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Clonal biology of caespitose grasses

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Introduction

Graminoids comprise one of the largest subgroups of clonal plants among
terrestrial angiosperms (Tiffney & Niklas, 1985). Caespitose graminoids
represent a unique growth form that is characterized by the compact spatial
arrangement of ramets within individual clones and the absence of rhi-
zomes or stolons. Caespitose graminoids occur on all continents from the
high Arctic to the Sub-Antarctic and are distributed over a wide range of
precipitation zones (Leith, 1978; Walter, 1979). This growth form is partic-
ularly dominant in the grassland biome which occupies 24 million km^2
including tropical and temperate grasslands, savannas and shrub steppe
(Leith, 1978).

The wide distribution and dominance expressed by caespitose
graminoids is somewhat surprising given that the majority of modern
monocot families are rhizomatous (Tiffney & Niklas, 1985). Rhizomes are
modified horizontal ramets located belowground that represent a mode of
clonal growth well suited for ramet dispersal, effective resource acquisition,
and resource storage (Grace, 1993). In contrast, caespitose graminoids
possess several attributes that could potentially limit their success, includ-
ing intense intraclonal competition for nutrients (Hartnett, 1993) and for
photosynthetically active radiation (Caldwell *et al.*, 1983; Ryel, Beyschlag
& Caldwell, 1993, 1994), and a limited ability to access heterogeneously dis-
tributed resources (Van Auken, Manwaring & Caldwell, 1992). This poses
the question, 'what structural and/or functional attributes contribute to the
ecological success of caespitose graminoids without the benefits conferred
by rhizomes?' The adaptive value of caespitose clones must be sufficient to
offset the benefits associated with rhizomes or this growth form would not
be so successful (e.g. Pedersen & Tuomi, 1995). Because they possess

minimal plasticity for ramet placement compared with rhizomatous and stoloniferous (produce modified horizontal ramets aboveground) species (e.g. de Kroon & van Groenendael, 1990), caespitose graminoids may be an ideal growth form in which to evaluate ecological success conferred by clonality.

A greater understanding of the processes and mechanisms influencing and/or regulating ramet demography within individual clones would increase insight into the ecological success of caespitose graminoids. For example, are ramets within individual clones interdependent or independent? What mechanism(s) regulates ramet densities, including recruitment and/or mortality, within clones? Do caespitose clones represent an alternative strategy to active foraging characteristic of rhizomatous and stoloniferous species? How does the spatial arrangement of ramets within individual clones influence growth efficiency? Answers to these questions are essential for a thorough understanding of the structure, function, and competitive ability expressed by this important and widely distributed group of clonal plants. Unfortunately, the biology of caespitose clones has received minimal attention compared with resource foraging by rhizomatous and stoloniferous species. However, the concept of foraging strategies within clonal plants has recently been broadened to incorporate the caespitose growth form (Hutchings & de Kroon, 1994; de Kroon & Hutchings, 1995).

The goals of this chapter are to evaluate mechanisms potentially capable of regulating ramet demography within caespitose clones and to assess mechanisms conferring ecological success to caespitose grasses. These two goals are related in that intraclonal regulation of ramet recruitment and density may optimize the growth efficiency of individual clones. Specific objectives are to:

1. establish the architectural constraints that define the caespitose growth form;
2. evaluate the status of mechanisms capable of regulating intraclonal ramet demography, including apical dominance, resource competition, physiological integration, the red:far-red ratio of solar radiation, and equitable resource acquisition among ramets within clones;
3. assess the relative magnitude and influence of intraclonal ramet competition;
4. survey the ability of caespitose clones to consolidate and monopolize resources within their immediate environment as a potential mechanism for their ecological success.

Architecture and demography of caespitose grasses

Clonal architecture

A thorough comparison of caespitose and rhizomatous or stoloniferous grasses requires some knowledge of the developmental morphology contributing to architectural variations among them. In grasses, the fundamental growth unit is the phytomer which consists of a blade, sheath, node, internode, and axillary bud (Etter, 1951; Langer, 1972; Dahl & Hyder, 1977). Ramets comprise a series of phytomers successively differentiated from individual apical meristems (White, 1979; Briske, 1991). This pattern of developmental morphology determines that grass clones are composed of an assemblage of phytomers organized within a variable number of ramets. Morphological variation of individual ramets is a consequence of the number and size of phytomers which comprise them. For example, variation in ramet architecture among grasses of various heights results from a modification in the size and/or number of phytomers determining cumulative ramet height and leaf area. Following a period of juvenile development, ramets are potentially capable of initiating subsequent ramets from axillary buds.

The capacity for physiological integration between juvenile and parental ramets is established at the time of ramet development. Inter-ramet vascular connections are formed soon after bud differentiation beginning with vascular traces of the prophyll (Hitch & Sharman, 1968a,b; Bell, 1976). Basal differentiation of these vascular traces eventually allows them to join the vascular system of the parental ramet, thus conferring the ability for inter-ramet resource allocation. Physiological processes governing resource availability and sink strengths determine the subsequent patterns of intra- and inter-ramet resource allocation once the vascular system has formed (Geiger, 1979). Inter-ramet carbon allocation patterns in grasses have been summarized by Pitelka & Ashmun (1985; also see Welker & Briske, 1992).

Architectural variation among plants is often determined by a small number of attributes including branch angles, internode length, and the probability of bud growth (Harper, 1981). Spatial arrangement of ramets within clones is a major determinant of architectural variation among grass growth forms (i.e. caespitose, rhizomatous and stoloniferous species), and is dependent upon the pattern of ramet development (Fig. 4.1). Intravaginal ramet development within the subtending leaf sheaths results in minimal inter-ramet distances and defines the caespitose (tussock, bunchgrass, or phalanx) growth form (White, 1979; Briske, 1991). Extravaginal ramet development proceeds laterally through the subtending
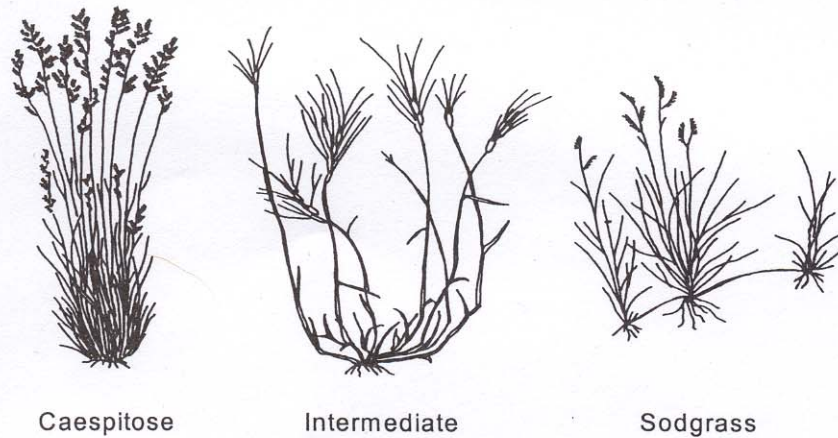
Caespitose   Intermediate   Sodgrass

