Nordic Society Oikos

Clonal Biology of the Temperate, Caespitose, Graminoid Schizachyrium scoparium: A Synthesis with Reference to Climate Change
Author(s): J. M. Welker and D. D. Briske
Source: *Oikos*, Vol. 63, No. 3 (Apr., 1992), pp. 357-365
Published by: Blackwell Publishing on behalf of Nordic Society Oikos
Stable URL: http://www.jstor.org/stable/3544961
Accessed: 25/11/2008 17:18

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at http://www.jstor.org/page/info/about/policies/terms.jsp. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at http://www.jstor.org/action/showPublisher?publisherCode=black.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit organization founded in 1995 to build trusted digital archives for scholarship. We work with the scholarly community to preserve their work and the materials they rely upon, and to build a common research platform that promotes the discovery and use of these resources. For more information about JSTOR, please contact support@jstor.org.

Blackwell Publishing and *Nordic Society Oikos* are collaborating with JSTOR to digitize, preserve and extend access to *Oikos.*

http://www.jstor.org

OIKOS 63: 357–365. Copenhagen

Clonal biology of the temperate, caespitose, graminoid Schizachyrium scoparium: a synthesis with reference to climate change

J. M. Welker and D. D. Briske

Welker, J. M. and Briske, D. D. 1992. Clonal biology of the temperate, caespitose, graminoid *Schizachyrium scoparium:* a synthesis with reference to climate change. – Oikos 63: 357–365.

Caespitose graminoids are characterized by the compact spatial arrangement of ramets within clones and the absence of rhizomes or stolons. Resource allocation is principally acropetal with established ramets supporting juvenile ramets during early development. However, after juvenile ramet maturation a responsive resource transfer system is maintained by a low level of continuous resource allocation between parental and juvenile ramets. Isotopic and severing experiments demonstrated that physiological integration in the caespitose graminoid *Schizachyrium scoparium* is restricted to individual ramet sequences consisting of three connected ramet generations as opposed to all ramets within the clone. This number of ramet generations comprising the physiological individual is determined by demographic variables influencing the recruitment and longevity of individual ramets. Restricted resource allocation among ramet sequences within clones is primarily caused by the disintegration of vascular connections among ramet sequences following death of the seminal ramet. The survival value conferred by a clonal architecture composed of an assemblage of autonomous physiological individuals growing within close proximity requires further evaluation but may center on intra-plant competitive interactions.

The response of this large sub-group of clonal plants to climate change will significantly impact community structure and function because of their diversity and dominance in numerous biomes. The impact of climate change on the caespitose graminoid growth form is difficult to anticipate because: 1) caespitose graminoids consist of both C_3 and C_4 species which will complicate the response of the growth form, 2) our understanding about the clonal biology and population ecology of this growth form is still evolving and 3) the modular construction of this growth form may result in variable responses at the ramet, clone and population levels of organization.

J. M. Welker, Inst. of Terrestrial Ecology, Merlewood Research Station, Grange-over-Sands, Cumbria LA11 6JU, England. – D. D. Briske, Dept of Rangeland Ecology and Management, Texas A&M Univ., College Station, TX 77843, USA.

The environmental impacts associated with changes in atmospheric composition continue to be of major concern to ecologists, social scientists and policy makers (Schneider 1989, Houghton et al. 1990, Welker et al. 1991a). Increasing concentrations of trace gases along with associated changes in temperature and precipitation will most likely alter the structure and function of terrestrial ecosystems (Melillo et al. 1990). However, even though plant taxa are assumed to respond individualistically to the changing climate, clonal plant responsiveness may have significant impacts on community structure and function because of their diversity and dominance in numerous biomes (Cook 1983, Bradshaw and McNeilly 1991, Huntley 1991).

Graminoids comprise one of the largest sub-groups of clonal plants among terrestrial angiosperms and are

Accepted 3 December 1991

characterized by a modular construction arising from the successive iteration of phytomers (White 1979, Tiffney and Niklas 1985, Briske 1991). Caespitose graminoids can be distinguished by the compact spatial arrangement of ramets within individual clones established by the emergence of juvenile ramets within the subtending leaf blades and sheaths of parental ramets. The capacity for inter-ramet resource allocation is established early in ramet development as vascular traces of successive leaf primordia join the vasculature of the parental axis at the nodes (Hitch and Sharman 1968, Bell 1976).

