

Size and ecological significance of the physiological individual in the bunchgrass *Schizachyrium scoparium*

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The size and ecological significance of the physiological individual were investigated in the bunchgrass *Schizachyrium scoparium* by experimentally manipulating the number of connected ramet generations within a hierarchy. Growth and demographic responses of juvenile ramets within the variously sized ramet hierarchies, including total hierarchy mass, were monitored at regular intervals. Growth of two-generation ramet hierarchies in a controlled environment and juvenile ramets within two-generation hierarchies in the field were suppressed by 58 and 26%, respectively, when severed from the clone. Parental ramets (secondary generation) incurred a 50% reduction in mass by sustaining growth of juvenile ramets within two-generation hierarchies. Severance of vascular connections between the primary ramet (common progenitor of the clone) and all secondary-tertiary hierarchies within the clone increased resource availability for the remaining experimental hierarchy which significantly increased juvenile ramet mass, leaf number and leaf area. Survivorship of juvenile ramets was not affected by severing ramet hierarchies from the clone, but leaf recruitment, ramet recruitment and juvenile ramet reproductive development were significantly suppressed. The ecological benefits derived from physiological integration within this species are largely confined to physiological individuals consisting of three connected ramet generations as opposed to the entire clone. Resource integration within the physiological individual enhances vegetative growth and reproductive development of juvenile ramets in the competitive environment created by the high density of established ramets characteristic of the caespitose growth form.

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Intraclonal resource allocation is known to confer several ecological benefits that may increase fitness in clonal plants (Pitelka and Ashmun 1985). Parental support of juvenile ramets (Callaghan 1984), amelioration of localized environmental stresses (Salzman and Parker 1985), increased efficiency of resource sampling in heterogeneous environments (Slade and Hutchings 1987a), and correlative inhibition of ramet recruitment (Pitelka 1984) have all been documented in several clonal species. However, the relative contribution of various ramet generations toward the expression of these ecolog-

ical benefits has only been evaluated in a small number of species.

It is not known whether intraclonal resource allocation involves all ramets within a clone or is confined to specific ramet groups (Watson and Casper 1984, Harper 1985). The assemblage of connected ramet generations functioning as an autonomous unit in the assimilation, allocation and utilization of resources within a clone has been designated the integrated physiological unit or physiological individual (Watson and Casper 1984). The size of the physiological individual (i.e., the number of

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Table 1. Mean and standard error of morphometric characters of primary, secondary and tertiary ramet generations in 16 wk-old clones of *Schizachyrium scoparium* at the initiation of a controlled environment experiment. N = 6 clones with a mean of 38 ramets per clone.

Morphometric Character	Ramet generation		
	Primary	Secondary	Tertiary
Ramet height (cm)	7.4 ± 1.3	11.9 ± 0.9	9.1 ± 1.5
Number of green leaves	6.8 ± 0.6	6.6 ± 0.9	4.3 ± 0.5
Shoot mass (g)	0.27 ± 0.05	0.57 ± 0.10	0.13 ± 0.02
Total root length (cm)	222.3 ± 42.6	248.1 ± 53.9	4.7 ± 2.9
Root number	14.5 ± 1.8	12.2 ± 1.7	0.8 ± 0.4
Root mass (g)	0.78 ± 0.18	0.96 ± 0.19	0.01 ± 0.01
Ramets per clone	1.0 ± -	8.3 ± 1.3	29.0 ± 4.2

connected ramet generations displaying resource integration) is determined primarily by vascular continuity within the clone (Watson and Casper 1984) and secondly by source-sink relations between and among ramet generations (Pitelka and Ashmun 1985).