Fig. 4.1. Architectural variation within the grass growth form originates from the pattern of juvenile ramet emergence. The caespitose growth form originates from intravaginal ramet development within surrounding leaf sheaths while extravaginal ramet development through the subtending leaf sheaths contributes to a more diffuse ramet arrangement represented by the intermediate growth form. Extravaginal ramet development is a prerequisite for rhizome and stolon development characteristic of the sodgrass growth form. (From Briske, 1991).

leaf sheath contributing to a greater inter-ramet distance within clones. This pattern of ramet development defines the intermediate growth form. Extravaginal ramet development is a prerequisite for development of the sodgrass (creeping, spreading, or guerrilla) growth form and inter-ramet distances may be further accentuated by the development of rhizomes and stolons. Architectural variation also determines how clones exploit their environment and interact with neighbours (Harper, 1981).

Clonal demography

Clonal growth and continued site occupation in perennial grasses results from a condition termed meristem dependence (Tomlinson, 1974). Active meristems are continually required to produce juvenile ramets to offset mortality losses associated with the relatively short longevity of these structures (≤ 2 years; Langer, 1972; Briske & Richards, 1995). Successive ramet recruitment produces a series of connected generations referred to as ramet hierarchies or families (Langer, 1972). The number of ramet generations comprising a hierarchy is determined by the rate of ramet recruitment and ramet longevity as influenced by genetic and environmental constraints. In the case of the C_4 caespitose grass, *Schizachyrium scoparium*, ramet hierar-

chies comprise three connected ramet generations (Welker, Briske & Weaver, 1991; Williams & Briske, 1991). Ramet hierarchies are restricted to three generations because the oldest ramet generation dies and decomposes prior to development of the quaternary ramet generation. However, ramet hierarchies have been shown to separate without ramet mortality in *Poa alpina*, suggesting the occurrence of active abscission between ramet generations (Wilhalm, 1995). Resource allocation from both of the older ramet generations within a hierarchy supports juvenile ramet establishment (Welker *et al.*, 1991; Williams & Briske, 1991; Welker & Briske, 1992).

The numbers of ramets per hierarchy and hierarchies per clone define the size and architectural configuration of caespitose clones. With increasing clone size and age, ramet hierarchies become separated as the initial ramet generations die and decompose (Gatsuk *et al.*, 1980; Olson & Richards, 1988). The hollow crown phenomena characteristic of many long-lived perennial caespitose grasses is very likely a natural consequence of the architectural development of clones and not a symptom of stress or disturbance (e.g. Briske, 1991; Danin & Orshan, 1995). Disproportionate ramet recruitment at the clone periphery eventually reduces axillary bud availability within the clone interior and limits ramet recruitment (Butler & Briske, 1988; Olson & Richards, 1988). The interior regions of clones may not be recolonized because of insufficient plasticity for ramet placement in this location.

Annual ramet replacement theoretically confers clones with potential immortality (Watkinson & White, 1986). Individual genets of *Carex curvula, Festuca rubra, F. ovina,* and *Holcus mollis* have been estimated to attain great longevities, perhaps exceeding 1000 years (Steinger, Körner & Schmid, 1996), and occupy large areas (Harberd, 1961, 1962, 1967). However, the few age estimates available for North American caespitose grasses indicate that maximum clone longevity does not exceed 50 years (Briske & Richards, 1995). Comparable evaluations of caespitose grasses in Kazakhstan, including *Festuca, Koeleria,* and *Stipa* spp., suggest maximum clone longevities of 30–80 years (Vorontzova & Zaugolnova, 1985; Zhukova & Ermakova, 1985). Estimates of relatively short life spans may partially result from the architectural development of caespitose clones and the charting procedures frequently used to monitor clone survival. Clonal expansion and subsequent fragmentation may yield estimates of premature clone mortality even though the genet continues to survive in the form of one or more remnants of the original clone (e.g. West, Rea & Harniss, 1979; Cain, 1990; Lord, 1993). Chronological estimates of the architectural development of *Deschampsia caespitosa* in northern Europe suggest that
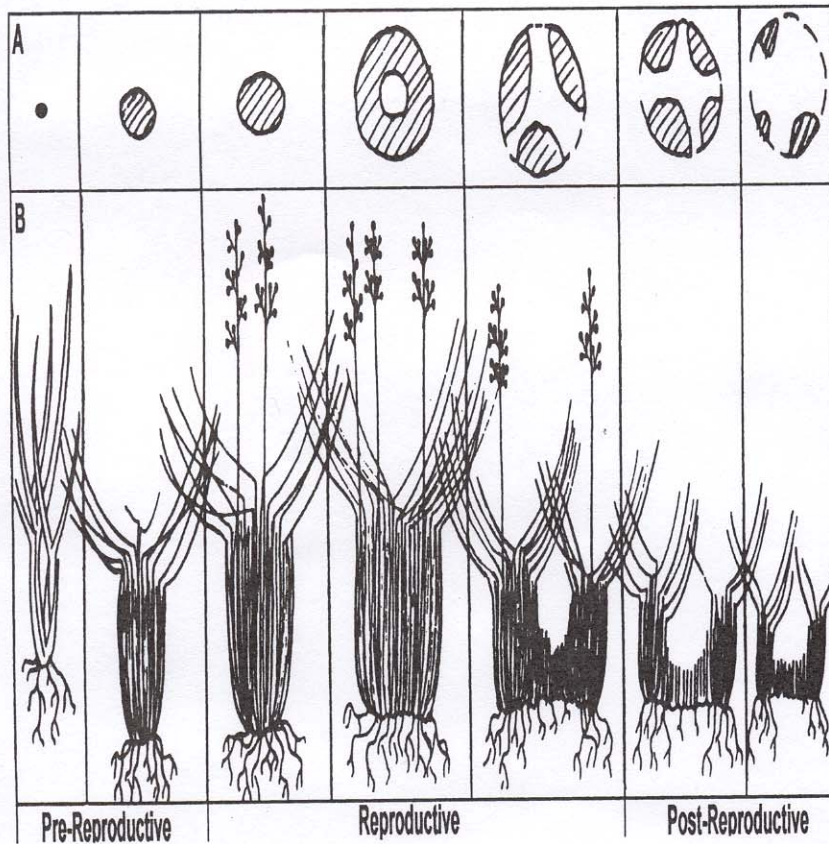
Fig. 4.2. Age estimates of the architectural development of *Deschampsia caespitosa* in northern Europe suggest that 35–60 years is required for clones to proceed from seedlings to senescence. Development of hollow crowns occurs in the reproductive stage and clonal fragmentation occurs in the post-reproductive stage. (From Gatsuk *et al.*, 1980).

