

An isotopic (^{15}N) assessment of intracolonial regulation in C_4 perennial grasses: ramet interdependence, independence or both?

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Summary

1 A series of three experiments was conducted with three C_4 perennial grasses, *Panicum virgatum* (short rhizomes forming distinct clones), *Schizachyrium scoparium* (caespitose) and *Bouteloua gracilis* (caespitose), to determine whether intracolonial regulation was characterized by interdependence, independence or a combination of both processes. Specific hypotheses tested were: (i) all ramets within individual clones are physiologically integrated; (ii) ramet hierarchies (several connected generations) within individual clones are capable of acquiring soil nitrogen equally from localized nutrient-rich pulses; and (iii) nitrogen is retained within individual hierarchies through allocation to sequentially developed ramet generations.

2 Mean ^{15}N atom percent excess values within labelled ramet hierarchies were 10–21-fold greater than in immediately adjacent ramet hierarchies, and 105–137-fold greater than in the remaining ramet hierarchies within clones for all three species. This pattern of ^{15}N distribution demonstrates that physiological integration does not occur among all ramets within individual clones and that ramet hierarchies function as integrated physiological individuals.

3 Ramets in closer proximity to a ^{15}N pulse in soils acquired disproportionately greater amounts of the isotope compared to more distant ramets within clones for all three species. Inequitable resource acquisition among ramet hierarchies establishes the potential for asymmetric intracolonial competition below-ground and the development of size inequalities among hierarchies.

4 Approximately 21.7%, 3.5%, 1.7% and 2.3% of the initial ^{15}N pool was allocated from the first ramet generation to the second and third (spring cohort), third (autumn cohort) and fourth generations, respectively. However, the magnitude of nitrogen allocation from parent to juvenile ramet generations was relatively consistent, with 17–32% of the ^{15}N pool within parental ramets allocated to juvenile ramets. Inter-generational ^{15}N allocation in *S. scoparium* clones therefore demonstrates a high degree of interdependence within individual ramet hierarchies.

5 Clones of the rhizomatous and two caespitose grasses investigated functioned as assemblages of autonomous ramet hierarchies, but ramet generations within individual hierarchies were effectively integrated. Consequently, intracolonial regulation in these temperate, perennial grasses is characterized by both ramet interdependence and independence. The occurrence of ramet independence throughout much of the life history of perennial grasses demonstrates the ecological importance of clonal fragments to genet and population maintenance and emphasizes that this may be the most relevant scale to investigate further the ecology of this important and widely distributed group of clonal plants.

Keywords: clonal biology, intracolonial competition, nitrogen allocation, physiological integration, sectoriality

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Introduction

The ecological interpretation of intraclonal regulation in clonal plants has shifted from one of exclusive ramet interdependence (e.g. Marshall & Sagar 1965; Pitelka & Ashmun 1985) to one encompassing ramet independence as a potential mechanism (e.g. Cain 1990; Kelly 1995). Physiological subdivision within clonal plants has been termed sectoriality, and emphasizes the combined benefits of independence (autonomy) and interdependence (integration) (Marshall 1996; Price *et al.* 1996; Vuorisalo & Hutchings 1996). Evidence for the limited occurrence of interdependence among ramets originates from various sources including isotopic labelling (Welker *et al.* 1991; Price *et al.* 1992), severing of vascular connections (Williams & Briske 1991; Hartnett 1993) and clonal architecture (Gatsuk *et al.* 1980; Wilhalm 1995; Briske & Derner 1998). This evidence has led to the hypotheses that physiological integration operates at a finer scale than that of the entire clone in several graminoid species (Briske & Butler 1989; de Kroon & Kwant 1991) and that ramet hierarchies (several connected ramet generations) function independently within clones (Welker *et al.* 1987, 1991; Williams & Briske 1991). Greater insight into the extent and significance of physiological integration is required to interpret more accurately mechanisms of ramet regulation, spatial organization of ramets within clones and the ecological success associated with various groups of clonal plants (i.e. phalanx vs. guerrilla strategies, *sensu* Lovett-Doust 1981).

If ramet hierarchies function as autonomous units within clones, then equitable resource sampling among ramet hierarchies within clones may potentially mediate the extent of intraclonal regulation. A broadly distributed root system associated with each ramet hierarchy may potentially enable all ramet hierarchies to access soil resources equitably within the immediate vicinity of individual clones. Therefore, a small-scale resource limitation or nutrient-rich pulse would equitably constrain or promote growth of all ramet hierarchies within a clone, rather than only the hierarchies nearest the resource pulse. It is conceivable that equitable resource acquisition among ramet hierarchies may minimize intraclonal competition, promote ramet interdependence and enhance growth efficiency of the clone.

