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# Intraclonal regulation in a perennial caespitose grass: a field evaluation of above- and below-ground resource availability

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**Summary**

**1** Intraclonal regulation of the $C_4$ caespitose perennial grass *Schizachyrium scoparium* was evaluated in response to various levels of above-ground (radiation intensity) and below-ground (soil volume) resource availability in the field for three successive growing seasons. We reasoned that the relative plasticity of clonal growth in response to various levels of resource availability may provide insight into the mechanism of intraclonal regulation.

**2** Six naturally occurring clones were randomly assigned to each of five treatments: (i) unrestricted soil volume (control); (ii) large soil volume in which roots were confined to a cylinder of soil with a radius four times that of the clone; (iii) small soil volume, twice the clone radius; (iv) large soil volume with radiation intensity reduced to 55% of ambient; and (v) small soil volume with reduced radiation intensity.

**3** Ramet recruitment increased within the first season following root confinement in large soil volumes, while ramet and leaf growth exhibited less plasticity. The effects of a reduction in radiation intensity were smaller, and, in contrast, increased ramet and leaf growth, but did not modify ramet recruitment.

**4** The pattern and magnitude of ramet mortality in clones confined to the large soil volume were similar to those of clones in unrestricted soil volume, indicating that intraclonal regulation was sufficient to reduce ramet recruitment and thus density to within the carrying capacity established by resource availability.

**5** Similar growth and ramet demography of clones in the unrestricted and small soil volumes suggest that unrestricted clones normally access resources from a soil volume similar to that of the small soil volumes.

**6** Rapid clonal growth in response to root confinement to large soil volumes, resource acquisition from a relatively small soil volume that contains the zone of resource accumulation, and the capacity for rapid expression of ramet plasticity provide circumstantial evidence that individual caespitose clones may respond to resource accumulation in soils beneath them.

*Key-words:* caespitose growth form, clonal biology, plant-induced soil heterogeneity, ramet recruitment, self-thinning

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## Introduction

Our limited knowledge concerning the regulation of intraclonal growth constrains our ecological understanding of clonal plants, including their patterns of growth and demography, intensity and mode of competition and distribution in response to spatial and temporal resource availability. None of the mechanisms proposed for intraclonal regulation has been supported by other than minimal or inconsistent evidence (Suzuki & Hutchings 1997; Briske & Derner 1998; Derner & Briske 1998). The interpretation of several of these proposed mechanisms is

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further influenced by the recognition that clonal plants are often organized as assemblages of autonomous physiological individuals, rather than as an effectively integrated assemblage of ramets. For many grasses, the absence of complete vascular continuity within mature clones suggests that individual ramets or limited numbers of connected ramet generations respond to resource availability via a form of decentralized intraclonal regulation (Harper 1985; Briske & Butler 1989; de Kroon & Kwant 1991; but see Laterra *et al.* 1997; Briske & Hendrickson 1998).

Resource availability, either directly or indirectly as mediated by competition, exerts a substantial influence on intraclonal growth and ramet demography. Grasses respond to intraspecific and interspecific competition by a suppression of ramet recruitment, rather than by increased ramet mortality (Briske & Butler 1989; Cheplick 1997). This response suggests that axillary bud outgrowth is very responsive to resource availability (Briske & Butler 1989; Hendrickson & Briske 1997) and that some form of intraclonal regulation exists to suppress bud growth before ramet density exceeds the carrying capacity of the environment, thus minimizing ramet self-thinning (Hutchings 1979). However, neither the nature of the regulatory mechanism nor the associated environmental resources or signals associated with resource availability have been determined.

Evidence that perennial caespitose grasses accumulate soil organic carbon and nitrogen in the soils directly beneath individual clones re-emphasizes the potential involvement of below-ground resource availability on intraclonal regulation (Hook *et al.* 1991; Vinton & Burke 1995; Derner *et al.* 1997). Even though such nutrient accumulation in soils beneath caespitose grasses has not been shown to benefit plant growth and fitness (Aguilera & Lauenroth 1995), correlation between nutrient accumulation beneath clones and ramet number per clone suggests a causal effect on clonal growth and structure (Derner *et al.* 1997). However, an increase in ramet recruitment or density in response to increased resource availability does not demonstrate a regulatory influence on clonal growth unless there is a disproportionate growth response relative to growth of the entire clone (Phillips 1975).

The compact spatial arrangement of ramets within caespitose clones contributes to, when rapid growth is possible, leaf area indices that are sufficient to induce intense intra- and interclonal competition for light (Caldwell *et al.* 1983; Ryel *et al.* 1994). Therefore, competition for light may be more critical than competition for below-ground resources in mesic grasslands that produce dense canopies, while the opposite may be true in semi-arid grasslands where water limits canopy development (Burke *et al.* 1998). However, competitive removal experiments have demonstrated increased growth, ramet recruitment and basal area expansion of caespitose grasses in mesic (Briske & Butler 1989; Tilman 1989; Hartnett 1993) but not in semi-arid environments (Olson & Richards 1989; Fowler 1995; McPherson 1997). Therefore, this disparity in results clearly indicates that the contribution of above- and below-ground resource availability to intraclonal growth and regulation requires further investigation.

We evaluated the effects of modified available soil volumes and light intensities on the plasticity of caespitose clones of the $C_4$ perennial grass *Schizachyrium scoparium*. Available soil volume was used as a proxy for soil resource availability and was modified by driving two sizes of plastic pipe into the soil around individual clones, to produce a fourfold variation in soil volume. We assumed that the large tube size would eliminate competing root systems and increase soil resource availability to the confined clones, while small tubes would reduce the soil volume explored by the clone's root system and decrease soil resource availability. Shadecloth filters were used to reduce radiation intensity above selected clones within each soil volume by approximately 50%. Variables at the leaf, ramet and canopy levels were monitored to assess the rate and magnitude of clonal growth at the various hierarchical levels in response to modified resource availability.