35–60 years is required for clones to progress from seedlings to senescent clones (Gatsuk *et al.*, 1980; Zhukova & Ermakova, 1985) (Fig. 4.2). The pre-reproductive, reproductive, and post-reproductive stages require approximately 5–10, 15–30, and 15–25 years to complete, respectively. Clones develop hollow crowns during the reproductive stage and may fragment into as many as 20 units during the post-reproductive stage. The progression of clonal development is assumed to be both species and habitat specific (Vorontzova & Zaugolnova, 1985; Zhukova & Ermakova, 1985; Wilhalm, 1995).

Although each clone fragment is potentially free living and capable of

continued ramet recruitment, contrasting views exist concerning their fate
and contribution to population maintenance. One interpretation indicates
that clonal fragments are relatively short-lived and that caespitose grass
populations are maintained largely by reproduction from seed (Vorontzova
& Zaugolnova, 1985; Zhukova & Ermakova, 1985). However, other inves-
tigators indicate that clonal fragments have a greater longevity (Lord, 1993;
Danin & Orshan, 1995) which enables them to contribute to genet existence
and population maintenance. Clonal fragmentation is a common charac-
teristic of perennial caespitose grasses in Europe (Wilhalm, 1995). All 24
species evaluated showed evidence of fragmentation into smaller units con-
sisting of several ramets each. A greater understanding of the fate of clonal
fragments is required because it may be the most relevant level at which to
investigate the ecology of clonal plants (Cain, 1990).

Mechanisms of ramet regulation within caespitose clones

In this section we evaluate five mechanisms associated with the regulation
of ramet recruitment and/or mortality within caespitose grass clones.
These mechanisms include: (1) apical dominance, (2) resource competition,
(3) physiological integration, (4) red:far-red ratio of solar radiation, and (5)
equitable resource acquisition by ramet hierarchies within clones. Apical
dominance and resource competition have long been recognized as mech-
anisms capable of regulating juvenile ramet growth from axillary buds
while the latter three mechanisms are more contemporary. A greater under-
standing of the mechanism(s) regulating intraclonal ramet demography
would increase insight into the structure and function of individual clones,
and more clearly establish whether ramet interdependence or independence
is the prevalent mode of intraclonal function.

Apical dominance

Apical dominance describes the physiological regulation of axillary bud
growth by the apical meristem region (Phillips, 1975; Cline, 1991). The
physiological mechanism termed the direct hypothesis of auxin action was
initially proposed by Thimann & Skoog (1933) shortly following the dis-
covery of the plant hormone auxin. This mechanism indicates that auxin
(indoleacetic acid), produced in the apical meristem and young leaves,
directly inhibits axillary bud growth. Apical meristem destruction or
removal is assumed to release axillary buds from hormonal inhibition and
stimulate ramet initiation by eliminating the source of auxin (Fig. 4.3). The
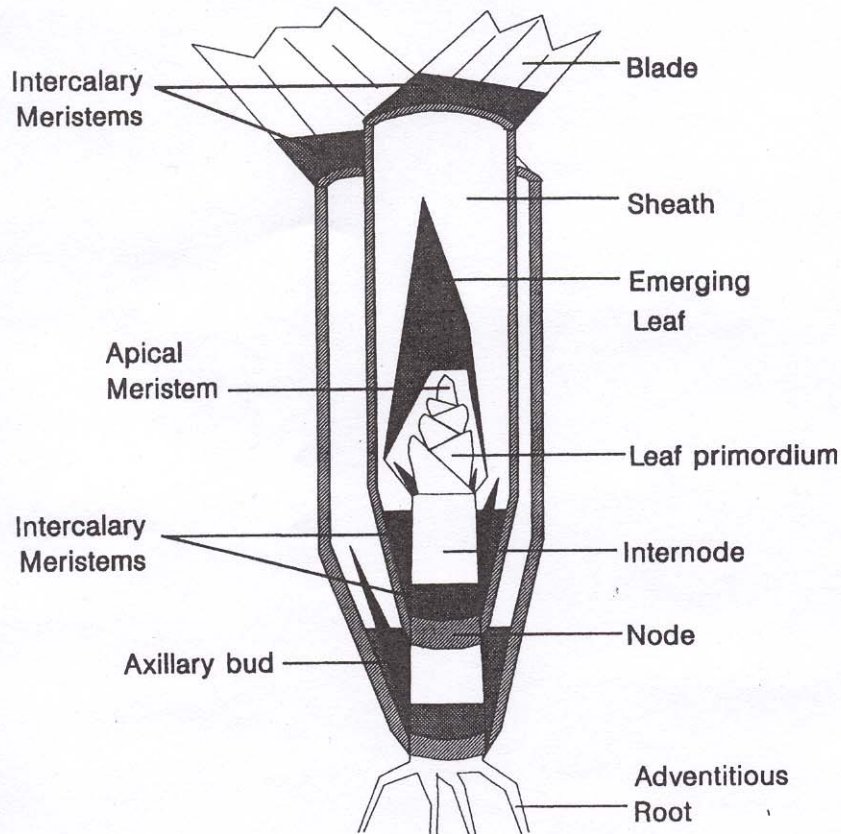
Fig. 4.3. Longitudinal view of a ramet base (crown) illustrating the apical meristem and an emerging leaf and ramet. A single axillary bud is differentiated with each phytomer from the apical meristem. (From Murphy & Briske, 1992).

direct hypothesis of auxin action continues to be a predominant interpretation of the physiological mechanism of apical dominance by grassland ecologists and resource managers (Murphy & Briske, 1992). However, the direct hypothesis was abandoned by plant physiologists during the 1950s because of experimental and interpretive inconsistencies and the demonstrated involvement of a second hormone, cytokinin. A hypothesis based on the auxin:cytokinin ratio has replaced the direct hypothesis as the current hormonally based interpretation of apical dominance (Cline, 1991; Murphy & Briske, 1992). This hypothesis indicates that auxin produced in the apical meristem region blocks the synthesis or utilization of cytokinin within axillary buds, inhibiting their growth (see Hutchings & Mogie,

1990). Despite wide acceptance, numerous issues remain unresolved concerning this hypothesis, suggesting that it may also be an incomplete interpretation of the physiological mechanism of apical dominance.

