parts (phytomers) differentiated from an individual apical meristem (syn. tiller; White, 1979). Clones were grown under these conditions for 8 months to develop several ramet hierarchies from the initially planted ramet (common progenitor of the clone).

Experimental clones were composed of an average of 36 ramets with primary, secondary and tertiary ramets comprising 11, 53 and 36% of the total number of ramets per clone, respectively (Table 1). Experimental ramet hierarchies consisted of (1) a primary ramet which developed from an axillary bud of the initially planted ramet, (2) secondary ramets which developed from the primary ramet, and (3) tertiary ramets which developed from secondary ramets (Fig. 1). An average experimental ramet hierarchy consisted of a single primary, four secondary and two tertiary

Table 1. Mean and standard error of morphometric parameters and nitrogen concentration of primary, secondary and tertiary ramet generations within 8-month-old clones of *Schizachyrium scoparium* at the conclusion of the investigation. $n = 18$ clones with a mean of 36 ramets per clone.

Clonal parameters	Ramet generation		
	Primary	Secondary	Tertiary
Morphometric parameters			
Ramets clone^{-1}	4·5 ± 1·1	20·2 ± 2·0	12·5 ± 1·6
Maximum height ramet^{-1} (cm)	58·7 ± 5·5	50·6 ± 1·1	36·8 ± 1·3
Live leaf number ramet^{-1}	7·2 ± 0·5	5·0 ± 0·1	4·0 ± 0·3
Shoot mass ramet^{-1} (g)	0·60 ± 0·09	0·21 ± 0·05	0·11 ± 0·04
Root mass ramet^{-1} (g)	1·37 ± 0·18	0·16 ± 0·05	0·09 ± 0·02
Maximum root length ramet^{-1} (cm)	60·0 ± 6·1	28·8 ± 1·12	10·9 ± 0·8
Root number ramet^{-1}	12·5 ± 0·5	5·6 ± 0·2	2·5 ± 0·3
Nitrogen concentration (%)			
Shoots	1·31 ± 0·12	1·45 ± 0·08	1·33 ± 0·10
Roots	1·35 ± 0·09	1·41 ± 0·11	1·35 ± 0·07

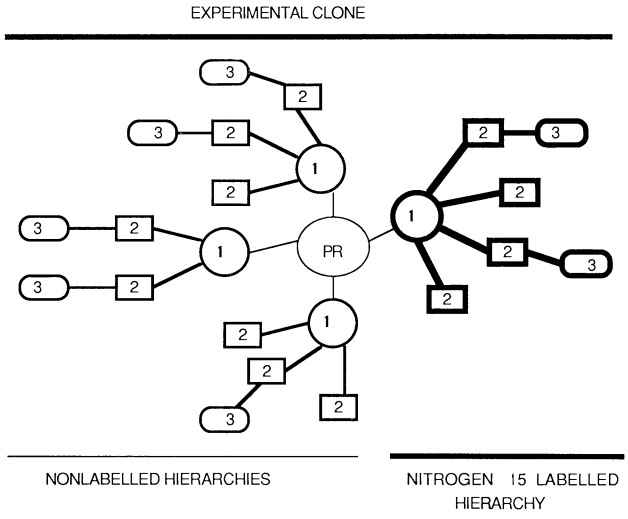

Fig. 1. Schematic representation of an experimental bunchgrass clone composed of four ramet hierarchies consisting of three connected ramet generations each. Initiation of all ramet hierarchies from a single planted ramet (progenitor ramet, PR) ensures vascular continuity within the clone. Labelled nitrogen (^{15}N) was introduced into a single hierarchy (bold designation) by root or foliar labelling of either the primary (1°) or secondary (2°) ramet generation. Inter-ramet distances have been exaggerated for clarity of presentation.

ramets while an average clone consisted of four ramet hierarchies. Morphological development was greatest in the chronologically oldest primary ramet generation with secondary and tertiary ramets showing progressively less development (Table 1). All ramet generations possessed adventitious roots and were assumed to be capable of absorbing soil nitrogen. Per cent nitrogen content did not vary significantly in live biomass among ramet generations or between roots and shoots.