Clonal organization as an assemblage of autonomous ramet hierarchies would necessitate effective physiological integration among ramets within hierarchies to minimize competitive interactions, increase residence time of limiting nutrients and reduce soil nutrient demand. In nitrogen-poor environments, efficient nitrogen allocation from old, senescing leaves to new, developing leaves has been interpreted as an adaptive mechanism (Hill 1980; Jonasson & Chapin 1985; Hocking 1995; Aerts 1996). Intergenerational nitrogen allocation has been documented in numer-

ous perennial grasses (e.g. Pitelka & Ashmun 1985; Welker & Briske 1992), graminoids (e.g. Jonsdottir & Callaghan 1990) and annual cereals (e.g. Simpson *et al.* 1982; MacKown *et al.* 1989). However, all of these investigations have evaluated the relative sink strengths of existing ramet generations over short time periods, rather than nitrogen retention through effective allocation within sequentially developed ramet generations.

The extent of ramet interdependence vs. independence may potentially be mediated by resource availability in specific habitats. Caraco & Kelly (1991) have proposed that intraclonal ramets may be integrated to a lesser extent in environments with high resource availability compared to those with low resource availability. It could be inferred from their models that juvenile ramets in high resource availability environments may become self-sufficient more rapidly because of efficient resource acquisition directly from the environment, while ramets in low resource availability environments may maintain interdependence for longer periods because of limited resource availability.

A series of three experiments was conducted to test whether intraclonal regulation in three C_4 perennial grasses was characterized by interdependence, independence or a combination of both processes. Specific hypotheses were: (i) all ramets within individual grass clones are physiologically integrated; (ii) ramet hierarchies within individual grass clones are capable of equitably acquiring soil nitrogen from localized nutrient-rich pulses peripheral to individual clones; and (iii) nitrogen is retained within individual hierarchies by efficient allocation to sequentially developed ramet generations. Hypotheses (i) and (ii) were tested with three C_4 perennial grasses, *Panicum virgatum* (short determinate rhizomes forming robust and spatially distinct clones; Hartnett 1993), *Schizachyrium scoparium* (caespitose) and *Bouteloua gracilis* (caespitose), that are distributed along an east-west environmental gradient in the North American Great Plains. Evaluation of a dominant species in each of three communities characterized by a wide range of resource availabilities (e.g. 2.5-fold variation in annual precipitation and soil organic carbon in the 0–10 cm soil depth; Zak *et al.* 1994) provided a more robust test of hypotheses (i) and (ii) compared to an evaluation of multiple species in a single community. Hypothesis (iii) required more intensive sampling and isotopic analyses, so it was tested with a single caespitose species, *S. scoparium*, in naturally occurring populations on the Texas A&M University campus. Experimental protocol focused on identification of presence/absence of a stable isotope of nitrogen (^{15}N) in the physiological integration and equitable resource acquisition experiments, and on the magnitude of ^{15}N transfer in the intergenerational nitrogen allocation experiment.

Site descriptions

The tallgrass community, Konza Prairie Research Natural Area, was located on a midslope topographical position in the Flint Hills of eastern Kansas, near Manhattan (39°05'N, 96°35'W). Vegetation is dominated by *Andropogon gerardii* Vitman, *Sorghastrum nutans* L., *Schizachyrium scoparium* and *P. virgatum* with a mean annual net primary productivity (ANPP) of 4000 kg ha⁻¹. Annual precipitation is 835 mm and annual mean temperature is 12.8 °C (Bark 1987). The midgrass community was located on a midslope topographical position in west-central Kansas at Fort Hays State University (38°52'N, 99°23'W), where *S. scoparium*, *A. gerardii* and *Bouteloua curtipendula* (Michx.) Kunth comprise the dominant species, and mean ANPP is 2200 kg ha⁻¹. This location has a mean annual precipitation of 588 mm and annual temperature of 11.9 °C (Hulett & Tomanek 1969). The shortgrass community site was located on a swale topographical position at the Central Plains Experimental Range (CPER) in north-central Colorado, approximately 60 km north-east of Fort Collins (40°49'N, 107°46'W). Mean annual precipitation is 321 mm and annual temperature is 8.6 °C (Lauenroth & Sala 1992). Vegetation is predominately (90%) *B. gracilis* (Milchunas *et al.* 1989), and mean ANPP is 1000 kg ha⁻¹. Long-term ungrazed (tallgrass since 1969, midgrass since 1908, and shortgrass since 1939) sites were sampled within each community.

The intergenerational nitrogen allocation experiment was conducted at the Texas A & M Native Plant and Animal Conservancy in east-central Texas near College Station (30°35'N; 96°21'W). This area is located within the Post Oak Savanna Resource Region (Gould 1975). Soils on this site are classified as montmorillonitic, thermic Udic Paleustalfs and have a fine sandy loam A horizon *c.* 17 cm thick. These soils are moderately well drained and occur on gently sloping uplands (1–5%) at an elevation of 150 m. Mean annual precipitation is 993 mm and mean annual temperature is 20.0 °C (Anderson & Briske 1995), with mean ANPP of 3500 kg ha⁻¹. The frost-free period averages 270 days and extends from March to November.