Tracer and severing experiments conducted with several caespitose graminoids confirm the supposition of partial clonal integration even though ramets grow within close proximity of one another in this growth form (Colvill and Marshall 1981, Briske and Butler 1989, Welker et al. 1991). Resource allocation has been demonstrated within ramet hierarchies composed of three connected ramet generations in *Uncinia meridensis* (Callaghan 1984) and *Schizachyrium scoparium* (Welker et al. 1987), five ramet generations in *Hordeum distichum* (Anderson-Taylor and Marshall 1983) and up to eleven generations in *Carex bigelowii* (Jónsdóttir and Callaghan 1988). Unfortunately, the ecological benefits conferred by physiological integration in clonal graminoids have received considerably less emphasis than patterns of resource allocation (but see Mattheis et al. 1976, Ong and Marshall 1979, Jónsdóttir and Callaghan 1988). Therefore, much of what is known concerning the size and ecological significance of the physiological individual within clonal graminoids is inferred from tracer experiments.

This investigation was conducted to evaluate the size and ecological significance of the physiological individual in the bunchgrass *Schizachyrium scoparium* using an alternative approach to isotopic labelling. Growth and demographic variables of juvenile ramets were monitored in variously sized ramet hierarchies severed from intact clones to create a series of potential physiological individuals. Both perennation and clonal expansion are dependent upon recruitment, establishment and growth of juvenile ramets, therefore, the ecological consequences of physiological integration are most appropriately monitored in this generation. Modification of resource allocation patterns by severing vascular connections between ramets provides a more direct indication of the ecological significance of physiological integration than does tracing the movement of isotopes in intact clones.

Materials and methods

Schizachyrium scoparium var. *frequens* is a perennial bunchgrass widely distributed throughout the eastern two-thirds of the U.S. (Gould 1975). However, it is most abundant in the True Prairie Association of the eastern Great Plains. The bunch or caespitose growth form originates from the intravaginal pattern of juvenile ramet development and complete absence of rhizomes and stolons. Clones are long-lived, possess the C₄ photosynthetic pathway and reproductive ramets attain heights up to 1.5 m. In central Texas, juvenile ramets are recruited in the spring and autumn in undisturbed populations. Ramets in the spring cohort frequently complete their life in one growing season while ramets of the autumn cohort overwinter and complete their life during the subsequent season (Briske and Butler 1989).

Controlled environment experiment

Schizachyrium scoparium clones were grown in 10 × 80 cm sections of PVC pipe filled with sandy loam soil within a controlled environment chamber. Each container was planted with one individual ramet crown (i.e., basal several cm of a ramet possessing an apical meristem and root primordia) randomly selected from a group of five naturally occurring clones. This propagation procedure circumvented the seedling stage of plant development to more closely mimic clonal expansion in the field. Both the soil and the field grown clones were collected from the Texas A&M Native Plant and Animal Conservancy located 3 km southwest of the Texas A&M University main campus. Transplant clones received 200 ml of distilled water daily and were supplied with a one-half strength Peter's 20-20-20 (N, P, K) solution at weekly intervals. Clones were grown with an 11-h photoperiod, quantum flux density of 750 μmol m⁻² s⁻¹ at the top of the plant canopy and a day/night temperature regime of 31/22°C. Clones were grown for 16 wk, beginning in August 1986, to develop the three connected ramet generations necessary for experimentation.