Nitrogen-15 labelling was conducted by locating a single, newly initiated adventitious root of a primary or secondary ramet in the vermiculite portion of the growth medium and directing it into a 25-ml plastic vial containing vermiculite 5 months following planting. At the time of ^{15}N labelling, the plastic vials were uncovered, the prospective root removed, washed with deionized water and submerged into a 25-ml glass vial filled with 99% excess $(^{15}NH_4)_2\ SO_4$ at 24 mM (Anderson-Taylor & Marshall, 1983; Welker *et al.*, 1987). Vials containing the root and isotopic solution were then placed back into the vermiculite, covered with masking tape to minimize solution loss and left in place throughout an 11-h photoperiod. Roots were then removed from the glass vials, rinsed and blotted dry, and placed back into the plastic vials and covered with vermiculite. Foliar labelling was implemented on a separate set of plants 2 days following the final harvest for the root labelling experiment. The uppermost fully expanded leaf of either a primary or secondary ramet was placed into a 25-ml glass vial containing isotopic solution in the same form and concentration as in root labelling and covered with clear tape for an 11-h photoperiod. Leaves were then removed from the vial, blotted dry and left intact.

Both root and foliar labelling experiments were arranged in a randomized block design and one-third of the plants were destructively harvested at 24, 72 and 120 h following labelling. Treatments consisted of labelling either primary or secondary generation ramets of designated ramet hierarchies within the clone. Labelled hierarchies were separated by ramet generation into their respective root and shoot tissues. Roots and shoots of non-labelled ramet hierarchies were composited by ramet generation for nitrogen analysis. Morphological characteristics of each ramet were recorded, including total extended height, number of live leaves, maximum root length and numbers of adventitious roots. Plant material was dried at 50 °C for 72 h for biomass determination and then ground with a Wiley Mill to pass through a 40-mm screen.

Nitrogen analyses were conducted following Kjeldahl procedures (Bremner, 1965). Samples were then prepared for ^{15}N analysis by re-acidification with 0·2 ml of 2 N HCl and evaporated to dryness in glass vacuum tubes. Percentage ^{15}N excess was determined by mass spectrometry (Bremner, 1965). Analysis of variance procedures were used to test for treatment effects including organ and generation labelled, harvest date, ^{15}N

mass among labelled and non-labelled hierarchies within a clone, and morphometric parameters among ramet generations. Nitrogen allocation patterns are presented as the relative distribution of ^{15}N mass between roots and shoots of individual ramets, among ramet generations within a hierarchy and among hierarchies within a clone. Relative distribution represents the ratio of ^{15}N mass with a specific organ and the total mass within the labelled hierarchy.

Results

Intrahierarchical ^{15}N distribution

The organ (shoot or root) and ramet generation (primary or secondary) labelled, either independently or in combination, significantly affected the relative distribution of ^{15}N in the shoots and roots of primary and secondary ramet generations within the experimental hierarchies (Table 2). Harvest date significantly ($P = 0{\cdot}09$) affected the relative distribution of ^{15}N in the roots of secondary ramets and interacted significantly ($P = 0{\cdot}08$) with generation and organ to affect the relative distribution of ^{15}N in tertiary ramets.

Root labelling. Relative distribution of ^{15}N mass within roots and shoots of secondary and tertiary ramets did not exceed 2% at 24 h following root labelling of the primary ramet (Fig. 2a). However, relative distribution values increased 10·5- and four-fold for shoots in the secondary and tertiary ramet generations, respectively, between 24 and 120 h following labelling. Nitrogen was allocated equitably to the roots and shoots of the secondary ramets, but preferentially allocated to the shoots of tertiary ramets. Approximately 50% of the total ^{15}N mass with the ramet hierarchies was allocated to secondary and tertiary ramets at 120 h following root labelling of the primary ramet.

Relative distribution of ^{15}N mass within shoots of tertiary ramets was three-fold greater at 24 h when ^{15}N was introduced into the roots of the secondary rather than the primary ramet generation (4·4 *vs* 1·5%; Fig. 2a and b), Relative distribution of ^{15}N mass in roots of tertiary ramets was six-fold greater (1·4 *vs* 9·1%) 24 h following secondary ramet labelling in comparison to primary ramet labelling. Relative distribution increased to 6·6% within the shoots, but decreased to 3·2% within the roots at 120 h. Tertiary ramets were importing essentially all of the nitrogen from the root labelled secondary ramet, to the exclusion of the primary ramet, at 120 h. Approximately, 90% of the ^{15}N mass, equally distributed between roots and shoots, was retained in the secondary ramet following root labelling of that generation. The largest fraction of ^{15}N mass allocated basipetally from roots of the secondary ramets to primary ramets was 10·5% at 24 h, but then decreased to less than 1% at 120 h.