Methods

PHYSIOLOGICAL INTEGRATION

Physiological integration among ramets within individual clones was evaluated by randomly selecting similar-sized clones of each species along a line transect in the respective plant community. Six, 10 and nine replicate clones were evaluated for *P. virgatum*, *S. scoparium* and *B. gracilis*, respectively (Table 1). Replicate clone number varied because of limitations in excavating entire *P. virgatum* clones to determine ramet hierarchies, and the death of a labelled parental

ramet in one *B. gracilis* clone. Clones were labelled with a 100 mM solution of (¹⁵NH₄)₂SO₄, containing 99% ¹⁵N excess, by injecting the solution between the two most fully expanded leaf sheaths of a single parental ramet within an individual clone (Dodd & van Amburg 1970). (¹⁵NH₄)₂SO₄ has previously been demonstrated to be absorbed effectively by *S. scoparium* (Welker *et al.* 1987, 1991). The solution was injected into ramets on two consecutive days, with equivalent amounts of solution, during the late afternoon (*c.* 17.00 h) to increase foliar absorption and decrease evaporative loss. Total solution volumes of 1.00, 0.45 and 0.10 ml were used for *P. virgatum*, *S. scoparium* and *B. gracilis* clones, respectively, to compensate for differences in clone biomass among species. Clones were labelled during the first week of June 1994 and then destructively harvested 34–36 days later. Clones of *S. scoparium* and *B. gracilis* were separated into three components: (i) the labelled ramet and its associated hierarchy (i.e. connected ramet generations); (ii) the four to five hierarchies immediately adjacent to the labelled hierarchy; and (iii) all remaining hierarchies. Difficulty in determining hierarchies in *P. virgatum* necessitated that clones be separated into: (i) the labelled ramet; (ii) the associated ramets within the hierarchy; and (iii) ramets in the remaining hierarchies. Heights of the labelled ramet were measured at the time of injection and prior to destructive harvest for all three species (Table 1). Rhizome lengths from the labelled ramet (2.9 ± 0.4 cm) and the interramet distance connecting the labelled parent and nearest ramet within the same hierarchy (7.4 ± 1.6 cm) were measured for *P. virgatum* clones.

Above-ground biomass was dried at 60 °C for 72 h and ground to pass a 40-mesh screen. Approximately 7.5 mg of biomass was placed in tin capsules and analysed for ¹⁵N atom percent using a Carlo-Erba NA-1500 elemental analyser interfaced with a VG-Isomass mass spectrometer (Isotope Services Inc., Los Alamos, NM). Nitrogen-15 abundances on samples near natural abundance reproduce to 0.0004% ¹⁵N. Mean (*n* = 6) background ¹⁵N atom percent values (*P. virgatum*: 0.3671 ± 0.0002, *S. scoparium*: 0.3648 ± 0.0003, *B. gracilis*: 0.3667 ± 0.0001) were subtracted from respective species samples to determine ¹⁵N atom percent excess values (Boutton 1991).

EQUITABLE RESOURCE ACQUISITION

Equitable resource acquisition among ramet hierarchies comprising individual clones was evaluated by injecting ¹⁵N into soils peripheral to individual clones. Fifty millilitres of a 100-mM (¹⁵NH₄)₂SO₄ solution, containing 69% ¹⁵N excess, was injected into soils at a depth of 20 cm in early June 1994. A lower percent ¹⁵N excess was used in this experiment to reduce costs associated with larger volumetric applications of the isotopic solution to soils. Solution was injected into

Table 1 Mean (\pm SE) values for three architectural attributes of three dominant C₄ perennial grasses along an east–west environmental gradient in the North American Great Plains. An individual parental ramet within each clone was labelled with ¹⁵N to evaluate the potential for physiological integration among all ramets within a clone. Ramet heights were initially measured on 4–8 June and again before destructive harvest on 8–12 July 1994

Species	Community	<i>n</i>	Basal area (cm ²)	Ramet height (cm)		Ramet number in hierarchy
				Initial	Final	
<i>Panicum virgatum</i>	Tallgrass	6	1658 \pm 72	48.9 \pm 3.7	61.7 \pm 3.5	4.7 \pm 1.0
<i>Schizachyrium scoparium</i>	Midgrass	10	215 \pm 13	19.1 \pm 0.8	18.9 \pm 0.9	2.8 \pm 0.2
<i>Bouteloua gracilis</i>	Shortgrass	9	151 \pm 9	27.9 \pm 1.5	25.0 \pm 1.5	2.0 \pm 0.2