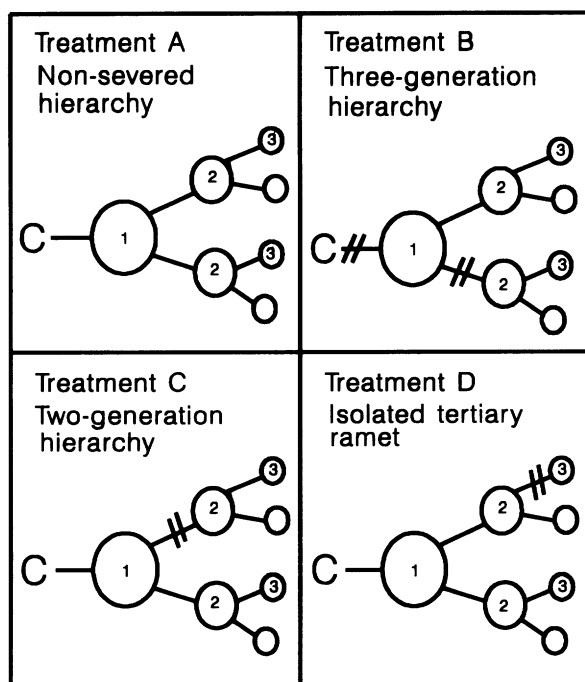


Fig. 1. Diagrammatic representation of four potential physiological individuals produced by severing three generation ramet hierarchies at various locations within clones of a caespitose graminoid. Hatch marks represent the point at which vascular attachments were severed and the letter C represents the remainder of the clone (additional secondary-tertiary generation hierarchies originating from the primary ramet). Inter-ramet distances have been exaggerated for clarity of presentation.

Six clones were destructively harvested to characterize clone architecture at the beginning of the experiment. Clones were composed of a mean of 29 tertiary, 8.3 secondary and a single primary ramet (Table 1). The two chronologically oldest ramets, the primary and secondary generation, displayed comparable morphological development and both were morphologically advanced relative to the younger tertiary ramets. Tertiary ramets initiate adventitious roots at about the third or fourth leaf stage in this species (Carman and Briske 1982). The occurrence of more developed morphometric variables in secondary than in primary generation ramets indicates the acceleration of primary ramet senescence. Ramets were defined as the sum of all subunitary parts (phytomers) differentiated from an individual apical meristem (syn. tiller).

Thirty-six clones were selected on the basis of architectural uniformity and randomly assigned to three severing treatments. Severing treatments produced the following ramet hierarchies which may potentially function as physiological individuals: 1) a three-generation hierarchy produced by severing all but one secondary ramet and a single associated tertiary ramet from the clone (Trt. B; Fig. 1), 2) a two-generation hierarchy

isolated from the clone (Trt. C) and 3) a single tertiary generation ramet isolated from the clone (Trt. D, used only in experiment 2). A ramet hierarchy consisting of three generations within the clone was used as a control to evaluate treatment responses (Trt. A). Each severing treatment and the control was replicated 12 times.

Leaf numbers and one-sided blade area were monitored by measuring the length and width of all live leaf blades present on tertiary ramets at 6-d intervals for 24 d. Shoot height, root number and total root length were recorded for ramets from the experimental hierarchies at the termination of the 24-d experiment. Shoots and roots of the respective ramet generations were oven-dried at 60°C for 48 h prior to dry-weight determination.

Field experiment

A field study was conducted within a *Schizachyrium scoparium*/*Paspalum plicatulum* dominated site on the Texas A&M Native Plant and Animal Conservancy in June 1986. The area is located 3 km southwest of the Texas A&M main campus in east central Texas and is characterized as part of the Post Oak Savanna vegetation zone (Gould 1975). Precipitation averages 950 mm annually and has a bimodal distribution with maxima in the spring and autumn. Mean long-term precipitation (30-yr average) for March through August is 61, 109, 112, 81, 61 and 58 mm, respectively. Precipitation in the 3 months preceding and during the investigation approximated the 30-yr average, but varied substantially from the long-term average for individual months. Precipitation was 14.7, 40.3 and 63.9% less than the 30-yr average for March, April and July, respectively, but exceeded the long-term average by 43.7, 25.9 and 46.5% for May, June and August, respectively (NOAA 1986).

A design similar to that used in the controlled environment experiment was implemented in the field with established plants on 5 June. Clones were selected within a representative size range characterized by 20 to 40 live ramets and a basal area of 50 to 100 cm². Eighteen clones were selected from each of four adjacent 8 × 4 m blocks within an area dominated by *S. scoparium*. Twelve clones from each block were randomly assigned to three treatments (Trts. A, C and D; Fig. 1) and four harvest dates. Treatment B was replaced by treatment D, an individual tertiary ramet severed from the clone, because of the limited number of three generation hierarchies present at this time of year (shoots of primary ramet generations were largely senescent). Ramet recruitment in the spring (April-May) provided a sufficient growth period for tertiary ramets to establish both root and shoot systems prior to severing (Carman and Briske 1982). Shoot mass of tertiary ramets within the experimental hierarchies were harvested on 8 and 25 June, 16 and 30 July, 1986, with the first harvest occur-