Specific hypotheses tested were that (i) ramet recruitment and density would be more plastic than either canopy or leaf variables in response to modified resource availability; (ii) intraclonal regulation would suppress the increase in ramet recruitment and density per clone and prevent ramet self-thinning in clones confined in the large soil volumes; (iii) intraclonal regulation would suppress ramet recruitment and density per clone, but substantial ramet mortality would occur in clones confined in the small soil volumes; and (iv) clonal growth would be sufficiently plastic to adjust to modified resource volumes within the first growing season following modification of resource availability. We reasoned that the expression of clonal plasticity in response to modified below-ground resource availability would provide (i) an indication of the potential contribution of resource accumulation in soils beneath individual clones to growth of this caespitose grass, and (ii) additional insight into the mechanism of intraclonal growth regulation.

## Field sites and methods

### STUDY SITE

The experiment was conducted on the Texas A & M Native Plant and Animal Conservancy in east-central Texas near College Station (30°35′ N; 96°21′ W), which is characterized as part of the Post Oak Savanna vegetation zone (Gould 1975). Soils on the

site were a Lufkin fine sandy loam (fine, montmorillonitic, thermic Veric Albaaqualf), an upland series formed from alluvium deposited over coastal plains sediments, commonly $\leq 20$ cm deep to a dense clay layer (Hallmark *et al.* 1986). Mean monthly temperature ranges from a low of 11 °C in January to a high of 29 °C in July. The frost-free period averages 270 days and extends from March through November. Long-term (46-year) precipitation is $1008 \pm 244$ (mean $\pm$ 1 SD) mm annually and has a bimodal distribution, with maxima in the spring and autumn. Mean long-term precipitation for the primary growth period of $C_4$ grasses, from May until July, is 273 mm; in 1995, 1996 and 1997 it was 132%, 45% and 96% of the 46-year average, respectively.

## METHODS

S*chizachyrium scoparium* var. *frequens* (C. E. Hubb.) Gould is a $C_4$ perennial caespitose grass that is widely distributed throughout the eastern two-thirds of the United States (Gould 1975). It is most abundant in the True Prairie Association of the eastern Great Plains. In central Texas, juvenile ramets are recruited in the spring and autumn in undisturbed populations. Ramets initiated in the spring cohort frequently complete their life during that growing season, while ramets initiated in the autumn cohort overwinter and complete their life during the subsequent growing season (Briske & Butler 1989).

Thirty *S.* sco*parium* clones with comparable basal areas (mean $\pm$ 1 SE, $76.2 \pm 4.1$ cm$^2$), ramet numbers ($50.1 \pm 3.5$) and conspecific neighbour proximity were selected in November 1994. Six replicate clones were randomly assigned to each of five treatments: (i) unrestricted soil volume (U, control); (ii) large soil volume (L); (iii) small soil volume (S); (iv) large soil volume with reduced photosynthetic photon flux density (PPFD; shading; L-SH); and (v) small soil volume with reduced PPFD (S-SH). Large soil volumes were imposed with a 0.4-m diameter (a radius four times that of clones) $\times$ 0.5-m long PVC tube, while small soil volumes were imposed with a 0.2-m diameter (a radius twice that of clones) $\times$ 0.5-m long PVC tube, centred around individual clones and driven into the soil in January 1995. The PVC tubes were assumed to confine the majority of the clone's root system because a dense claypan exists at 0.2 m soil depth (Hallmark *et al.* 1986). Shade treatments were imposed by erecting $1 \times 1$ m shadecloth filters 0.6 m above the soil surface, and were initiated on 2 May and ended on 15 July in all 3 years. Filters were raised to 0.9 m above the soil surface on 1 July in each year to accommodate culm elongation of reproductive ramets. Shade treatments reduced PPFD in the vicinity of clones by approximately 50% when solar angles were relatively high. PPFD and red : far-red (R:FR), calculated as the ratio of spectral photon fluxes at $660 \pm 5$ nm and $730 \pm 5$ nm (Smith 1982), were measured near the centre of clones at the soil surface, immediately above the clone canopy, directly beneath the shadecloth, and above the shadecloth (i.e. ambient) on one-half of the clones ($n = 3$) assigned to each of the shade treatments. Reported PPFD and R:FR values obtained from each clone are means of two scans made between 12:00 and 13:00 h at 2-week intervals with an LI-1800 portable spectroradiometer (calibrated at LI-COR Inc., Lincoln, NE) equipped with a remote cosine-corrected probe. The probe was orientated parallel to the soil surface during radiation measurements. Mid-day (15:00–16:00 h) leaf xylem pressure potentials were taken bi-weekly on two leaves from each of three randomly chosen unshaded clones in the unrestricted, large and small soil volume treatments, with a pressure bomb, in 1995 and 1996 (PMS Instrument Company, Corvallis, OR). Mid-day values were recorded to reflect maximum development of water stress in a diurnal period.