the soil at 1, 2 or 3 clone diameters away from the north-periphery of large and small basal area clones ($n = 36$ for each size class) to evaluate the linear distance over which equitable resource acquisition may operate (Table 2). Clones were bisected in an east–west direction at the clone base and the endpoints were marked with coloured nails to facilitate clone orientation relative to the location of ¹⁵N placement. Anatomical connections among ramets in half (18) of the clones in each size class per species were severed along this line with a metal blade driven to a depth of 10 cm to sever rhizomes within *P. virgatum* clones and to a depth of 2.5 cm to sever above-ground ramet connections in both *S. scoparium* and *B. gracilis* clones. The effect of severing on root systems was not evaluated, but potential damage was limited by the shallow depth of severing. Severing vascular connections eliminated the potential for physiological integration among all ramets within an individual clone and ensured that ramets within a clone segment acquired ¹⁵N label via root absorption. Ramets in the clone segment nearer the ¹⁵N pulse will be referred to as pulse ramets, while ramets further from the ¹⁵N pulse will be referred to as non-pulse ramets. Above-ground biomass was harvested in mid-July (peak biomass) from all clones by clone segment 34–36 days

after ¹⁵N placement in soil. Sample preparation and ¹⁵N analysis for the pulse and non-pulse segments were conducted as previously described.

INTERGENERATIONAL NITROGEN ALLOCATION

Intergenerational nitrogen allocation within individual ramet hierarchies was evaluated by randomly selecting 20 similar-sized *S. scoparium* clones in each of two ungrazed communities. Ten clones were randomly assigned to each of the following destructive harvest dates: 21 November 1994, 3 July 1995, 11 November 1995 and 9 June 1996. A single parental (first generation) ramet, randomly chosen within each clone, was labelled with 0.50 ml of a 100-mM solution of (¹⁵NH₄)₂SO₄, containing 99% ¹⁵N excess, during the second week of May 1994, as described previously for the physiological integration experiment. The presence of sequentially recruited ramets from the labelled parental ramet was evaluated monthly and marked with colour-coded wire loops when they were initiated. Ramets recruited from the labelled parental ramet during the 2-year period were separated into individual generations at each harvest date. Sample preparation and ¹⁵N analysis for shoot biomass from

Table 2 Mean (\pm SE) basal area and location of ¹⁵N placement into soil at 1, 2 or 3 clone diameters from the periphery of two size classes ($n = 36$) of three dominant C₄ perennial grasses along an east–west environmental gradient in the North American Great Plains. ¹⁵N acquisition by ramets within clones provided an evaluation of the ability of autonomous ramet hierarchies to access resources equitably from nutrient-rich pulses within the immediate vicinity of individual clones

Species	Community	Clone size	Basal area (cm ²)	¹⁵ N distance from clone (cm)		
				Clone diameter		
				1 ×	2 ×	3 ×
<i>Panicum virgatum</i>	Tallgrass	Small	894 \pm 27	33	67	100
		Large	1630 \pm 65	45	90	135
<i>Schizachyrium scoparium</i>	Midgrass	Small	103 \pm 11	10	20	30
		Large	194 \pm 13	17	34	51
<i>Bouteloua gracilis</i>	Shortgrass	Small	96 \pm 7	9	18	27
		Large	358 \pm 24	21	42	63

each ramet generation within the labelled hierarchy were conducted as described previously. Pools of ^{15}N , calculated by multiplying the mass (g) of plant tissue, N concentration of plant tissue and ^{15}N atom percent excess, were used to identify the magnitude of inter-generational nitrogen allocation (Boutton 1991).

Statistical analyses

PHYSIOLOGICAL INTEGRATION

Data from the physiological integration experiment were analysed using Page's test, which is a distribution-free test for ordered alternatives based on Friedman rank sums (Hollander & Wolfe 1973, p. 147). We tested the null hypothesis that the three components of each clone would contain similar ^{15}N atom percent excess against the one-sided alternative hypothesis, indicating that the amount of ^{15}N atom percent excess among clone components would be ranked as: injected hierarchy > neighbour hierarchies > remaining hierarchies.

EQUITABLE RESOURCE ACQUISITION

Data from the equitable resource acquisition experiment were analysed as a split-plot design with size class and sever/non-sever treatments as the main factors, and distance of ^{15}N pulse from clone periphery as the split factor. The error term used to test the main factors was the interaction of the main factors, while the split factor and interactions were tested with the residual error (Steel & Torrie 1980, p. 377). Data were analysed using GLM procedures (SAS Institute Inc. 1988) and means were separated by Bonferroni *t*-tests when a factor was significant ($P < 0.05$). Ratios of ^{15}N atom percent excess for pulse : non-pulse clone segments were log transformed prior to analysis to normalize residuals; means and standard errors are reported after back-transformation. Least significant means (LSMEANS) were used to determine if the ratios of pulse : non-pulse clone segments were significantly different from 1:1.

INTERGENERATIONAL NITROGEN ALLOCATION

Data from the intergenerational nitrogen allocation experiment were analysed as a factorial design (harvest date by ramet) with GLM procedures (SAS Institute Inc. 1988). Comparisons between ramet generations for shoot mass and ^{15}N pools were done with a *t*-test at each harvest date.