Foliar labelling. Relative distribution of ^{15}N mass within shoots of secondary ramets was 5·4-fold greater than in shoots of tertiary ramets 24 h following foliar labelling of the primary ramet (4·0 *vs* 0·6; Fig. 2c). Values increased to 5·1 and 1·9% for shoots of secondary and tertiary ramets,

Table 2. Partial analysis of variance table for relative distribution of ^{15}N mass in shoots and roots of three ramet generations within a labelled hierarchy. Labelled nitrogen was introduced into the hierarchy through root or foliar (organ) labelling of either a primary or secondary ramet generation and destructively harvested at 24, 72 and 120 h. $n = 3$ for each of the four generation × organ labelling combinations.

Generation and organ	Source of variation	*F*	*P*
Primary ramets			
Shoots	Generation × organ	147·6	0·0001
Roots	Generation	14·2	0·0009
	Organ	3·2	0·0869
Secondary ramets			
Shoots	Generation × organ	64·7	0·0001
Roots	Organ	73·1	0·0001
	Harvest date	2·6	0·0939
Tertiary ramets			
Shoots	Organ	21·7	0·0001
Roots	Generation × organ × harvest date	3·1	0·0811

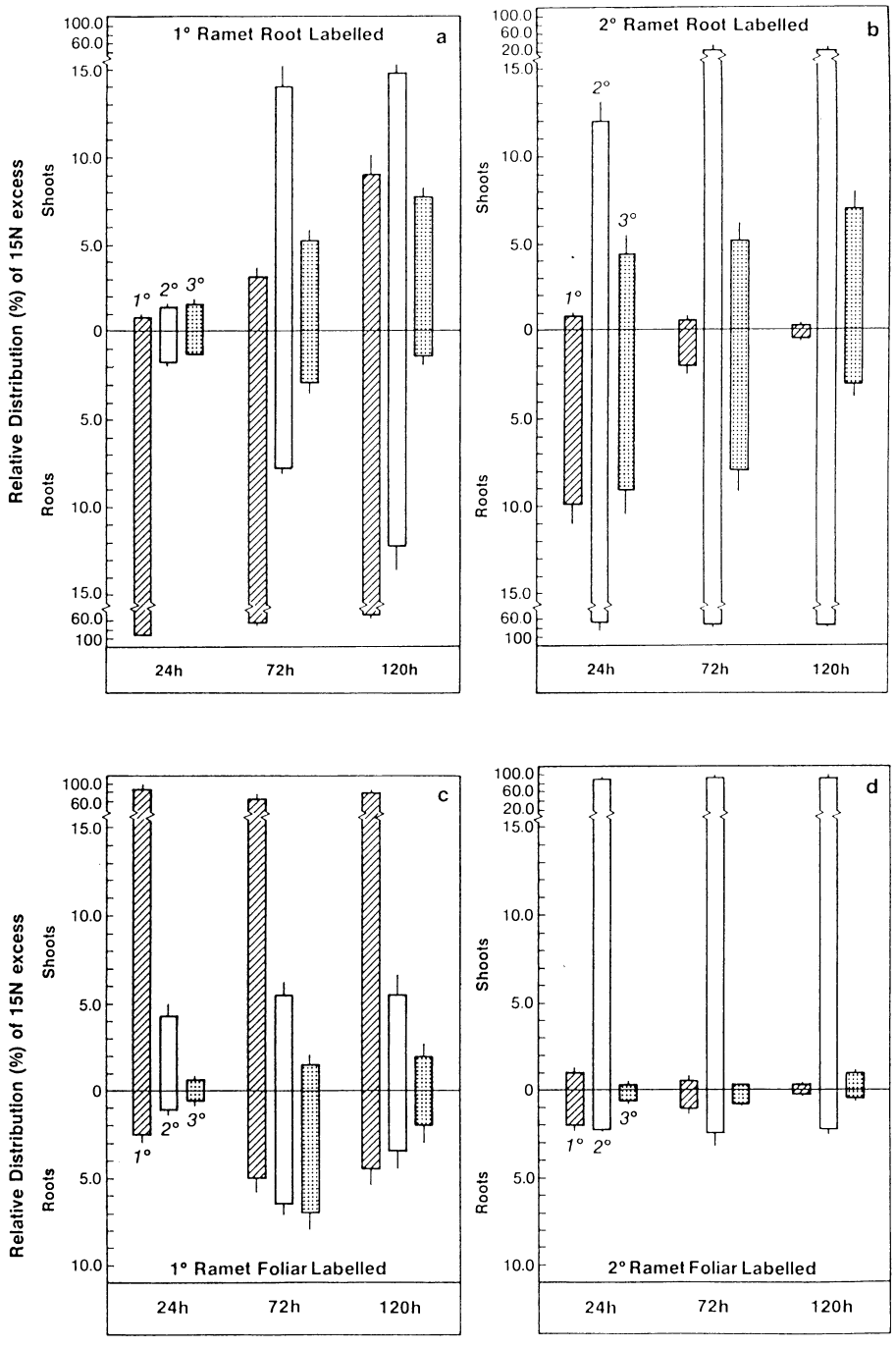

Fig. 2. Relative distribution (%) of the total mg of ^{15}N mass in shoots and roots of primary (1°), secondary (2°), and tertiary (3°) generation ramets 24, 72 and 120 h following (a) 1° root labelling, (b) 2° root labelling, (c) 1° foliar labelling and (d) 2° foliar labelling. Vertical lines represent 1 standard error of the mean.

respectively, at 120 h. Approximately, 88·2% of the ^{15}N mass was retained in the primary ramets (roots) 120 h following foliar labelling of that ramet.

Minimal amounts of ^{15}N mass were present in either the primary or tertiary ramets following foliar labelling of the secondary ramet generation (Fig. 2d). Primary ramets imported the greatest amounts of ^{15}N 24 h following labelling, 1 and 2% in the shoots and roots, respectively. Shoots of tertiary ramets displayed the greatest relative distribution of ^{15}N mass at 120 h, but values did not exceed 2%. Less than 4% of the labelled nitrogen was allocated basipetally from the foliar labelled

secondary ramet to the primary ramet or acropetally to the tertiary ramets within the sequence. Approximately, 96% of the ^{15}N mass was retained within the shoots of the secondary ramet.

Interhierarchical ^{15}N distribution