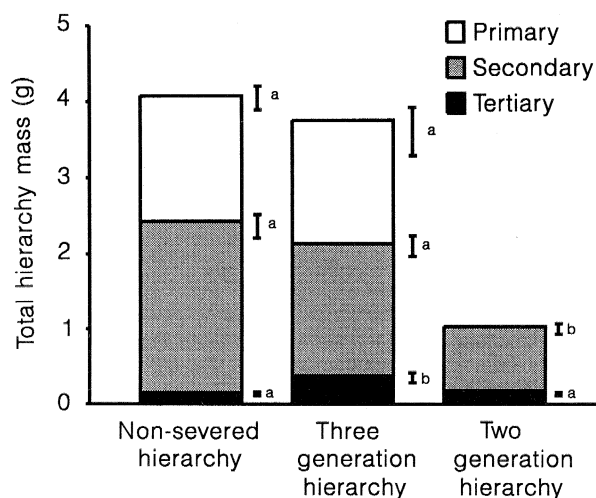


Fig. 2. Total biomass of experimental ramet hierarchies and component ramet generations of non-severed, three-generation and two-generation ramet hierarchies 24 d following severing in a controlled environment experiment. Vertical bars represent one standard error of generation means. Comparable ramet generations among treatments labelled with the same letter do not differ significantly ($P > 0.05$).

ring on the day after implementation of severing treatments.

Leaf blade area of tertiary ramets was estimated by regressing blade length to blade area at weekly intervals ($\text{Area} = -0.38 + 0.34 (\text{Length})$; $R^2 = 0.77$). Blade area was measured with a leaf area meter following each of the four destructive harvests. Severing treatments A, C and D were applied to the six remaining plants in each block to evaluate demographic responses (Fig. 1). Tertiary ramets were evaluated by monitoring the following variables at two week intervals for 80 d: 1) ramet survivorship, 2) number of live leaves, 3) cumulative number of leaves recruited, 4) net number of juvenile ramets recruited (recruitment minus mortality) and 5) ramet reproductive status (vegetative or reproductive).

Statistical analysis

The controlled environment experiment was analyzed as a completely randomized design and the field experiment as a randomized block design. A split-plot analysis was applied to all experiments when repeated measurements were made on the same experimental unit. Whole-plot factors included severing treatment and block. The subplot factor in all cases was sampling date. Analysis of variance procedures were used to evaluate statistical differences between severing and sample date effects with the exception of demographic responses which were analyzed with a Chi-square procedure (Ott 1984). Fisher's Least Significant Difference Test was

used for separation of means when significant treatment differences were indicated.

Results

Controlled environment experiment

Restricting the size of the potential physiological individual by severing significantly affected biomass accumulation within the experimental ramet hierarchies. Total biomass of the isolated two-generation hierarchies (tertiary + secondary mass) was 58% less than the combined mass of similar ramets within non-severed hierarchies at the end of the 24 d experiment ($P < 0.05$, Fig. 2). Restricted growth of parental ramets (secondary generation) accounted for the entire mass reduction within the two-generation hierarchies while mass of the tertiary ramets was unaffected. Total hierarchy weights were not statistically different between the isolated three-generation and non-severed hierarchies despite a