Results

PHYSIOLOGICAL INTEGRATION

Mean ^{15}N atom percent excess values within labelled ramet hierarchies were 10–21-fold greater than in

immediately adjacent ramet hierarchies, and 105–137-fold greater than in the remaining ramet hierarchies within clones for all three species (Table 3). The one-way trend of ^{15}N distribution within clones from labelled hierarchy > neighbour hierarchies > remaining hierarchies was highly significant ($P < 0.001$) for all three species (Page's L statistic was 83, 140 and 126 for *P. virgatum*, *S. scoparium* and *B. gracilis*, respectively).

EQUITABLE RESOURCE ACQUISITION

Severing of individual clones did not significantly affect ^{15}N acquisition from any pulse location for any species. The ratio of ^{15}N atom percent excess for pulse : non-pulse clone segments was significantly greater than 1:1 for both size classes of *P. virgatum* clones at the one diameter ^{15}N pulse location (Table 4). However, ratios were not significantly greater than 1:1 at the two- and three-diameter ^{15}N pulse locations for either large or small clones. The much lower ratios at the two- and three-diameter ^{15}N pulse locations were associated with large reductions in the amount of ^{15}N incorporated into clones compared to the one-diameter ^{15}N pulse location (Table 5). Pulse : non-pulse ^{15}N atom percent excess ratios were significantly greater than 1:1 for both size classes of *S. scoparium* clones at all three ^{15}N pulse locations (Table 4). The ratio of ^{15}N atom percent excess in pulse : non-pulse clone segments increased with pulse distance for this species because the amount of ^{15}N incorporated into the clone segment nearer the ^{15}N pulse location remained relatively high compared to the clone segment opposite the ^{15}N pulse (Table 5). Small clones of *B. gracilis* had ^{15}N atom percent excess ratios in pulse : non-pulse clone segments that were significantly greater than 1:1 at all three ^{15}N pulse locations, while ^{15}N atom percent excess ratios in large clones exceeded 1:1 at only the one diameter ^{15}N pulse location (Table 4). Low ^{15}N atom percent excess ratios in this species again reflected low amounts of ^{15}N acquisition by both pulse and non-pulse segments (Table 5).

INTERGENERATIONAL NITROGEN ALLOCATION

Nitrogen-15 was allocated from the labelled first (parental) generation ramet to all three subsequently developed ramet generations within autonomous ramet hierarchies (Table 6). Significantly greater ^{15}N atom percent excess and ^{15}N pools occurred in the older than in the younger ramet generation at each harvest date. The labelled first ramet generation possessed the greatest ^{15}N atom percent excess and ^{15}N pool, as anticipated. Approximately 18%, 32%, 20% and 17% of the ^{15}N pool was allocated from parent to juvenile ramet generations at each harvest date, respectively (Table 6). Approximately 21.7%, 3.5%,

Table 3 Mean (\pm SE) ^{15}N atom percent excess values within clone components of three dominant C_4 perennial grasses along an east–west environmental gradient in the North American Great Plains following labelling of an individual parental ramet within each clone. Asterisks indicate a significant ($P < 0.001$, Page's test) downward distribution trend from the labelled hierarchy to the remaining hierarchies

Species	Community	Clone component	^{15}N atom percent excess
<i>Panicum virgatum</i>	Tallgrass	Labelled ramet	3.6734 \pm 0.7089*
		Associated ramets	0.3884 \pm 0.2803
		Remaining hierarchies	0.0268 \pm 0.0163
<i>Schizachyrium scoparium</i>	Midgrass	Labelled hierarchy	2.3065 \pm 0.2811*
		Adjacent hierarchies	0.1372 \pm 0.0299
		Remaining hierarchies	0.0218 \pm 0.0048
<i>Bouteloua gracilis</i>	Shortgrass	Labelled hierarchy	3.0848 \pm 0.1760*
		Adjacent hierarchies	0.1459 \pm 0.0308
		Remaining hierarchies	0.0282 \pm 0.0054

Table 4 Mean (\pm SE) ratios of ^{15}N atom percent excess in pulse (P) : non-pulse (NP) segments of small and large clones of three dominant C_4 perennial grasses along an east–west environmental gradient in the North American Great Plains ($n = 36$ per size class per species). ^{15}N solution was injected into the soil at 1, 2 or 3 clone diameters from the periphery of each clone to create a nutrient-rich pulse. See Table 2 for injection distances and Table 5 for ^{15}N atom percent excess values. Asterisks indicate ratios that are significantly ($P < 0.05$) different from 1:1