The fraction of ^{15}N mass allocated from labelled to non-labelled hierarchies within individual clones was significantly affected by the organ (shoot or root, $P = 0{\cdot}038$) and ramet generation (primary or secondary, $P = 0{\cdot}002$) through which ^{15}N was introduced (Table 3). Interhierarchical allocation represented 7·1 and 4·0% of the total ^{15}N mass introduced into individual ramet hierarchies when the primary ramet was labelled via the root or shoot, respectively. In contrast, only 2·4 and 0·5% of the ^{15}N mass was allocated interhierarchically when a secondary ramet generation was labelled via the root or shoot, respectively. The vast majority of ^{15}N mass, 93–99% (range = 91·1–99·5%), remained within the ramet hierarchy into which it was initially introduced.

Discussion

The relative distribution of ^{15}N within clones of *S. scoparium* indicates that physiological integration is restricted to individual ramet hierarchies consisting of a minimum of three anatomically attached generations. A majority (>93%) of the ^{15}N introduced into individual experimental ramet hierarchies remained within the labelled hierarchies as opposed to being allocated to associated hierarchies within the clone (Table 3). The propensity for acropetal resource allocation appears to be the predominant factor limiting resource allocation between hierarchies within young clones possessing complete vascular continuity. An absence of complete clonal integration has been suggested following tracer investigations with *Andropogon scoparius* (syn. *S. scoparium*; Dodd & Van Amburg, 1970), *Lolium perenne* (Colvill & Marshall, 1981) and severing of vascular connections within clones of *S. scoparium* (Briske & Butler, 1989; D. Williams & D.D. Briske, unpublished observations).

A greater percentage of nitrogen was allocated between ramet hierarchies when ^{15}N was introduced into the primary rather than the secondary ramet generation or when ^{15}N was introduced into roots rather than shoots of either ramet generation (Table 3). The secondary ramet generation and shoot systems of both generations functioned as strong sinks retaining large amounts of nitrogen. A similar ranking of sink strengths has been observed in ramet hierarchies of *Lolium perenne* with ^{14}C (Danckwerts & Gordon, 1987). Labelled ramets retained a large portion of the ^{15}N indicating that proximity to the nitrogen source is an important consideration influencing intraclonal resource allocation (Wardlaw, 1968).