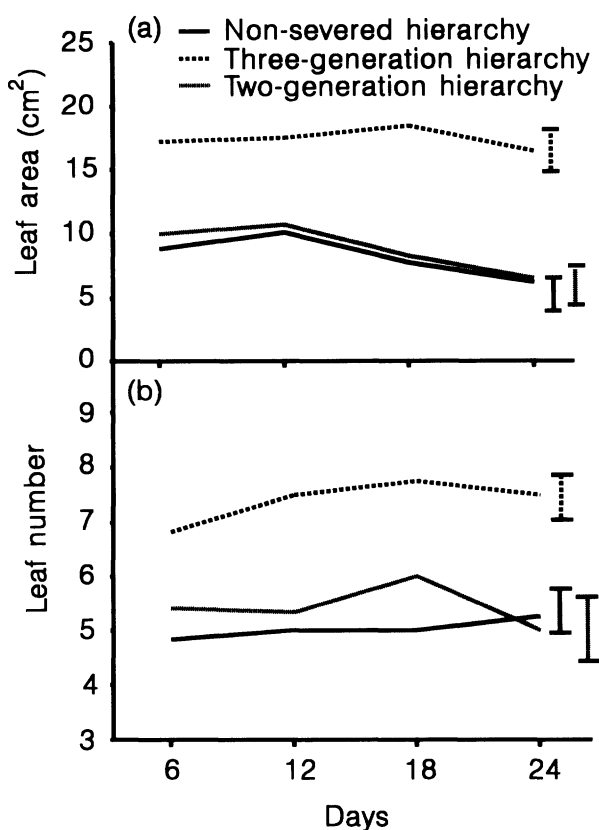


Fig. 3. Mean (a) leaf area and (b) number of green leaves present on tertiary ramets in non-severed, three-generation and two-generation ramet hierarchies in a controlled environment experiment. Vertical bars represent the maximum standard error of treatment means.

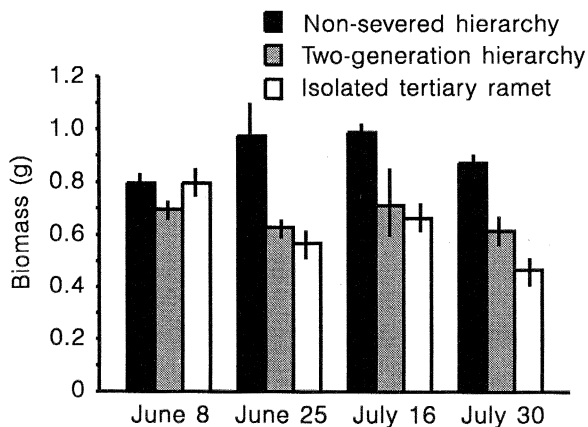


Fig. 4. Mean aboveground biomass of tertiary ramets in non-severed hierarchies, two-generation hierarchies and isolated tertiary ramets in a field experiment. Vertical bars represent one standard error of the treatment means.

two-fold increase in tertiary ramet mass within the isolated three-generation hierarchy (Fig. 2). Ramets of all generations survived throughout the 24 d experiment regardless of the severing treatment imposed.

Mean tertiary ramet biomass in the isolated three-generation hierarchies 24 d following severing was 112 and 151% greater than that in the two-generation and non-severed hierarchies, respectively ($P < 0.01$, Fig. 2). A significantly greater proportion of the biomass accumulated by tertiary ramets in the isolated three-generation hierarchies was distributed belowground ($P < 0.05$). Root: shoot biomass ratios averaged 0.14 ± 0.04 , 0.82 ± 0.33 and 0.19 ± 0.07 in the non-severed, three-generation and two-generation hierarchies, respectively.

Tertiary ramet leaf area in the three-generation hierarchy was 94 and 110% greater than in the two-generation and non-severed hierarchies, respectively ($P < 0.05$, Fig. 3a). Tertiary ramets within the three-generation hierarchies possessed, on average, 1.6 more live leaves than those within the two-generation or non-severed hierarchies ($P < 0.05$, Fig. 3b).

Field experiment

Restricting the potential physiological individual to a two-generation ramet hierarchy or an isolated tertiary ramet in field established clones of *S. scoparium* reduced shoot mass of tertiary ramets (Fig. 4). Biomass differences were not statistically significant when all harvest dates were incorporated into the model ($P = 0.31$), but tertiary ramet mass was reduced 26% ($P = 0.07$) when the final harvest date was analyzed independently. Similar weights of tertiary ramets among treatments on the initial harvest date (8 June) apparently masked the treatment differences in the

larger model. The trend of decreasing biomass in isolated tertiary ramets indicates that leaf senescence exceeded leaf growth as the growing season progressed.