Species	Community	Basal area (cm^2)	Ratio of ^{15}N atom percent excess in P:NP clone segments		
			1 clone diameter	2 clone diameters	3 clone diameters
<i>Panicum virgatum</i>	Tallgrass	894 \pm 27	101.9 \pm 46.0*	3.2 \pm 0.8	1.4 \pm 0.1
		1630 \pm 65	11.3 \pm 6.2*	2.5 \pm 1.2	1.2 \pm 0.1
<i>Schizachyrium scoparium</i>	Midgrass	103 \pm 11	20.1 \pm 10.6*	37.9 \pm 17.2*	102.8 \pm 67.9*
		194 \pm 13	21.7 \pm 12.7*	25.1 \pm 14.1*	90.1 \pm 54.8*
<i>Bouteloua gracilis</i>	Shortgrass	96 \pm 7	8.2 \pm 4.5*	4.5 \pm 1.4*	7.1 \pm 3.4*
		358 \pm 24	10.1 \pm 4.3*	1.6 \pm 0.2	1.5 \pm 0.4

Table 5 Mean (\pm SE) ^{15}N atom percent excess values ($\times 10^3$) for pulse (P) : non-pulse (NP) segments of small and large clones of three dominant C_4 perennial grasses along an environmental gradient in the North American Great Plains. ^{15}N solution was injected into the soil at 1, 2 or 3 clone diameters from the periphery of each clone to create a nutrient-rich pulse. See Table 4 for statistical results and Table 2 for injection distances

Species	Community	Basal area (cm^2)	Clone segment	^{15}N atom percent excess values ($\times 10^3$)		
				1 clone diameter	2 clone diameters	3 clone diameters
<i>Panicum virgatum</i>	Tallgrass	894 \pm 27	P	444.7 \pm 125.3	15.6 \pm 13.9	1.8 \pm 0.3
			NP	39.4 \pm 24.3	7.4 \pm 2.9	1.4 \pm 0.2
	1630 \pm 65	P	66.8 \pm 46.0	16.9 \pm 13.1	2.7 \pm 0.3	
		NP	5.6 \pm 1.7	3.8 \pm 0.7	2.3 \pm 0.2	
<i>Schizachyrium scoparium</i>	Midgrass	103 \pm 11	P	5351.7 \pm 1105.7	2625.1 \pm 525.0	1236.3 \pm 486.5
			NP	1970.1 \pm 666.5	931.3 \pm 393.5	321.1 \pm 145.0
	194 \pm 13	P	2733.6 \pm 471.3	809.5 \pm 308.3	144.9 \pm 78.3	
		NP	849.3 \pm 232.8	185.6 \pm 63.2	7.8 \pm 4.5	
<i>Bouteloua gracilis</i>	Shortgrass	96 \pm 7	P	372.9 \pm 135.7	22.2 \pm 10.0	3.8 \pm 2.1
			NP	147.9 \pm 65.9	3.6 \pm 1.0	1.6 \pm 0.6
	358 \pm 24	P	45.9 \pm 19.9	6.8 \pm 2.3	6.1 \pm 1.9	
		NP	4.8 \pm 0.9	3.7 \pm 0.7	3.9 \pm 0.2	

Table 6 Mean (\pm SE) values for shoot mass (g), shoot nitrogen (%), ^{15}N atom percent excess, and ^{15}N pools (mg) for four ramet generations within individual hierarchies of *S. scoparium* clones at four harvest dates over a 2-year period. A parental (first) ramet generation was labelled with ^{15}N within each clone ($n = 40$) to determine the efficiency with which nitrogen is retained within individual ramet hierarchies through allocation to sequentially developed ramet generations. Asterisks indicate significant ($P < 0.05$, t -test) differences between ramet generations within a harvest date

Harvest date	Variable	Ramet generation within an individual hierarchy				
		First	Second	Third (spring)	Third (autumn)	Fourth
November 1994	Mass (g)	1.16 \pm 0.49*	0.29 \pm 0.10			
	Nitrogen (%)	0.34 \pm 0.01*	0.65 \pm 0.06			
	^{15}N excess	3.41 \pm 0.88*	1.55 \pm 0.41			
	^{15}N pool (μg)	134.49 \pm 4.31*	29.22 \pm 2.46			
July 1995	Mass (g)		0.35 \pm 0.09	0.50 \pm 0.10		
	Nitrogen (%)		0.37 \pm 0.03	0.43 \pm 0.03		
	^{15}N excess		0.77 \pm 0.13*	0.22 \pm 0.06		
	^{15}N pool (μg)		9.97 \pm 0.35*	4.73 \pm 0.18		
November 1995	Mass (g)			0.80 \pm 0.34*	0.18 \pm 0.09	
	Nitrogen (%)			0.39 \pm 0.02*	0.73 \pm 0.06	
	^{15}N excess			0.29 \pm 0.06*	0.17 \pm 0.04	
	^{15}N pool (μg)			9.05 \pm 0.41*	2.23 \pm 0.22	
June 1996	Mass (g)				1.08 \pm 0.43	0.70 \pm 0.20
	Nitrogen (%)				0.40 \pm 0.04*	0.64 \pm 0.07
	^{15}N excess				0.35 \pm 0.10	0.07 \pm 0.02
	^{15}N pool (μg)				15.12 \pm 1.72*	3.14 \pm 0.28

1.7% and 2.3% of the initial ^{15}N pool was allocated from the first ramet generation to the second and third (spring cohort), third (autumn cohort) and fourth generations, respectively. Variability in ^{15}N values within a generation between harvest dates was a result of clone and/or ramet variability associated with harvesting separate clones on sequential dates.