Five uniformly sized ramets per clone were chosen and marked with colour-coded wire loops on 2 May in all three years. Non-destructive measurements of ramet height, number of leaf blades and total blade length per ramet were taken bi-weekly. Ten additional ramets, with variable heights, from nearby clones were harvested destructively on each sampling date to develop linear regression equations between leaf blade area and leaf blade length and ramet mass and between total leaf blade length and ramet height (Appendix 1, in the *Journal of Ecology* archive on WWW; see the cover of a current issue for the address). Leaf blade areas were obtained with a leaf area meter (model CI-202; CID Inc., Vancouver, WA). Peak above-ground biomass was estimated for each clone by multiplying the number of ramets per clone on 15 July of each year by the predicted mean ramet mass at that date. Ramet recruitment was assessed bi-weekly by counting juvenile ramets recruited from each marked parental ramet. Cumulative recruitment is the summation of bi-weekly recruitment from each initially marked parent. Basal area and ramet number were determined for all clones on 2 May and 15 July in all three years. Although mean basal area and ramet number did not differ significantly between treatments on the initial sampling date, considerable variation occurred between clones in three soil volume treatments (mean basal area: 81, 76 and 87 cm$^2$; mean ramet number per clone: 60, 44 and 51; for unrestricted, large and small soil volume treatments, respectively). Mean values for these clonal variables were expressed as percentage relative change from the initial value measured within each treatment to account for this variation between treatments.

The circumference of the clone canopy increased from the base to the top (inverted frustum of a cone), and canopy volume per clone, which was estimated bi-weekly, was calculated using the equation:

$$V = 1/3\Pi h(r^2 + rR + R^2)$$

where $V$ = volume; $h$ = distance from soil surface to top of clone canopy (canopy height); $r$ = radius of basal area occupied by clone; and $R$ = radius of area at top of clone canopy (canopy radius)

Three additional clones were selected and allocated to each of the unrestricted, large and small soil volume treatments. Soil cores (0.02 × 0.6 m) were taken directly beneath each of these clones and at the mid-point location between the clone periphery and the PVC tube edge for those clones in the large and small volume treatments, on 27 July 1996. Ten additional cores were taken from interstitial areas for determination of soil bulk density using the core method (Van Remortel & Shields 1993). Soil from each core was divided into four depths: 0–5, 5–15, 15–30 and 30–50 cm, sieved to separate plant material and fragments greater than 2 mm in diameter, and placed in a refrigerator. Available nitrate and ammonium was determined by weighing out 7-g subsamples of soil, extraction with 50 ml of 2 N KCl for 30 min on an orbital shaker, and filtration through Whatman number 40 paper. The extracts were refrigerated until analysed on a Technicon AutoAnalyser II (Technicon Industrial Systems, Tarrytown, NY). The remainder of each soil sample was dried at 50 °C for 3 days, ground with a ring pulverizer (model TE250; Angstrom Inc., Belleville, MI) and analysed for carbon and nitrogen using a Carlo-Erba NA-1500 (Fisons Instruments, Danvers, MA) elemental analyser. Pool sizes of carbon, nitrogen and available nitrogen were calculated (i) directly beneath the basal area of clones and (ii) for the remainder of the soil volume within the PVC tube.

### STATISTICAL ANALYSES

The effect of modified soil volumes on *S. scoparium* leaf, ramet and clone variables was analysed as a completely randomized design using soil volumes and sampling date as factors. The effect of shading on clones was analysed as a split-plot design with soil volumes and radiation treatment with reduction or control levels for each variable comprising the main factors, and date designated as the split factor. The error term used to test 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 with Bonferroni *t*-tests when a factor was significant ($P < 0.05$). Mean values from the five marked ramets were used in analyses. Preliminary analyses indicated multiple year interactions, so subsequent analyses were run separately by year. Comparisons between clones in the large and small soil volume treatments for total soil nitrogen, organic carbon and available nitrogen concentrations and pools were conducted with *t*-tests. Leaf water potential data within each year were analysed as a two-way ANOVA with sample date and soil volume as factors.

## Results

### RADIATION ENVIRONMENT AND SOIL RESOURCES

Shade treatments reduced mid-day PPFD by 55% and R:FR by 9% in both soil volume treatments compared with ambient values (Table 1). Ambient PPFD and R:FR were 2146 $\mu$mol m$^{-2}$ s$^{-1}$ and 1.1, respectively. Mean PPFD and R:FR for shaded clones were not significantly different between large and small soil volume treatments at any position measured.

**Table 1** Mean (± SE, $n$ = 3) photosynthetic photon flux density (PPFD) and red:far-red (R:FR) ratio measured near the centre of clones at the soil surface (base), immediately above the clone canopy (top), directly beneath the shadecloth (beneath) and above the shadecloth (ambient) for *Schizachyrium scoparium* clones confined to large and small soil volumes in the field. PPFD and R:FR measurements were made between 12:00 and 13:00 h on 1 May 1995 with a LI-1800 portable spectroradiometer equipped with a remote cosine-corrected probe held parallel to the soil surface. Mean values measured at the same position were not significantly different ($P > 0.05$) between the two soil volumes

| | PPFD ($\mu$mol m$^{-2}$ s$^{-1}$) | | R:FR | |
|---|---|---|---|---|
| Position | Large soil volume | Small soil volume | Large soil volume | Small soil volume |
| Base | 121.8 (23.7) | 178.4 (42.9) | 0.55 (0.053) | 0.58 (0.070) |
| Top | 754.5 (42.9) | 785.5 (11.9) | 0.95 (0.007) | 0.96 (0.017) |
| Beneath | 976.1 (65.5) | 1020.9 (101.1) | 1.00 (0.015) | 0.99 (0.010) |
| Ambient | 2132.3 (26.9) | 2160.3 (17.4) | 1.09 (0.004) | 1.09 (0.001) |

Concentrations of available $NO_3^-$ for all soil samples were less than 1 p.p.m. Therefore, only $NH_4^+$ concentrations were used to calculate available nitrogen pools within the large and small soil volumes. Pools of total nitrogen, soil organic carbon and $NH_4^+$ were significantly greater for the large soil volumes (28.46, 367.48 and 0.49 kg, respectively) than for the small soil volumes (7.59, 116.08 and 0.16 kg, respectively). Calculated total nitrogen, soil organic carbon and $NH_4^+$ pools were 3.8, 3.7 and 3.7 times greater, respectively, in the large compared with the small soil volume treatments given the fourfold difference in soil volume between treatments.