The ability of apical dominance to explain ramet recruitment in grasses is less consistent than generally recognized, regardless of the underlying physiological mechanisms. Apical meristem removal does not consistently promote ramet initiation in grasses and ramet initiation may occur in plants with intact apical meristems (Murphy & Briske, 1992). However, forage grasses adapted to mesic, fertile environments (e.g. *Lolium perenne*) frequently do increase ramet initiation in response to plant defoliation and grazing (e.g. Grant, Barthram & Torvell, 1981). The mechanism(s) associated with these contrasting responses is unknown. The large number of potentially intervening variables, including environmental conditions, species-specific responses, stage of phenological development, and frequency and intensity of defoliation, also minimizes the likelihood of consistent ramet initiation in response to defoliation. These inconsistencies indicate that the traditional concept of apical dominance is an overly restrictive interpretation of ramet regulation in perennial grasses.

Resource competition

Resource competition exerts a substantial influence on ramet recruitment in grass clones (Briske & Butler, 1989; Hartnett, 1993). Presumably competition influences resource availability and, therefore, ramet recruitment and/or mortality. Ramet recruitment is strongly influenced by both intraclonal and interclonal competition in populations of caespitose grasses (Briske & Butler, 1989; Cheplick & Salvadori, 1991). Clone size and distribution also mediate competitive interactions and influence ramet initiation and clonal expansion (Briske & Anderson, 1990). A high density of small *Schizachyrium scoparium* clones exhibited greater relative increases in ramet density and basal area expansion than did a comparable number of ramets arranged in a low density of large clones. These responses apparently were mediated through a specific regulation mechanism, as opposed to increased efficiency of resource acquisition, because annual shoot biomass production was comparable for all three combinations of clone size and ramet distribution evaluated. Greater ramet recruitment from the high density of small clones was very likely a function of the greater clonal periphery associated with a large number of small clones (Briske & Anderson, 1990). The majority of juvenile ramet recruitment occurs on the

periphery, rather than the interior, of individual clones (Olson & Richards, 1988; Briske & Butler, 1989).

Resource availability has been associated with regulation of ramet recruitment based on a correlative relationship between the rate and magnitude of ramet recruitment and resource availability. However, it is impossible to conclude from such evidence that ramet recruitment is regulated by resource availability as opposed to being one component of an overall growth increase (Murphy & Briske, 1992). Higher nutrient concentrations in axillary buds released from inhibition in comparison with their inhibited counterparts do not necessarily imply a causal relationship. Greater nutrient concentrations in growing buds may more accurately reflect the result, rather than the cause, of axillary bud growth (Rubinstein & Nagao, 1976). Consequently, it is difficult to deny the involvement of resource availability in the regulation of ramet recruitment, but it has yet to be established that ramet recruitment is specifically regulated by resource availability (Murphy & Briske, 1992).

Physiological integration

Physiological integration among ramets has been proposed to function as a mechanism capable of regulating ramet recruitment within clones (Hutchings, 1979; Pitelka, 1984; Hutchings & Bradbury, 1986). Resource integration among ramets within clones presumably provides a mechanism to: (1) equitably distribute resources among ramets, (2) minimize inter-ramet competition, and (3) optimize the efficiency of resource acquisition from the local environment (Caraco & Kelly, 1991). Although the occurrence of inter-ramet resource allocation is well documented in grasses (Pitelka & Ashmun, 1985), substantial evidence has accumulated to indicate that resource integration does not occur among all ramets within caespitose clones (Briske & Butler, 1989; de Kroon & Kwant, 1991).

Experiments conducted with three dominant grass species (*Panicum virgatum, Schizachyrium scoparium* and *Bouteloua gracilis*) along an east–west environmental gradient in the North American Great Plains demonstrate that physiological integration is confined to individual ramet hierarchies, rather than throughout all ramets within clones (Derner & Briske, 1998). A vast majority of the stable isotope of nitrogen (^{15}N) introduced into individual parental ramets remained within the labelled ramet hierarchies, rather than being allocated to associated ramet hierarchies within the clone. These findings confirm that intraclonal integration is not complete and support previous hypotheses drawn from ^{15}N experiments with
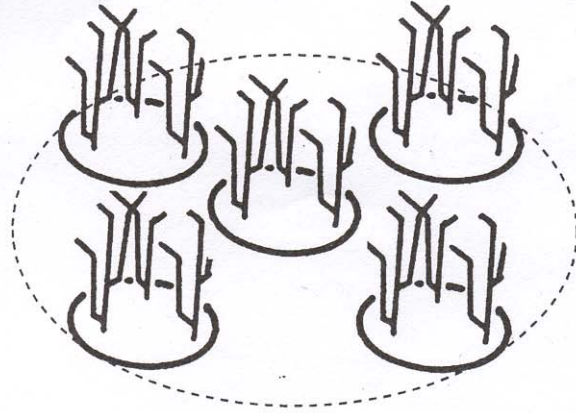
Fig. 4.4. Clones of temperate, caespitose grasses are organized as assemblages of autonomous ramet hierarchies, rather than as a sequence of completely integrated ramets. The benefits of physiological integration are restricted to individual ramet hierarchies (solid circles), which consist of approximately three connected ramet generations, while interhierarchical competition occurs for soil resources accumulated directly beneath the basal area of individual clones (dashed circle).

containerized *S. scoparium* clones and experiments severing vascular connections among ramets within established clones in the field (Welker *et al.*, 1987, 1991; Williams & Briske, 1991).

Partial resource integration can be explained on the basis of the developmental architecture of caespitose clones. Most investigations of inter-ramet resource allocation in grasses have been conducted with young plants established from seed (e.g. Pitelka & Ashmun, 1985). The potential for complete resource integration exists in young plants because all ramets possess vascular connections with the seminal ramet produced from the embryo. This provides complete vascular continuity throughout the entire clone. However, the seminal ramet dies during the second or third growing season, disrupting complete vascular continuity within older clones (Briske & Butler, 1989). Annual grasses are anticipated to maintain complete vascular continuity because longevity of the seminal ramet equals that of the clone.