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). The growth form is particularly dominant in the grassland biome which occupies 24 million km^2 including tropical and temperate grasslands, savannas and shrub steppe (Leith 1978). The grassland biome has been projected to increase in response to a doubling of atmospheric CO_2 concentration by encroaching on substantial portions of the boreal forest and tundra biomes (Emanuel et al. 1985). Even though these projections do not consider the associated effects of modified precipitation patterns (e. g. Manabe and Wetherald 1987) and predictions of CO_2-induced temperature vary substantially (e. g. Schneider 1989), they do emphasize the potential for large shifts in graminoid distribution, especially in mid- and high latitudes. This paper summarizes current knowledge of the clonal biology of the temperate, caespitose, graminoid growth form and develop general inferences concerning the potential impacts of climate change on this growth form.

Materials and methods

Research results are based on experimentation with two model species; *Schizachyrium scoparium* var. *frequens* Hubb. and *Paspalum plicatulum* Michx. *S. scoparium* is distributed throughout the eastern two-thirds of the U.S. while *P. plicatulum* only occurs in the southeast U.S., but is also distributed throughout Central and South America (Gould 1975). Patterns and magnitudes of intraclonal resource allocation were investigated with both radioactive and stable isotopes (Welker et al. 1985, Welker et al. 1987, Welker et al. 1991b). Carbon allocation was investigated by labelling with the short-lived isotope $^{11}CO_2$ at the Duke University Phytotron (Magnuson et al. 1982, Welker et al. 1985). This technique provides the capacity for continuous carbon monitoring in real time within intact plants. Plants were grown under controlled conditions at the Duke Phytotron for up to six months under well watered conditions by which time individual clones of *Schizachyrium scoparium* and *Paspalum plicatulum* consisted of a primary ramet with a series of secondary juvenile ramets. The upper most fully developed leaf of the primary ramet was placed in a water cooled photosynthetic cuvette and continuously generated $^{11}CO_2$ was pumped through a gas impervious line from the nearby Van DeGraff nuclear accelerator to the plant growth cabinent and into the leaf cuvette (Welker et al. 1985). Selective defoliation or shading was initiated following the attainment of a steady state isotopic equilibrium in plants. A steady state condition is equal to the carbon-11 activity in plant organs when the rate of isotope import from the labelled leaf is equal to the radioactive decay in the importing organ. This condition provides an absolute reference for interpretation of carbon allocation patterns and allocation responses after defoliation and shading.

Nitrogen allocation was investigated by labelling with the stable isotope ^{15}N (Bremner 1965, Welker et al. 1987, Welker et al. 1991b). Roots or leaves of specific ramet generations were immersed in a ^{15}N solution (24 mM 99% ^{15}N excess as NH_4SO_4) for an 11-h photoperiod. Roots and shoots of specific ramet generations and ramet sequences (several connected ramet generations originating from a common parent) were harvested at 24, 72 and 120 h following labelling and percentage ^{15}N excess was determined by mass spectrometry (Bremner 1965). Nitrogen allocation is presented as the relative distribution of ^{15}N mass which represents the ratio of ^{15}N mass within a specific organ and the total ^{15}N mass within either the labelled ramet sequence or clone. The amount of total nitrogen allocated between the roots and shoots of various ramets within a sequence was estimated by multiplying the total mg of nitrogen (^{14}N + ^{15}N) within a specific organ by the relative distribution of ^{15}N allocated from a donor ramet to a receptor ramet at 120 h following labelling.

The ecological significance of physiological integration was investigated in both 16-wk-old clones grown in a controlled environment and established clones in the field, by severing vascular connections between ramets as an alternative approach to isotopic labelling (Williams and Briske 1991). Vascular connections between specific ramet generations were severed to create a series of potential physiological individuals (number of connected ramet generations functioning as an autonomous unit i.e., Watson and Casper 1984) consisting of one, two or three ramet generations. Shoot and root growth and demographic variables of juvenile ramets were monitored at regular intervals to evaluate the ecological significance of physiological integration within the variously sized ramet sequences relative to comparable ramet generations within intact clones.

Ramet demography was investigated in established clones in the field to determine patterns of ramet recruitment, phenological development and survivorship (Briske and Butler 1989). In addition, the relative contributions of interclonal and intraclonal interference to the regulation of ramet populations were independently investigated following the removal of neighbouring clones and thinning of ramets with clones,