Discussion

Restriction of physiological integration to individual ramet hierarchies and inequitable resource acquisition among ramet hierarchies demonstrated the occurrence of intracolonial ramet independence in clones of all three perennial grasses investigated along the environmental gradient. Consequently, hypotheses (i) and (ii), stating that all ramets within clones are physiologically integrated and that ramet hierarchies within clones are capable of equitably acquiring soil nitrogen from nutrient-rich pulses peripheral to individual clones, respectively, were rejected. Ramet interdependence was demonstrated by effective nitrogen allocation among sequentially developed ramet generations within individual ramet hierarchies over a 2-year period; therefore, we were unable to reject hypothesis (iii). These data collectively demonstrate a high degree of ramet independence at the level of the entire clone, but a high degree of interdependence within individual ramet hierarchies comprising these clones.

Minimal ^{15}N distribution among ramet hierarchies establishes that these clones exist as an assemblage of autonomous ramet hierarchies and that ramet hierarchies function as 'integrated physiological units'

(*sensu* Watson & Casper 1984; Watson 1986). Autonomy among ramet hierarchies develops when the seminal ramet, which is the common progenitor of all intracolonial ramets, dies during the second or third year and eliminates complete vascular continuity among ramets within clones. At this point, increased structural complexity of clones precipitates the shift from complete ramet interdependence to independence (e.g. Tuomi & Vuorisalo 1989; Price *et al.* 1992). Resource allocation within ramet hierarchies occurs primarily from older to younger generations (e.g. Welker *et al.* 1987, 1991; Bullock *et al.* 1994), supporting vegetative growth and reproductive development of juvenile ramets in the competitive environment created by the high density of established ramets (Williams & Briske 1991). Architectural evaluation of 24 perennial caespitose species in Europe has indicated that grass clones comprise 2–35 individual units consisting of several ramets each (Wilhelm 1995). This pattern of clonal organization further suggests that independence among ramet hierarchies may be a common characteristic of caespitose grasses.

Acquisition of ^{15}N from soils by ramets in closer proximity to nutrient-rich pulses was not affected by severing of individual clones, but it was significantly greater than for ramets located farther from the nutrient-rich pulse for both size classes of all three species when the pulse was located at one clone diameter from the clone periphery. This response was also significant when the ^{15}N pulse was located two and three diameters from the clone periphery for both size classes of *S. scoparium* and the small size class of *B. gracilis*. In addition, ramets within *S. scoparium* clones had substantially greater ^{15}N atom percent excess values

compared to the other two species. This suggests that *S. scoparium* may have a greater N absorption capability compared to either *B. gracilis* or *P. virgatum* (e.g. Tilman 1989). Lateral root distributions of these three species are similar (0.7–1.0 m) and each species possesses a similar percentage of root biomass in the upper 30 cm of soil (Weaver 1954, p. 163). However, *S. scoparium* clones possess greater root biomass in the upper 0–5 cm soil depth compared to the other two species (Weaver & Clements 1938, p. 315; Derner *et al.* 1997). In cases where ^{15}N absorption did not differ in response to ramet proximity to nutrient-rich pulses, minimal amounts of ^{15}N were absorbed by all ramets (e.g. large clones of *B. gracilis*). Minimal ^{15}N acquisition by *P. virgatum* when the ^{15}N pulse was located two and three diameters from the clone periphery may have resulted from a greater plant density and intensity of competition in the tallgrass community (e.g. Tilman 1989). Lower ^{15}N absorption may have been mediated by greater primary productivity and the uniform distribution of plant cover in the tallgrass community (Sims *et al.* 1978).

Inequitable resource acquisition among ramet hierarchies in all three species indicates that ramets located in closer proximity to heterogeneously distributed soil resources potentially gain a competitive advantage over ramets located at a greater distance from nutrient-rich pulses. Inequitable resource acquisition of below-ground resources among ramet hierarchies establishes the potential for asymmetric competition within clones (Connolly & Wayne 1996; Schwinning 1996). Asymmetric competition among ramet hierarchies within clones may potentially contribute to size inequalities among ramets (de Kroon *et al.* 1992), as opposed to symmetric competition which may potentially promote size equalization among ramets (Hutchings & Barkham 1976; Ekstam 1995). However, it has been hypothesized that asymmetric competition among ramets within clones may be expressed as symmetric competition among clones because conspecific clones possess comparable competitive abilities (de Kroon *et al.* 1992). This hypothesis may be modified to indicate that asymmetric competition among ramet hierarchies may potentially produce symmetric competition within individual clones of the grass species we investigated.