## CLONAL GROWTH AND BIOMASS PARTITIONING

Growth variables for all three soil volume treatments showed a similar general pattern, with approximately equal values in the unrestricted and large treatments and lower values in the small treatment (Table 2). Year by year variation differed, however. Canopy volume showed a soil volume × year interaction with significant interactions for all 3 years in the unrestricted soil volumes, and a significant interaction associated with reduced canopy volume in the driest of the 3 years (1996) in

**Table 2** Mean (± SE, $n = 6$) values for leaf, ramet and clone level variables of *Schizachyrium scoparium* clones grown in the field with modified resource availabilities. Resource availability treatments were unrestricted (U), large (L), large and shade (L-SH), small (S) and small and shade (S-SH) soil volumes. All tabulated values were collected on the last sampling date (15 July) in each year. Values within each year for soil volume treatments (U, L and S) followed by the same uppercase letter, and values within each year for comparisons involving radiation intensity (L vs. L-SH and S vs. S-SH) followed by the same lowercase letter are not significantly different ($P > 0.05$)

| | | Resource availability treatments | | | | |
|---|---|---|---|---|---|---|
| Variable | Year | U | L | L-SH | S | S-SH |
| Clone level | 1995 | | | | | |
| Biomass (g) | | 55.7 (7.9)$^{A}$ | 54.2 (11.7)$^{Aa}$ | 81.5 (13.4)$^{a}$ | 17.2 (3.9)$^{Bx}$ | 25.3 (4.3)$^{x}$ |
| Canopy volume ($\times 10^4$ cm$^3$) | | 3.71 (0.35)$^{A}$ | 4.94 (0.39)$^{Ba}$ | 5.65 (0.37)$^{a}$ | 1.55 (0.17)$^{Cx}$ | 2.32 (0.38)$^{x}$ |
| Ramet level | | | | | | |
| Cumulative recruitment (juveniles/parent) | | 0.69 (0.14)$^{A}$ | 1.50 (0.31)$^{Ba}$ | 1.52 (0.30)$^{a}$ | 0.53 (0.23)$^{Bx}$ | 0.65 (0.15)$^{x}$ |
| Height (cm) | | 39.5 (2.0)$^{A}$ | 39.6 (3.1)$^{Aa}$ | 54.1 (5.1)$^{b}$ | 27.5 (2.8)$^{Bx}$ | 36.5 (3.2)$^{y}$ |
| Mass (g) | | 0.80 (0.06)$^{A}$ | 0.80 (0.09)$^{Aa}$ | 1.25 (0.16)$^{b}$ | 0.43 (0.09)$^{Bx}$ | 0.71 (0.10)$^{y}$ |
| Leaf level | | | | | | |
| Number of blades | | 6.0 (0.5)$^{A}$ | 7.3 (0.6)$^{Aa}$ | 9.9 (1.4)$^{a}$ | 4.4 (0.4)$^{Bx}$ | 5.3 (0.5)$^{x}$ |
| Total blade length (cm) | | 104.4 (8.9)$^{A}$ | 111.7 (7.6)$^{Aa}$ | 144.2 (11.7)$^{b}$ | 79.6 (11.1)$^{Bx}$ | 114.0 (13.7)$^{y}$ |
| Total blade area (cm$^2$) | | 45.7 (4.0)$^{A}$ | 49.0 (3.4)$^{Aa}$ | 63.6 (5.3)$^{b}$ | 34.5 (5.0)$^{Bx}$ | 50.0 (6.2)$^{y}$ |
| Clone level | 1996 | | | | | |
| Biomass (g) | | 24.5 (2.4)$^{A}$ | 25.2 (3.2)$^{Aa}$ | 23.7 (2.7)$^{a}$ | 10.1 (1.5)$^{Bx}$ | 10.1 (0.8)$^{x}$ |
| Canopy volume ($\times 10^4$ cm$^3$) | | 1.75 (0.13)$^{A}$ | 1.94 (0.21)$^{Aa}$ | 1.93 (0.17)$^{a}$ | 0.84 (0.10)$^{Bx}$ | 0.93 (0.13)$^{x}$ |
| Ramet level | | | | | | |
| Cumulative recruitment (juveniles/parent) | | 0.46 (0.15)$^{A}$ | 0.43 (0.28)$^{Aa}$ | 0.20 (0.10)$^{a}$ | 0.30 (0.17)$^{Ax}$ | 0.23 (0.15)$^{x}$ |
| Height (cm) | | 40.4 (1.0)$^{A}$ | 41.7 (2.6)$^{Aa}$ | 40.1 (1.3)$^{a}$ | 31.8 (2.3)$^{Bx}$ | 34.6 (1.8)$^{x}$ |
| Mass (g) | | 0.42 (0.02)$^{A}$ | 0.44 (0.04)$^{Aa}$ | 0.42 (0.02)$^{a}$ | 0.29 (0.03)$^{Bx}$ | 0.33 (0.03)$^{x}$ |
| Leaf level | | | | | | |
| Number of blades | | 3.1 (0.2)$^{A}$ | 2.5 (0.2)$^{Ba}$ | 3.1 (0.2)$^{a}$ | 2.1 (0.3)$^{Bx}$ | 2.3 (0.3)$^{x}$ |
| Total blade length (cm) | | 58.3 (4.4)$^{A}$ | 45.3 (4.1)$^{Ba}$ | 55.7 (6.8)$^{a}$ | 27.7 (5.7)$^{Cx}$ | 33.9 (7.7)$^{x}$ |
| Total blade area (cm$^2$) | | 27.0 (2.2)$^{A}$ | 20.6 (2.0)$^{Ba}$ | 25.7 (3.3)$^{a}$ | 12.0 (2.8)$^{Cx}$ | 15.0 (3.8)$^{x}$ |
| Clone level | 1997 | | | | | |
| Biomass (g) | | 64.0 (12.2)$^{A}$ | 83.0 (22.7)$^{Aa}$ | 54.6 (8.1)$^{a}$ | 24.9 (7.7)$^{Bx}$ | 30.5 (2.2)$^{x}$ |
| Canopy volume ($\times 10^4$ cm$^3$) | | 5.20 (0.58)$^{A}$ | 5.99 (0.89)$^{Aa}$ | 5.76 (0.42)$^{a}$ | 1.74 (0.24)$^{Bx}$ | 2.45 (0.24)$^{x}$ |
| Ramet level | | | | | | |
| Cumulative recruitment (juveniles/parent) | | 0.26 (0.09)$^{A}$ | 0.40 (0.15)$^{Aa}$ | 0.40 (0.14)$^{a}$ | 0.30 (0.19)$^{Ax}$ | 0.35 (0.14)$^{x}$ |
| Height (cm) | | 46.8 (3.0)$^{A}$ | 51.2 (3.9)$^{Aa}$ | 54.4 (4.9)$^{a}$ | 35.8 (3.8)$^{Bx}$ | 49.0 (2.6)$^{y}$ |
| Mass (g) | | 0.97 (0.13)$^{A}$ | 1.16 (0.17)$^{Aa}$ | 1.30 (0.21)$^{a}$ | 0.50 (0.16)$^{Bx}$ | 1.07 (0.11)$^{y}$ |
| Leaf level | | | | | | |
| Number of blades | | 6.1 (0.5)$^{A}$ | 5.7 (0.6)$^{Aa}$ | 6.8 (0.7)$^{a}$ | 3.6 (0.3)$^{Bx}$ | 5.8 (0.3)$^{y}$ |
| Total blade length (cm) | | 101.5 (8.0)$^{A}$ | 90.3 (5.2)$^{Aa}$ | 115.3 (8.2)$^{b}$ | 70.4 (10.0)$^{Bx}$ | 96.6 (6.7)$^{y}$ |
| Total blade area (cm$^2$) | | 48.1 (3.9)$^{A}$ | 42.6 (2.5)$^{Aa}$ | 54.9 (4.0)$^{b}$ | 32.9 (4.9)$^{Bx}$ | 45.8 (3.3)$^{y}$ |