Nitrogen-15 was allocated throughout the three generation ramet hierarchies within 24 h of labelling regardless of the ramet generation or organ into which nitrogen was initially introduced (Fig. 2). Both the primary and secondary ramet generations allocated nitrogen acropetally to juvenile, tertiary ramets. Primary and secondary ramet generations allocated comparable amounts of ^{15}N to juvenile ramets at 120 h when root labelled, but the primary ramet generation allocated a 2·6-fold greater amount of ^{15}N to juvenile ramets following shoot labelling. The propensity for acropetal resource allocation was presumably established by the relative sink strengths or water potential gradients among ramets within the hierarchy (Pitelka & Ashmun, 1985; Lang & Thorpe, 1986). Juvenile ramets arise from the distal portion of the hierarchy and only possess a limited capacity for water and nutrient acquisition because of limited

Table 3. Mean and standard error of the percentage of ^{15}N mass retained within the labelled ramet hierarchy or allocated to associated ramet hierarchies within the clone 5 days following labelling. Nitrogen was introduced into a single hierarchy per clone by either root or foliar labelling of a primary or secondary generation ramet. $n = 3$ for each of the four generation × organ labelling combinations.

	Root labelled	Foliar labelled
Primary ramet labelled		
Labelled hierarchy	92·9 ± 0·9	96·0 ± 1·8
Non-labelled hierarchies	7·1 ± 0·8	4·0 ± 1·9
Secondary ramet labelled		
Labelled hierarchy	97·6 ± 2·4	99·5 ± 0·2
Non-labelled hierarchies	2·4 ± 2·1	0·5 ± 0·1

root development during the initial stages of growth (Carman & Briske, 1982).

Basipetal nitrogen allocation, from secondary to ontogenetically older primary ramet generations, was observed, but only accounted for 1% of the ^{15}N mass within ramet hierarchies at the end of the experiment (Fig. 2b and d). These data corroborate the low levels of basipetal carbon allocation previously observed in several graminoid species (Clifford, Marshall & Sagar, 1973; Myahoza, Marshall & Sagar, 1973; Lauer & Simmons, 1988). Jonsdottir & Callaghan (1988, 1989) have suggested that basipetal resource allocation within clones of *Carex bigelowii* may support the root systems of recently senesced ramets thereby enhancing the capacity to acquire water and soil-derived nutrients. The majority of the basipetally allocated nitrogen within ramet hierarchies of *S. scoparium* was incorporated into root systems of primary ramets which possessed the greatest number of roots and greatest vertical penetration into the soil on a ramet generation basis (Fig. 2b and d, Table 1). Consequently, basipetal resource allocation from the secondary ramet generation may potentially sustain the longevity and function of the primary generation root system following shoot senescence.

Both root and foliar labelling yielded similar conclusions concerning the size of the physiological individual. However, a larger proportion of the ^{15}N acquired by foliar labelled ramets were retained within the ramets in comparison with root labelled ramets regardless of whether the primary or secondary generation was labelled (Fig. 2). These data indicate that a higher proportion of nitrogen absorbed by the shoot system was incorporated into metabolic compounds within the labelled ramet (Simpson, Lambers & Dalling, 1982). Catabolism of these compounds, associated with leaf senescence for example, may eventually remobilize nitrogenous compounds for intrahierarchical allocation. Jonasson & Chapin (1985) have indicated that sequential leaf development of graminoids may provide an efficient mechanism for nutrient conservation in infertile tundra environments. Similarly, nutrients may be allocated from senescing ramets within a hierarchy to ontogenetically younger ramets enhancing nutrient conservation and carbon acquisition in clonal graminoids (Field, 1983; Thorne & Wood, 1987; Lauer & Simmons, 1988). Root absorbed nitrogen was the predominant source of nitrogen allocated intraclonally within the 5-day experiment (Fig. 2). The contribution of remobilized nitrogen (foliar labelled) may have increased given additional time for leaf senescence and protein degradation (Field, 1983).

Clones of *S. scoparium* consist of an assemblage of independent physiological individuals as opposed to a system of completely integrated ramets. Physiological individuals within this species consist of a minimum of three connected ramet generations exhibiting acropetal resource allocation from both ontogenetically older ramet generations to juvenile ramets. This pattern of resource allocation within the physiological individual is required to ensure juvenile ramet establishment within the competitive environment established by the compact spatial arrangement of ramets within this growth form.

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