Resource allocation among only those ramets within individual ramet hierarchies indicates that ramet hierarchies function autonomously within clones, rather than as a sequence of completely integrated ramets (Fig. 4.4). Consequently, the benefits of physiological integration are restricted to these connected generations. Therefore, ramet hierarchies comprise the physiologically integrated individual in this growth form (*sensu* Watson &

Casper, 1984). Low levels of resource allocation observed between ramet hierarchies may result from the occurrence of mycorrhizal connections among root systems of ramet hierarchies (Newman, 1988; Fischer Walter *et al.*, 1996). Documentation of partial clonal integration within caespitose grasses requires that an alternative mechanism of intraclonal ramet regulation be identified and investigated.

Equitable resource acquisition among ramet hierarchies

Competitive interactions among ramet hierarchies within clones, rather than physiological integration among them, may potentially regulate ramet recruitment and density. A broadly distributed root system associated with each ramet hierarchy may potentially enable all ramet hierarchies to access resources equitably from small patches within the immediate vicinity of individual clones. Therefore, a small-scale resource limitation or pulse would equitably constrain or promote growth of all ramet hierarchies within a clone, rather than only the hierarchies nearest the resource patch. Consequently, equitable resource acquisition among ramet hierarchies may minimize intraclonal competition, promote ramet interdependence, and enhance growth efficiency of individual clones.

Experiments conducted with three dominant grass species along an east–west environmental gradient in the North American Great Plains documented that ramet hierarchies within individual clones did not exhibit equitable resource acquisition. Placement of ^{15}N in the soil at three locations peripheral to clones demonstrated that ramets in closer proximity to the nitrogen pulse exhibited significantly greater nitrogen acquisition than did those further away from the nitrogen pulse (Derner & Briske, 1998). Vascular connections within clones were severed perpendicular to the location of the ^{15}N pulse to ensure that ramets acquired ^{15}N by root absorption, rather than by physiological integration from associated hierarchies. Inequitable resource acquisition among ramet hierarchies demonstrates that hierarchies are independent and that intense competition potentially occurs among hierarchies within clones. Therefore, equitable resource acquisition is not a viable mechanism of intraclonal ramet regulation.

Red:far-red radiation ratio

Perception of an environmental signal, rather than resource availability or acquisition, may regulate intraclonal ramet recruitment and density.

Depressions in the red:far-red ratio (R:FR; 660 ± 5 nm:730 ± 5 nm) of solar radiation from values typical of sunlight have been proposed as a potential mechanism capable of regulating ramet initiation within perennial grasses (Deregibus *et al.*, 1985; Casal, Deregibus & Sanchez, 1985). A suppression of ramet initiation in response to the R:FR ratio was first demonstrated with seedlings of *Lolium perenne* and *L. multiflorum* in a controlled environment (Deregibus, Sanchez & Casal, 1983) and *Paspalum dilatatum* plants in the field (Deregibus *et al.*, 1985). However, in spite of the rapidly growing acceptance of the R:FR hypothesis (Casal *et al.*, 1985, 1987*a,b*; Casal, 1988; Skinner & Simmons, 1993), additional understanding of three important processes is required to determine accurately the ecological significance of the R:FR as an environmental signal capable of regulating ramet initiation and growth in caespitose grasses.

First, experiments designed to demonstrate the direct regulation of ramet initiation by the R:FR signal under field conditions have not produced consistent results. An increase in the R:FR beneath canopies of *P. dilatatum* increased ramet initiation by three times compared with control plants at the end of the growing season (Deregibus *et al.*, 1985). However, *Sporobolus indicus* plants in the same investigation were less responsive to supplemental red radiation. Similarly, a reduction in the R:FR at the bases of three morphologically distinct *Festuca rubra* ecotypes reduced ramet initiation in only two of the ecotypes during a six-month experiment (Skálová & Krahulec, 1992). A field experiment conducted with clones of *S. scoparium* demonstrated that irradiation with either red or far-red radiation at the clone bases throughout the photoperiod for 12 consecutive weeks did not significantly affect ramet initiation from existing buds on parental ramets (Murphy & Briske, 1994). The unresponsiveness of mature *S. scoparium* clones in the field is even more intriguing given that seedlings of this species produced the anticipated responses of increased leaf elongation and reduced ramet initiation following irradiation with end-of-day far-red radiation (J. S. Murphy & D. D. Briske, unpubl. manu.).

Second, the sites and locations of R:FR photoperception remain controversial and have very likely been misidentified as the axillary buds and/or sheaths at the ramet base (Casal *et al.*, 1985, 1987*a*; Deregibus *et al.*, 1985), rather than immature leaf blades located within the canopy (Skinner & Simmons, 1993). It is difficult to envisage how either sheaths or buds could efficiently function as sites of R:FR signal perception because (1) these organs are largely shielded from the ambient radiation environment by encircling older leaves (Dale, 1988) and (2) the axillary bud subtending each leaf does not develop into a new ramet until that leaf has ceased expansion

(Skinner & Nelson, 1994). If emerging leaf blades function as the predominant site of photoperception, it potentially minimizes the ecological significance of the R:FR as a density-dependent signal because the site of photoperception and low R:FR would spatially coincide only in young juvenile ramets and seedlings beneath clone canopies (Murphy & Briske, 1994).

Third, the mechanism by which low R:FR suppresses ramet initiation has not been clearly established. Although low R:FR suppression of ramet initiation has been demonstrated to occur without a reduction in the rate of leaf appearance (Casal, 1988; Skinner & Simmons, 1993), and therefore, axillary bud availability, an alternative mechanism of ramet suppression has not been identified. A plausible explanation of bud suppression following exposure to low R:FR is the temporary diversion of carbon (e.g. Yanovsky *et al.*, 1995) from axillary buds to support enhanced leaf development. Ramet suppression in response to low R:FR may be restricted to the early stages of seedling and ramet growth when competition between leaves and buds for a limited carbon supply is sufficient to affect juvenile ramet growth (J. S. Murphy & D. D. Briske, unpubl. manu.). Therefore, ramet suppression in response to low R:FR may not be a pervasive mechanism exclusively regulating axillary bud growth throughout the life of a ramet.

Summary of potential regulation mechanisms

An evaluation of the intraclonal mechanisms potentially capable of regulating ramet demography reveals that little is known about their mode of operation or relative contribution. The direct hypothesis of apical dominance is outdated from a physiological perspective and the response of ramet recruitment to apical meristem removal is less consistent than generally recognized. Physiological integration is restricted to individual ramet hierarchies and, therefore, incapable of regulating ramet recruitment within entire clones. Autonomous ramet hierarchies are not capable of equitably sampling resources, indicating that this process does not mediate interhierarchy competition to regulate ramet densities within clones. Additional information is required to define the mechanisms and ecological significance of the red:far-red ratio of solar radiation on ramet demography. Competition appears to exert the greatest influence on ramet populations, but it is uncertain whether competition exerts disproportionate effects on ramet recruitment relative to the overall influence on clonal growth.