both the large and small soil volumes. Shade treatments did not significantly affect canopy biomass or volume in any soil volume treatment.

Similarly, ramet height and mass did not differ between clones in large and unrestricted soil volumes, but both were reduced in clones in the small soil volumes (Table 2). For all treatments, the ramet level variables of height and mass were significantly greater in the final year of the investigation than in the previous 2 years. Ramet height and mass were significantly greater in the shade than non-shade treatments for clones in small soil volumes in the two wettest years, but not the drought year.

Blade length, area and number were again similar between clones in large and unrestricted soil volumes in the two wetter years, with clones in these two treatments having larger leaf variables than clones in small soil volumes (Table 2). Leaf variables were 50–70% lower in the drought year for all treatments. Blade length and area were approximately 30% greater in shaded compared with unshaded clones within a soil volume treatment; however, shade did not significantly affect leaf number in any soil volume treatment, with the exception of clones in the small soil volumes in 1997.

Growth responses at different hierarchical levels within clones were compared by calculating the ratios for leaf, ramet and clone variables in large compared with small soil volumes (Table 3). Clone canopies, representing a product of ramet- and leaf-level responses, showed the greatest growth response. Ratios for canopy biomass and volume in the large and small soil volume treatments ranged between 3.15 and 3.44 in the two wetter years. These values approached the ratios of soil volume and soil organic carbon and nitrogen pools between the two soil volume treatments. Ratios for ramet variables in the large and small soil volume treatments ranged between 1.31 and 1.86, with the exception of ramet mass in 1997 (ratio = 2.32). Ratios for large:small soil volume treatments were relatively constant among leaf variables, at approximately 1.5.

### RAMET DEMOGRAPHY

Relative ramet number per clone in the large soil volumes increased in the year following imposition of the soil volume treatments, while ramet number per clone in both the unrestricted and small soil volumes remained relatively constant until the final year of the investigation, when they both showed a 25% increase in May (Fig. 1a). Ramet number per clone showed seasonal fluctuation that was greatest (50%) in the large soil volumes; highest ramet numbers occurred in the spring, followed by a rapid decline in the summer. Ramet number per clone was similar in the unrestricted and small soil volumes, with both values approximately 60% lower than in the large soil volumes at the end of the investigation. Ramet mortality, as evidenced by the decrease in ramet number per clone, only occurred in clones in the small soil volume in the first year, in clones of both the large and small soil volumes in the second year, and in clones of all three treatments in the third year.