All tertiary ramets, regardless of the severing treatment imposed, survived throughout the 80-d observation period. Several other demographic variables, however, were detrimentally affected by severing vascular attachments. Reproductive development was observed in a significantly greater proportion of tertiary ramets within non-severed hierarchies when compared to tertiary ramets within isolated hierarchies. Reproductive development occurred in 13 of 16, 7 of 16 and 7 of 13 tertiary ramets in the non-severed hierarchy, two-generation hierarchy and isolated tertiary ramet treatments, respectively ($P < 0.05$). Tertiary ramets in non-severed hierarchies also exhibited greater rates of leaf recruitment ($P < 0.01$, Fig. 5a). The mean cumulative number of leaves produced by tertiary ramets during the 80-d observation period was 5.0 ± 0.40 , 3.9 ± 0.52 and 3.5 ± 0.45 for the non-severed hierarchy, two-generation hierarchy and isolated tertiary ramet treatments, respectively. Tertiary ramets attached to the clone initiated a significantly greater number of ramets when compared to tertiary ramets within isolated hierarchies ($P < 0.05$, Fig. 5b). The mean cumulative number of ramets

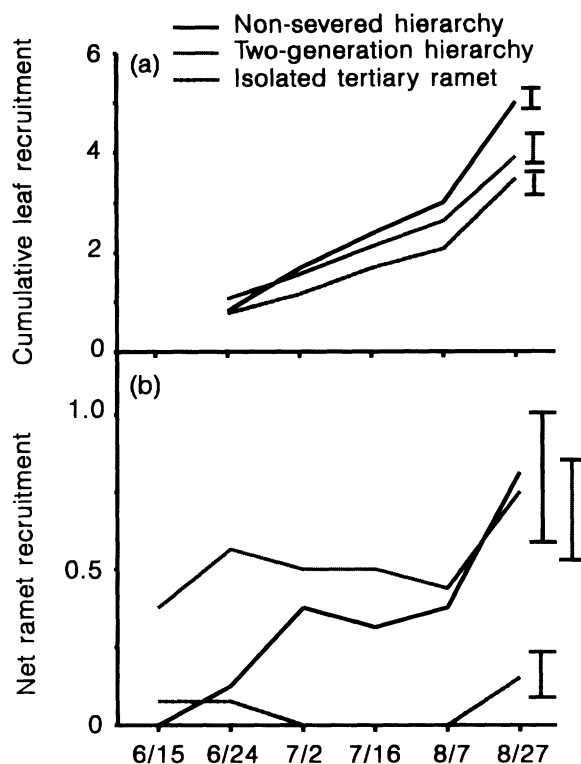


Fig. 5. (a) Cumulative leaf recruitment and (b) net ramet recruitment of tertiary ramets in non-severed hierarchies, two-generation hierarchies and isolated tertiary ramets in a field experiment. Vertical bars represent the maximum standard error of treatment means.

recruited per parental ramet during the 80-d observation period was 0.81 ± 0.37 , 0.75 ± 0.31 and 0.15 ± 0.10 for non-severed, two-generation and isolated tertiary ramet treatments, respectively.

Discussion

Experimental manipulation of the number of connected ramet generations within clones of *S. scoparium* affected fitness-related characters by influencing both vegetative growth and reproductive development of juvenile ramets. Reproductive development of juvenile ramets was more severely affected by a reduction in resource allocation from older ramet generations than ramet recruitment in established clones. Reproductive development was reduced by 47% within two-generation hierarchies while ramet recruitment was unaffected in similar sized hierarchies. However, ramet recruitment was reduced by 81% when tertiary ramets were isolated from the clone in comparison with comparable ramets in intact clones (Fig. 5b). These data confirm that juvenile ramet growth and clonal expansion in caespitose graminoids are dependent upon physiological integration in a similar manner to that demonstrated in several clonal herbs (e.g., Hartnett and Bazaz 1983, Slade and Hutchings 1987b) and rhizomatous graminoids (e.g., Mattheis et al. 1976, Jónsdóttir and Callaghan 1988).