The search for a sole physiological (e.g. apical dominance) or ecological

(e.g. red:far-red ratio) mechanism of intraclonal ramet regulation may have limited progress towards understanding the regulation of ramet demography within grasses. Regulation of this important demographic process by a single mechanism would potentially constrain morphological plasticity within the wide range of habitats occupied by the caespitose growth form. Alternatively, intraclonal ramet regulation may be a multivariable process regulated by several interacting physiological and environmental variables. However, a multivariable model has received minimal research emphasis (Phillips, 1975; Murphy & Briske, 1992). In addition, the ramet hierarchy, rather than the entire clone, may be a more appropriate scale at which to investigate intraclonal ramet regulation.

Evaluation of intraclonal ramet competition

Inter-ramet competition may occur, both aboveground and belowground, at each of the following hierarchical locations: (1) within individual hierarchies, (2) among hierarchies within a clone, (3) among hierarchies within intraspecific, and (4) interspecific clones (Harper, 1985; Briske & Butler, 1989). Although the relative contributions of inter-ramet, intraclonal, and interclonal competition to clonal structure and function have not been established, the relative intensities of intraclonal and interclonal competition have been demonstrated to be comparable in several caespitose grasses (Briske & Butler, 1989; Kelley, 1989; Cheplick & Salvadori, 1991). Comparable competitive intensities within, compared with between, clones suggest that potentially intense competitive interactions may occur among autonomous ramet hierarchies within clones.

Intense competitive interactions among ramet hierarchies are established by the absence of physiological integration and non-equitable acquisition of soil resources among these genetically identical structures (Derner & Briske, 1998). However, negative competitive interactions among ramet hierarchies may increase the competitive ability of individual clones by the development of a resource depletion zone (Harper, 1985), which is consistent with the phalanx strategy of clonal plant growth (Lovett Doust, 1981). In contrast, interactions among ramets within individual hierarchies are assumed to be positive, rather than negative (Table 4.1). The benefits of physiological integration within autonomous ramet hierarchies appear to exceed the detrimental effects of competition among these connected ramet generations.

Mechanisms of competitive interactions among hierarchical levels of clonal structure are also unclear. It is uncertain whether competition

Table 4.1. *A generalized comparison between intrahierarchical and interhierarchical ramet interactions in caespitose grass clones*

Ramet interactions within hierarchies are assumed to convey a net positive effect to individual ramets, while interactions among ramet hierarchies are assumed to convey a net negative effect to individual ramets.

Attribute	Intrahierarchical ramet interactions	Interhierarchical ramet interactions	References
Response	Positive	Negative	See citations below
Physical structure	Several connected ramet generations, defines the ramet hierarchy	Several autonomous ramet hierarchies, defines the clone	Welker *et al.*, 1991 Williams & Briske, 1991 Wilhalm, 1995
Physiological integration	Present	Absent	Pitelka & Ashmun, 1985 Welker *et al.*, 1987, 1991 Derner & Briske, 1998
Resource acquisition	Allocation from older to younger ramet generations	Non-equitable among intraclonal hierarchies	Pitelka & Ashmun, 1985 Welker *et al.*, 1991 Derner & Briske, 1998
Consequence	Enhanced juvenile ramet growth and reproduction	Comparable competitive intensities within and between conspecific clones	Briske & Butler, 1989 Kelley, 1989 Cheplick & Salvadori, 1991

among ramets within clonal plants is symmetric and contributes to size equalization among ramets (Hutchings & Barkham, 1976; Ekstam, 1995) or whether it is asymmetric and contributes to size inequalities among ramets (de Kroon, Hara & Kwant, 1992). Asymmetric competition for light is assumed to be most common at high plant densities where a potential shift may occur from self-shading to neighbour shading (Schwinning, 1996). Leaf area indices as high as 3.4 have been documented in caespitose grasses which result in substantial self-shading (Caldwell *et al.*, 1983; Ryel *et al.*, 1993; 1994). Inequitable patterns of resource acquisition below-ground also establish the potential for asymmetric competition within caespitose clones (Schwinning, 1996). It has been hypothesized that asymmetric competition among ramets within clones may produce symmetric competition among clones because conspecific clones possess comparable competitive abilities and they possess a limited ability to overtop and shade one another (de Kroon *et al.*, 1992). Additional insight into the relative magnitude and consequences of hierarchical competitive interactions may yield a greater understanding of demographic regulation and spatial organization of ramets within caespitose clones and the ecological success of this widely distributed group of clonal plants.

Interactions among autonomous units within clonal plants have also been evaluated in a cooperative, rather than a competitive, manner. Support for this interpretation is based on the assumption that antagonistic relationships are less stable than mutualistic ones (Hardwick, 1986) and that intraclonal competitive interactions represent a mechanism to optimize internal resource allocation (Sachs, Novoplansky & Cohen, 1993). The perspective of cooperative interaction among ramets within clones shifts emphasis from the advantages of interdependence to the advantages of independence (Kelly, 1995). However, the arguments proposed to justify ramet, and in this case ramet hierarchy, independence in clonal plants do not appear entirely applicable to caespitose grass clones. Production and maintenance costs of vascular connections are minimal in comparison with those of strongly rhizomatous species, and the possibility of traumatic breakage appears limited within clones characterized by relatively small basal areas (<1000 cm^2). However, the risk of disease and pathogen injury may be minimized by the absence of complete clonal integration in caespitose clones (e.g. Cook, 1985; Kelly, 1995). Benefits associated with optimal resource allocation are also minimized because each ramet produces its own root system and is capable of resource acquisition to support the shoot system (Sachs *et al.*, 1993). Yet, independence among ramet hierarchies appears to be a natural consequence of the developmental architecture of

caespitose clones, indicating that the majority of caespitose grasses exist as fragments, rather than entirely integrated clones (e.g. Wilhalm, 1995).