Relative basal area per clone increased in both the first and third years of the investigation for all soil volume treatments (Fig. 1b). Clones maintained constant basal areas in the second year, which coincided with a severe regional drought. Clones in the unrestricted and small soil volumes maintained similar basal areas per clone, which were approximately 50% less than the basal areas of clones in the large soil volume treatments at the end of the investigation.

Relative ramet density was significantly greater for clones in the large compared with the small soil volumes for all sample dates except May 1997

**Table 3** Ratios of leaf, ramet and clone level variables in the large vs. small soil volumes ($n$ = 6 each) on 15 July 1995, 1996 and 1997 for *Schizachyrium scoparium* clones grown in the field. Mean values for all variables are presented in Table 2

| | Large : small soil volume ratios | | |
|---|---|---|---|
| Variable | 1995 | 1996 | 1997 |
| Clone level | | | |
| Biomass | 3.15 | 2.50 | 3.33 |
| Canopy volume | 3.19 | 2.31 | 3.44 |
| Ramet level | | | |
| Cumulative recruitment | 2.83 | 1.43 | 1.33 |
| Height | 1.44 | 1.31 | 1.43 |
| Mass | 1.86 | 1.52 | 2.32 |
| Leaf level | | | |
| Number of blades | 1.66 | 1.19 | 1.58 |
| Total blade length | 1.40 | 1.64 | 1.28 |
| Total blade area | 1.42 | 1.72 | 1.29 |

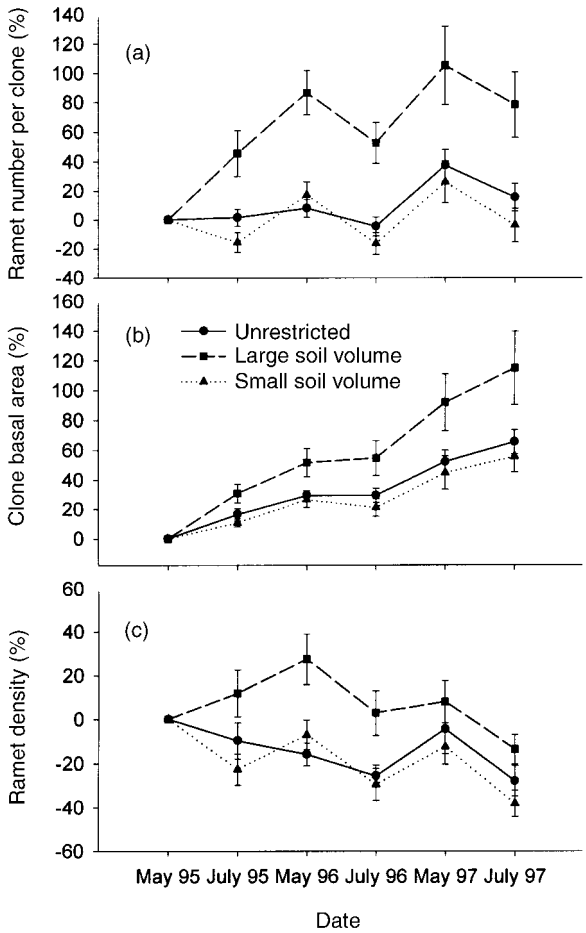


**Fig. 1** Mean (± SE, $n = 6$) relative change in (a) ramet numbers per clone, (b) basal area per clone and (c) ramet density per clone for the perennial caespitose grass *Schizachyrium scoparium*, grown in three soil volumes for three successive growing seasons. Values represent the percentage change from May 1995 mean measurements, which were (a) ramet number per clone, 60, 44 and 51; (b) basal area, 81, 76 and 87 $cm^2$; and (c) ramet density, 0.78, 0.63 and 0.60 per $cm^2$ for unrestricted, large and small soil volumes, respectively.

(Fig. 1c). Ramet densities for clones in the unrestricted and small soil volumes did not differ significantly at any sampling date. Ramet density showed a significant increase of approximately 30% for clones in large soil volumes during the first year, but then decreased during the following 2 years. Clones in the unrestricted and small soil volumes showed a gradual decrease in ramet densities of 28% and 38%, respectively, over the duration of the investigation.

Cumulative ramet recruitment was significantly greater in clones grown in the large compared with the small soil volumes for the last three sampling dates of the first year following confinement of soil volumes (Fig. 2). Recruitment data are only shown for the first growing season (1995) because treatment means did not differ significantly in subsequent years (Table 2). Ramet recruitment for clones in the unrestricted soil volumes was significantly lower than that in the large soil volumes on only the last sampling date shown. The more rapid rate of ramet recruitment displayed by clones grown in the large soil volumes was maintained throughout the initial growing season compared with clones in the other two treatments. Shade did not significantly affect cumulative ramet recruitment in any soil volume treatment.

### LEAF XYLEM PRESSURE POTENTIALS

Leaf xylem pressure potentials in the first growing season did not differ significantly between clones in the various soil volume treatments, with the exception of 9 June when clones in the unrestricted and small soil volumes had a more negative potential than clones in the large volumes (Fig. 3). Leaf pressure potentials were substantially more negative in the second year of the investigation, reflecting the below average precipitation during this period. During this growing season, clones in the unrestricted soil volumes had significantly higher potentials from 9 June onwards than clones in either large or small soil volumes, which did not differ significantly.