In contrast to the other demographic variables evaluated, ramet survivorship was not reduced by severing even when individual tertiary ramet generations were isolated from the clone. The advanced ontogeny of tertiary ramets at the time of severing may have enabled them to survive and continue growth at a reduced rate (Fig. 5a). Tertiary ramets possessed four to five live leaves and several senescent leaves at the time severing treatments were imposed. This surpasses the three to four leaf stage necessary for adventitious root development in this species, indicating that ramets were able to acquire resources from the soil in addition to assimilating carbon (Carman and Briske 1982).

Severance of vascular connections between the primary ramet (common progenitor of the clone) and the remainder of the clone to produce three-generation hierarchies resulted in a competitive release of resources by eliminating sinks associated with additional secondary-tertiary hierarchies. Therefore, a larger proportion of the resources within the primary generation were available for allocation to the sole remaining secondary-tertiary ramet hierarchy (Fig. 2). The competitive release of resources significantly increased biomass, leaf number and leaf area in tertiary ramets of three generation hierarchies (Fig. 3a).

The ecological significance of physiological integration on juvenile ramet growth was restricted to secondary-tertiary ramet hierarchies while total hierarchy mass

was influenced by three generations of connected ramets. Even though the mass of secondary-tertiary ramet hierarchies was reduced by 58% within 24 d of severing, it was the parental (secondary generation) ramet, rather than tertiary ramet, which incurred the entire growth restriction (Fig. 2). Apparently, tertiary ramets generate the greatest sink strength within the hierarchy enabling them to maintain resource import and growth at a rate comparable to juvenile ramets in intact clones. Consequently, these data indicate that the physiological individual in this bunchgrass consists of a minimum of three connected ramet generations. This interpretation is consistent with the one drawn from isotopic labelling experiments indicating that intraclonal resource allocation was restricted to three generation ramet hierarchies within *S. scoparium* (Welker et al. 1991). Acropetal resource allocation within ramet hierarchies of *S. scoparium* apparently minimizes the potential for complete clonal integration by restricting resource allocation to individual ramet hierarchies.

The number of ramet generations comprising the physiological individual is apparently determined by demographic processes controlling the recruitment and longevity of ramets originating from a common progenitor. Recruitment of a spring and autumn ramet cohort each year in ungrazed populations of *S. scoparium* coupled with a maximum ramet longevity of 16 months establishes the two to three generation ramet hierarchies observed in this species (Butler and Briske 1988, Briske and Butler 1989). Primary generation ramets senesce and die prior to recruitment of the quaternary ramet generation thereby maintaining physiological individuals of a relatively constant size. Successively younger ramet generations then assume the role of acquiring and allocating resources to juvenile ramets within the hierarchy. Graminoid species capable of recruiting a greater number of ramet cohorts per year (e.g. Anderson-Taylor and Marshall 1983) or possessing greater ramet longevity will possess larger physiological individuals (e.g. Jónsdóttir and Callaghan 1988), but would very likely convey ecological benefits similar to those observed in *S. scoparium*.

The ecological benefits derived from physiological integration within this species are largely confined to physiological individuals consisting of three connected generations as opposed to the entire clone. However, resource import and utilization by juvenile ramets within the physiological individual should be viewed as a prerequisite for the caespitose growth form, rather than the survival value conferred by the growth form. Physiological integration is essential for juvenile ramet establishment and growth within the competitive environment created by the high density of mature ramets within the caespitose growth form. The more relevant ecological question appears to be, "what selective advantage it attained by the growth of numerous physiological individuals within close proximity?" The intensity of resource competition among physiological indi-

viduals within a clone undoubtedly exceeds that resulting from interspecific competition.

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