Nitrogen was allocated among sequentially developed ramet generations within ramet hierarchies throughout the 2-year investigation, even though minimal integration existed among ramet hierarchies within clones. The percentage of ^{15}N pools (2–21%) allocated from the primary generation parental ramet to subsequently developed juvenile ramet generations over this time period is similar to the estimated total amount of nitrogen allocated among ramet generations in a short-term (5 day) labelling experiment with this species (Welker & Briske 1992). Decreases in ^{15}N atom percent excess and ^{15}N pools of ramet shoots over the 2-year period very probably resulted

from ^{15}N allocation to root systems (e.g. Clark 1977; Li *et al.* 1992) and nitrogen losses to shoot litter and root turnover (Wetselaar & Farquhar 1980; Berendse *et al.* 1992; Vazquez de Aldana *et al.* 1996). However, the magnitude of nitrogen allocation from parent to juvenile ramet generations was relatively consistent, with 17–32% of the ^{15}N pool within parental ramets being allocated to juvenile ramets at each harvest date. Nevertheless, the efficiency of intergenerational nitrogen allocation is substantially less than that of nutrient allocation among sequentially developing graminoid leaves (Jonasson & Chapin 1985) and nutrient resorption from senescing leaves of aborescent species (Aerts 1996). Nitrogen retention within caespitose grasses provides empirical evidence to support the occurrence of a consolidator strategy in clonal plants (de Kroon & Schieving 1990). However, the relatively low magnitude of intergenerational nitrogen allocation suggests that the majority of nitrogen incorporated into ramets over their life span originates from direct absorption via the root system.

Increased recognition of clonal plants as assemblages of autonomous units or fragments has shifted emphasis in clonal plant ecology and evolution from the advantages of interdependence to the advantages of independence (Kelly 1995). Unfortunately, the arguments proposed to justify ramet and, in this case, ramet hierarchy, independence in clonal plants do not appear directly applicable to grasses, especially those with a caespitose growth form. For example, production and maintenance costs of vascular connections between ramet generations are minimal in comparison to those of strongly rhizomatous species, and the possibility of traumatic breakage appears limited within clones characterized by relatively small basal areas (< 1000 cm²; Tables 2 and 4). However, the risk of disease and pathogen injury (e.g. Cook 1985; Kelly 1995) may be minimized by the absence of complete clonal integration in this growth form. The occurrence of ramet independence among hierarchies throughout much of the life history of clonal grasses verifies the ecological contribution of clonal fragments to genet and population maintenance (e.g. Lord 1993; Danin & Orshan 1995) and emphasizes that this may be the most relevant scale at which to investigate further the ecology of clonal plants (Cain 1990).

Several important inferences can be drawn from these data concerning sectoriality in perennial grass clones, and many of them contradict current assumptions regarding sectoriality in perennial grasses (Watson & Casper 1984; Vuorisalo & Hutchings 1996). First, sectoriality may be as common in mature grass clones as it is in herbaceous and arborescent dicots. Secondly, sectoriality appears to be a consequence of the developmental morphology of clonal growth rather than of physiological processes (e.g. source-sink relationships; Marshall 1996; Vuorisalo & Hutchings 1996). Thirdly, sectoriality exhibits minimal

flexibility in response to resource availability and is characteristic of both caespitose and determinate rhizomatous grass growth forms. Fourthly, no evidence exists to suggest that sectoriality occurs at more than one level (i.e. intrahierarchical) in individual grass clones (e.g. Wijesinghe 1994). Sectoriality within perennial grasses originates with the death of older ramet generations after they have contributed to the establishment of juvenile ramets to maintain the clone. In this context, there may be minimal adaptive value associated with independence among ramet hierarchies within mature perennial grass clones (Briske & Butler 1989; Briske & Derner 1998).

Ramet interdependence within hierarchies, combined with ramet independence within clones, establishes the occurrence of multilevel hierarchies necessary for 'group modulated selection' (Tuomi & Vuorisalo 1989). This represents a unique type of group selection in which the semiautonomy of ramets, or ramet hierarchies in this case, determines that they are appropriate interactive units for phenotypic selection in addition to that of the entire clone. Consequently, phenotypic selection in partially integrated clonal plants can be assumed to consist of two component forces. The first process operates entirely at the level of the ramet and is analogous to phenotypic selection in unitary plants. The second process operates at the level of the clone to modify ramet reproduction. This suggests that phenotypic selection in these clones may potentially be a product of ramet births, deaths and reproductive output mediated by the clone. Greater recognition of the mechanisms and consequences of ramet \times ramet hierarchy \times clone interactions are required to increase our knowledge of intracolonial regulation and ecological success of clonal plants.

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