## Discussion

Clones of the caespitose grass *S. scoparium* responded rapidly to root confinement in large soil volumes compared with unrestricted clones. Clone responses to root confinement in small soil volumes and reductions in light intensity were smaller compared with unrestricted and unshaded clones, respec-

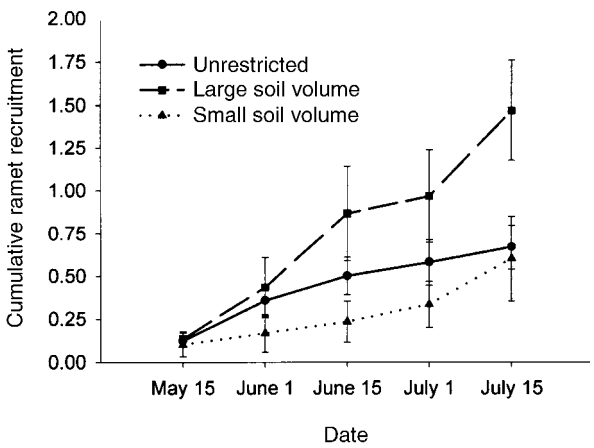


**Fig. 2** Mean (± SE, $n = 6$) cumulative ramet recruitment (juveniles per marked parental ramet) during 1995 for the perennial caespitose grass *Schizachyrium scoparium*, grown in three soil volumes.

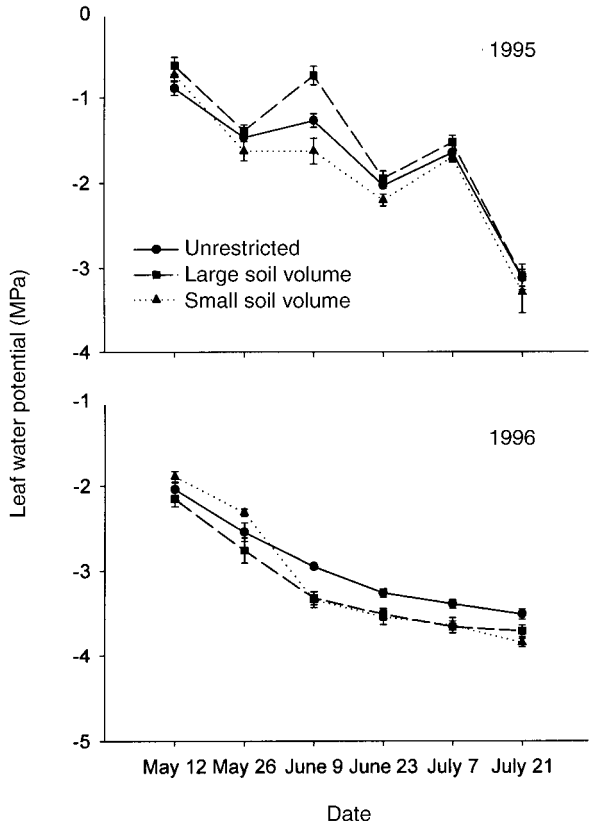


**Fig. 3** Mean ($\pm$ SE, $n = 6$) mid-day (13:00–14:00) leaf water potentials for clones of the perennial caespitose grass *Schizachyrium scoparium*, grown in three soil volumes in the field. Values were collected for the first two seasons of an investigation spanning three growing seasons.

tively. In the case of large soil volumes, ramet recruitment increased after root confinement and led to an increase in clonal growth, while ramet and leaf growth exhibited less plasticity in response to below-ground resource availability, thus supporting hypothesis (i). In contrast, a reduction in radiation intensity increased leaf and ramet growth, but it did not modify ramet recruitment or canopy variables. The pattern and magnitude of ramet mortality in clones in the large soil volume were similar to that of the unrestricted clones in the final 2 years of this investigation, indicating that intraclonal regulation was sufficient to maintain ramet densities within the carrying capacity of the given environment, as predicted by hypothesis (ii). The similarity in ramet recruitment, number and mortality in the small soil volumes and in unrestricted clones suggests that clones normally access soil resources from a cylinder of soil with a radius approximately twice that of individual clones. This suggests that soil volume was not restricted sufficiently to provide a valid test of hypothesis (iii). Clonal growth did indeed adjust to soil volume and shade treatments within the first growing season following root confinement, indicating that caespitose clones possess sufficient plasticity to respond rapidly to modified levels of resource availability, as suggested by hypothesis (iv).

Clones possessed sufficient plasticity to incorporate additional resources rapidly into a greater number of ramets during the first growing season without an increase in ramet height or mass. Ramet recruitment and number per clone, even in clones in the large soil volume, did not increase in the second or third growing season, indicating that clones had fully adjusted to resources within the large soil volume during the first growing season following root confinement. This response is consistent with previous investigations showing greater growth responses of grasses and graminoids to reduced competition and increased resource availability (Lapham & Drennan 1987; Briske & Butler 1989; Cheplick 1997; but see Hartnett 1993). An increase in ramet recruitment in response to increased resource availability conforms to the reserve meristem hypothesis presented by Aarssen (1995) as an ecological explanation for the role of apical dominance in plants. Enough axillary buds were presumably available to enable rapid growth and establishment of new ramets when clones were confined in large soil volumes (Hendrickson & Briske 1997). Ramet recruitment was greatly reduced in these clones after the first year, suggesting that the need for self-thinning was minimized because bud activation was suppressed in the subsequent seasons. Unfortunately, the specific resources and physiological mechanism(s) contributing to bud activation remain unknown (Cline 1991; Murphy & Briske 1992; Coenen & Lomax 1997).