Organization of caespitose grass clones as assemblages of autonomous ramet hierarchies establishes the potential for 'group modulated selection' (Tuomi & Vuorisalo, 1989; Cheplick, 1993) in this growth form. This represents a unique type of group selection in which the semi-autonomy of ramets, or ramet hierarchies in this case, determines that they are appropriate interactive units for selection in addition to that of the entire clone. Consequently, 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 selection in unitary plants. The second process operates at the level of the clone to modify ramet reproduction. This suggests that selection in caespitose clones may potentially be a product of ramet births, deaths, and reproductive output mediated by the clone. Greater insight into the mechanism(s) of clone–ramet interaction is required to effectively evaluate this concept.

Consolidator strategy

The most plausible interpretation of the ecological success of the caespitose growth form has been attributed to effective resource monopolization within the immediate environment of clones. This strategy of clonal plant growth is described as the consolidator strategy and is characterized by the following attributes: (1) the capacity for resource storage within clones, (2) density-dependent patterns of ramet recruitment and mortality, (3) limited architectural plasticity based on the absence of rhizomes and stolons, (4) a high degree of physiological integration among ramets, and (5) competitive superiority (de Kroon & Schieving, 1990). However, two of these attributes, extensive physiological integration and substantial carbon and nitrogen storage capacity, are not entirely applicable to caespitose grasses. The absence of rhizomes very likely limits storage capacity for labile carbon and nitrogen within caespitose clones (e.g. Grace, 1993), but direct comparisons have not been conducted. An alternative location for resource storage may be in soils beneath clones, rather than within clones. Greater pools of soil organic carbon (SOC) and total nitrogen (N) beneath compared with between *S. scoparium* clones in tallgrass and midgrass communities, and beneath compared with between *B. gracilis* clones in a shortgrass community verify that these two caespitose species accumulate nutrients in soils beneath clones as opposed to entirely within clones (Derner, Briske & Boutton, 1997). Nutrient accumulation is restricted vertically to the upper

portion of the soil (0–5 cm) and horizontally within the basal area occupied by clones (Fig. 4.5). Greater pools of SOC and N in soils beneath, compared with between, caespitose clones have been documented in mesic and semi-arid environments (Hook, Burke & Lauenroth, 1991; Jackson & Caldwell, 1993; Rice *et al.*, 1994; Vinton & Burke, 1995).

Accumulation of SOC and N in soils beneath caespitose clones potentially conveys two distinct advantages to this growth form that further supports the existence of the consolidator strategy. First, larger pools of SOC and N in soils beneath clones may provide a mechanism for resource monopolization and maintenance of competitive dominance in grasslands and savannas. Resource monopolization may result from nutrient immobilization in litter and root detritus within close proximity to clones, thereby limiting availability to associated vegetation (Wedin & Tilman 1993; Berendse, 1994; Wedin, 1995). Second, accumulation of SOC and N beneath clones may provide an alternative mechanism for density-dependent ramet regulation by increasing nutrient availability within the immediate vicinity of clones. However, ramet recruitment and shoot biomass of *S. scoparium* clones exhibited proportional increases to a threefold increase in available soil N, imposed by augmenting soil volumes available to established clones in the field (J. D. Derner & D. D. Briske, unpubl. manu.). Proportional increases in ramet recruitment with increasing N availability indicates that ramet recruitment is an important component of morphological plasticity and that N accumulation beneath clones affects growth, but does not necessarily function as a mechanism of ramet regulation. Consequently, resource accumulation beneath clones may be more important as a mechanism of resource monopolization to reduce competition from associated vegetation than as a mechanism of increased nutrient availability and intraclonal ramet regulation.

Ecological implications

Greater pools of SOC and N within the 0–5 cm soil depth beneath caespitose clones of *S. scoparium*, but not beneath rhizomatous clones of *P. virgatum*, within a tallgrass community, suggest that the consolidator strategy may be comprised of two functional categories. The absence of increased pools of either SOC or N at any soil depth beneath, compared with between, *P. virgatum* clones may be a consequence of its clonal architecture. This species possesses a large amount of shoot biomass belowground in the form of short rhizomes that are long-lived and known to function as sites of carbon and nitrogen storage (Hartnett, 1989, 1993).
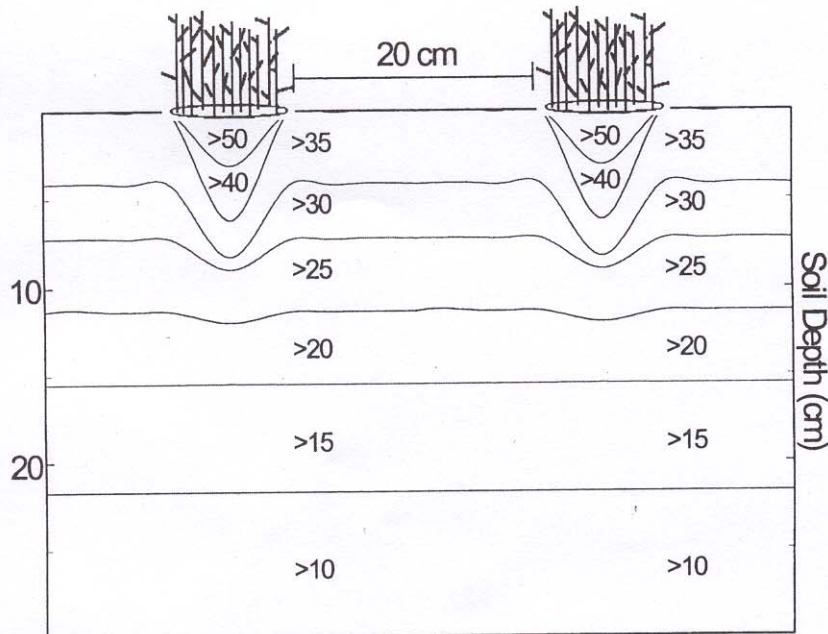
Fig. 4.5. Mean concentrations ($n=10$) of soil organic carbon (g kg^{-1}) within soils beneath and between a pair of *Schizachyrium scoparium* clones in a long-term ungrazed grassland community near Hays, Kansas. Soil cores were collected from three locations: directly beneath each clone, the interstitial centre, and near the periphery of each clone. Soil cores were separated into three depths: 0–5, 5–15 and 15–30 cm. Logistic regression equations were developed to determine the pattern of soil organic carbon accumulation beneath clones.

Caespitose consolidator strategists may partially rely on nutrient accumulation in soils beneath clones to maintain competitive dominance, whereas rhizomatous consolidator strategists may store nutrients within rhizomes, rather than soils. Both plant categories may effectively accumulate and utilize nutrients to support early season growth (Bobbink, den Dubbelden & Willems, 1989) and minimize aboveground nitrogen losses by herbivory, fire, and volatilization during periods of limited water availability (Heckathorn & DeLucia, 1994). However, direct comparisons of nutrient storage pools between rhizomatous and caespitose grasses have not been conducted.