Clones within the large soil volumes showed significant increases in ramet recruitment, ramet number, clone basal area and clone volume relative to unrestricted clones, while other variables, including ramet height and mass and leaf variables, were similar between clones in these two treatments. These differences in variable responses can probably be explained by the fact that variables that increased significantly following root confinement in the large soil volumes were directly influenced by ramet recruitment (e.g. ramet number and canopy volume), while variables that were not significantly affected were associated with growth of ramets (e.g. ramet mass and leaf blade area). Canopy biomass was an exception because, although dependent on recruitment, it did not differ significantly between clones in large and unrestricted soil volumes. Large standard errors for ramet number per clone in both the large and unrestricted soil volumes probably contributed to the insignificant treatment effect on canopy volume.

A greater expression of plasticity in ramet recruitment from axillary buds located at the soil surface, than in ramet growth from previously activated api-

cal meristems within the clone canopy, supports the hypothesis that the developmental rate of apical meristems is less sensitive than that of axillary buds to resource availability (Watson *et al.* 1997). Biomechanical constraints associated with the support of vertical structures may limit the range of plasticity shown by individual ramets (Huber 1996). Furthermore, in productive grassland environments, the capacity for effective lateral spread and space occupation may be of greater adaptive value than vertical growth (Lovett Doust & Lovett Doust 1982).

In contrast to greater ramet density of *S. scoparium* clones confined within large soil volumes, clones of the rhizomatous perennial grass *Panicum virgatum* developed ramets of greater size and reproductive development, rather than increased ramet numbers, in response to nitrogen fertilization (Hartnett 1993). Contrasting growth responses by *S. scoparium* and *P. virgatum* clones to increased below-ground resource availability may represent a case of interspecific variation in clonal plasticity, as demonstrated by Dong & Pierdominici (1994). Alternatively, contrasting growth responses between clones subjected to different soil volumes and nitrogen fertilization suggest that soil nitrogen may not have been the only soil resource influencing ramet recruitment. Hartnett (1993) suggested that soil water may be a more critical resource than soil nitrogen in influencing growth of perennial grass clones in mesic environments following removal of competitors and addition of nitrogen. However, in this investigation, soil water appeared to influence leaf and ramet growth to a greater extent than it did ramet recruitment.

Limited ramet mortality occurred in clones in the small soil volumes in the first year, as evidenced by decreases in ramet number and density per clone from May to July compared with unrestricted clones. However, no ramet mortality occurred in clones in the large soil volume until the second year, which was associated with a regional drought. The drought in the second year makes it difficult to determine whether ramet mortality occurred because clones recruited more ramets than the environment could support, or whether severe reductions in water availability contributed directly to mortality. Ramet mortality occurred to a similar extent in clones of all soil volume treatments in the third year of the investigation, suggesting that a mechanism of intraclonal regulation was operating to maintain ramet recruitment within the carrying capacity of the environment following modification in soil volumes. Ramet mortality and an associated decrease in ramet density per clone frequently occur in clones of this species during mid-summer (Briske & Butler 1989).

Self-thinning in *S. scoparium* clones may be minimized by extensive physiological integration between ramets, at least within individual ramet hierarchies, even though physiological integration does not occur between all ramets within the clone (Welker *et al.* 1991; Derner & Briske 1998). This interpretation is consistent with the hypothesis that intraclonal ramet density may be at least partially regulated by physiological integration (Hutchings 1979; Suzuki & Hutchings 1997), but it may apply at a finer scale than that of the entire clone (de Kroon & Kwant 1991; Derner & Briske 1998). The alternative interpretation, that self-thinning may be constrained by regulation of the number and size of physiologically independent units within clones, appears less plausible.

Increased growth of both ramets and leaves in response to shading within both the large and small soil volumes demonstrates that below-ground resource availability exerted greater control on clonal growth than light intensity did under the conditions of this experiment. A reduction in light intensity probably increased growth by increasing water-use efficiency in the shaded microenvironment. The occurrence of greater ramet height and leaf blade area in shaded compared with unshaded clones, even though clones within both soil volume treatments had similar xylem pressure potentials, provides indirect evidence for this interpretation. Clones in the large soil volumes had access to four times as much water as clones in the small soil volumes, but nevertheless clones in the large soil volumes had more favourable xylem pressure potentials than clones in the small soil volumes on only one sampling date in 1995. Apparently, clones in the large soil volumes increased their rate of soil water absorption compared with clones in the small soil volumes by proportionally increasing canopy biomass and transpirational area (Nobel 1981; Anderson & Briske 1995). Enhanced growth of a $C_4$ perennial grass in response to shading has been attributed to an increase in the availability of both water and nitrogen associated with increased mineralization (Cruz 1997). Late-seral $C_4$ perennial grasses have been shown to maintain substantial ramet recruitment at light intensities comparable (60% ambient) with those imposed in this experiment (Everson *et al.* 1988).

The occurrence of comparable cumulative ramet recruitment, ramet number, ramet density and basal area per clone in the unrestricted and small soil volumes at the end of the investigation suggests that unconfined clones acquired resources from a cylinder of soil with a radius approximately twice that of the clone. This soil volume contains soils with the largest accumulations of soil organic carbon and nitrogen directly beneath caespitose clones (Hook *et al.* 1991; Derner *et al.* 1997). Competition from

conspecific and heterospecific root systems may constrain root exploration to a smaller soil volume, even though caespitose grasses can acquire nutrients from distances of at least 0.5 m from the clone periphery (Tilman 1989; Derner & Briske 1998). Resource acquisition from a relatively small soil volume directly beneath clones, and the capacity for a high degree of clonal plasticity in response to soil resource availability, provides circumstantial evidence to support the inference that the growth and structure of caespitose clones may potentially be mediated by resource accumulation in soils beneath clones of this growth form.

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