Nutrient accumulation in soils beneath caespitose clones may function as a passive alternative to a more active foraging strategy based on the assumption that the benefits of exploratory search for resources do not outweigh associated costs of rhizome and/or stolon construction and

maintenance (e.g. Hutchings & de Kroon, 1994; de Kroon & Hutchings, 1995). Nutrient accumulation beneath caespitose clones may have minimized selection for an active foraging strategy associated with the development of rhizomes and/or stolons. The costs associated with ramet placement beyond the immediate vicinity of individual clones may exceed the potential benefits in this growth form. These costs would be expected to increase with continued site occupation because patch 'worth' beneath clones increases through time (e.g. Burke, Lauenroth & Coffin, 1995; Derner *et al.*, 1997). Physiological plasticity, including root proliferation (Robinson, 1996) and increased absorption kinetics (Crick & Grime, 1987; Jackson & Caldwell, 1989, 1992), is anticipated to be more important than morphological plasticity for effectively accessing nutrients in association with the consolidator strategy (e.g. Crick & Grime, 1987; Campbell & Grime, 1989; Jonasson & Chapin, 1991). Physiological plasticity may be more cost effective than morphological plasticity based on greater construction and maintenance costs associated with rhizome and/or stolon development.

While caespitose clones can occupy a broad range of seral positions in grasslands and savannas, they frequently comprise the dominant late-seral species (e.g. Lovett Doust & Lovett Doust, 1982). Do caespitose grasses attain dominance in these systems because they are characterized by minimal disturbances (de Kroon & van Groenendael, 1990) and/or because the risks of clone mortality are highly predictable (Hutchings and Bradbury, 1986)? This interpretation is based on the assumption that clones composed of highly aggregated ramets may be killed by a single lethal event (Cook, 1979; Schmid, 1990). However, no clear patterns emerge to correlate the distribution of caespitose grasses with disturbance regimes, climatic patterns or edaphic variables in grasslands and savannas. It is plausible, however, that caespitose grasses exhibit greater abundance in less productive habitats compared with rhizomatous species (e.g. Pugnaire & Haase, 1996). Resource accumulation in soils beneath clones may convey a more cost-effective mechanism of resource foraging than resource accumulation in rhizomes as resource availability decreases. Alternatively, rhizomatous grasses may dominate more productive habitats where the benefits of rhizome production outweigh the associated construction costs to optimize clonal fitness. In an east–west gradient across the Great Plains of North America, for example, caespitose grasses (*Bouteloua, Stipa* and *Schizachyrium*) express greater dominance than do rhizomatous species (*Andropogon, Panicum* and *Sorghastrum*) in the more xeric portions of the gradient (Sims, Singh & Lauenroth, 1978). If this distributional pattern

were verified in this and other regions, it would substantiate that resource accumulation in soils beneath individual clones is an important mechanism conferring ecological success to caespitose grasses.

Managerial implications

Degradation of late-seral caespitose grass populations in response to intensive long-term herbivory is well documented (Briske & Richards, 1995). Degradation is characterized by a reduction in mean basal area per clone and an increase in clone density very likely resulting from the fragmentation of individual large clones (Butler & Briske, 1988). Herbivore-induced population degradation may potentially be mediated by the reduction of SOC and N accumulation in soils beneath individual clones. Long-term intensive herbivory may reduce nutrient pools beneath clones by limiting availability of photosynthetic and/or meristematic tissues necessary for growth, and may thereby decrease organic matter input into soils in the immediate vicinity of clones (e.g. Berendse, Elberse & Geerts, 1992). A reduction in SOC and N pools beneath clones may potentially limit their ability to monopolize resources in the form of low-quality litter and maintain their competitive dominance. However, a reduction in SOC and N pools beneath clones following intensive herbivory would require decades based on the time required for organic matter turnover in temperate regions (Schimel *et al.*, 1994). Therefore, herbivore-induced population degradation of caespitose grasses must initially be mediated by the suppression of plant function because population structure of caespitose grasses can be modified by intensive herbivory within several years (Butler & Briske, 1988).

Herbivore-induced reductions of SOC and N in soils beneath clones may also have important implications for the restoration of severely degraded populations of caespitose grasses. Slow and incomplete recovery of degraded caespitose grass populations (e.g. Dyksterhuis, 1946; Riegel *et al.*, 1963) may be a consequence of the reduction in SOC and N pools beneath individual clones which minimizes clone function and competitive ability. Carbon addition to soil for purposes of N immobilization may be required to shift the competitive advantage from opportunistic mid-seral species, which often dominate grasslands following degradation, back to consolidator strategists. For example, N fertilization effectively negated the ability of the dominant caespitose grass, *S. scoparium,* to immobilize N in litter and root detritus and placed it at a competitive disadvantage with associated mid-seral perennial grasses within several years (Tilman & Wedin, 1991; Wedin, 1995). Increased N immobilization has been associated with

the progression of succession in several communities (McLendon & Redente, 1992).

Summary

Although mechanisms of intraclonal ramet regulation have received more research emphasis than mechanisms conferring ecological success to caespitose grasses, a functional interpretation of intraclonal demographic regulation has not yet been developed. The search for a single regulatory mechanism, as opposed to a multivariable approach, may have retarded development of an unified ecological interpretation for this important demographic process. Organization of caespitose clones as assemblages of autonomous ramet hierarchies suggests that the ramet hierarchy may be the appropriate level at which to investigate potential mechanisms of intraclonal ramet regulation. Interactions among ramets within individual hierarchies are assumed to convey a positive growth response because the benefits of physiological integration appear to exceed the detrimental effects of competition among connected ramet generations. In contrast, the absence of physiological integration, and the inability of genetically identical ramet hierarchies to acquire soil resources equitably, potentially produces intense intraclonal competition.

The ability of caespitose clones to monopolize resources through accumulation of soil organic carbon and total nitrogen directly beneath clones represents the most plausible mechanism for the ecological success of this growth form. Additional research is required to identify the environmental constraints and trade-offs associated with this mode of resource monopolization relative to a more active foraging strategy characteristic of rhizomatous and stoloniferous grasses. Recognition that caespitose grasses are composed of autonomous ramet hierarchies suggests that future advances in clonal biology of caespitose grasses will result from investigation of intraspecific and interspecific interactions among ramet hierarchies and their potential contributions to clone, genet and population maintenance.

Acknowledgements

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