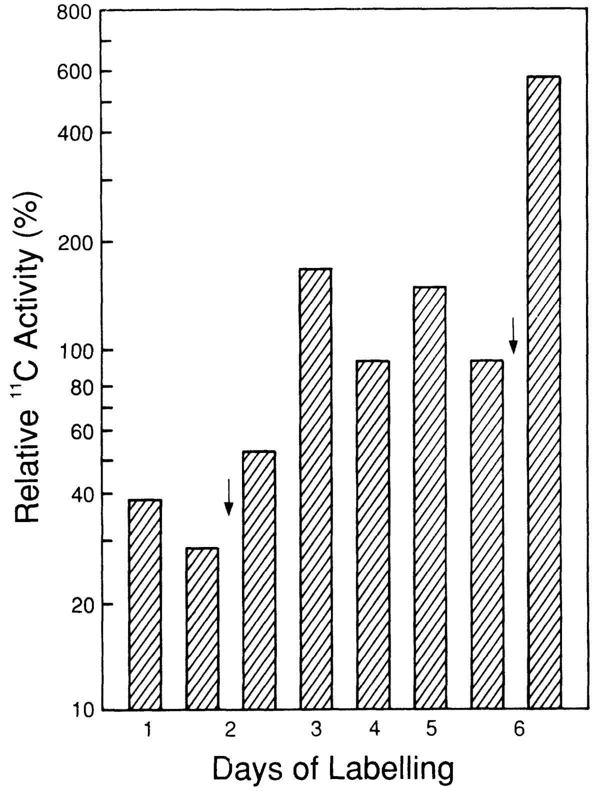

Fig. 1. Carbon-11 activity in a juvenile ramet of *Schizachyrium scoparium* relative to the ^{11}C activity of the labelled parental ramet during a 6 d period. Each bar represents the mean ^{11}C activity during a 360 min labelling period. The juvenile ramet was initially defoliated on day 2 and again on day 6 as indicated by the arrows. Labelling was conducted in both the morning and afternoon before and following defoliation on days 2 and 6. Activities greater than 100% indicate that the ^{11}C activity of the juvenile ramet is greater than that of the labelled parental ramet due to carbon accumulation.

respectively. Ten ramets, five in the interior and five on the periphery of each clone, were marked and monitored for two growing seasons to document patterns of ramet demography.

Results

Interdependence of juvenile ramets

Carbon was continuously transported from parental ramets labelled with $^{11}CO_2$ to all connected juvenile ramets of both *S. scoparium* and *P. plicatulum* at a stage of ramet development when carbon independence was anticipated (Welker et al. 1985). Juvenile ramets possessed a minimum of two adventitious roots, four leaves and ranged from 16–31 cm in height. Carbon-11 activity was generally greatest in the most ontogenetically advanced juvenile ramets of both species. Carbon-11 activities averaged across all nonlabelled juvenile ramets were 9.5% ± 2.6% and 20.7% ± 9.5% of the steady state values recorded for labelled ramets of *S. scoparium* and *P. plicatulum*, respectively. Juvenile ramets maintained physiological integration with their parental ramets following substantial shoot and root development with no indication of a complete cessation of carbon import.

Responsiveness of carbon allocation to ramet perturbation

Partial defoliation of juvenile ramets connected to labelled parental ramets increased ^{11}C activity to values 36% greater than those of the steady state level within 20–30 min in *P. plicatulum* (Welker et al. 1985). Shading juvenile ramets connected to labelled parental ramets also increased ^{11}C activity by a maximum of 70% over that of steady state activities within a comparable time period. Similarly, ^{11}C activities within juvenile ramets decreased to values comparable to those of steady state levels within 20–30 min following an increase in irradiance of previously shaded ramets.

Carbon-11 activity of individual juvenile ramets of *S. scoparium* was continuously monitored for a 6 d period during which time they were partially defoliated on day two and again on day six (Fig. 1). The initial defoliation increased ^{11}C activity by 85% within 3 h and a maximum activity 180% greater than that of the labelled ramet occurred 24 h following defoliation. A second defoliation which removed all leaf blade tissue that had regrown during the intervening 4 d period increased ^{11}C activity 440% above that of the labelled parental ramet 170 min following defoliation. These responses demonstrate the rapid increases in sink strength induced by defoliation and the synergistic effect of successive defoliation events on the patterns of carbon allocation between parental and juvenile ramets.

Extent of intraclonal resource allocation

Nitrogen was distributed throughout the roots and shoots of three connected ramet generations of *S. scoparium* within 24 h following exposure of an adventitious root of either the primary or secondary ramet generations to ^{15}N solution (Welker et al. 1987, Welker et al. 1991b). Both primary and secondary ramet generations of *S. scoparium* allocated nitrogen to juvenile, tertiary ramets (Welker et al. 1991b). However, relative distributions of ^{15}N between shoots and roots of tertiary ramets were 3- and 6-fold greater, respectively, 24 h following labelling when ^{15}N was introduced into the roots of the secondary rather than the primary ramet generation ($P = 0.08$). Basipetal nitrogen allocation, from secondary to ontogenetically older primary ra-

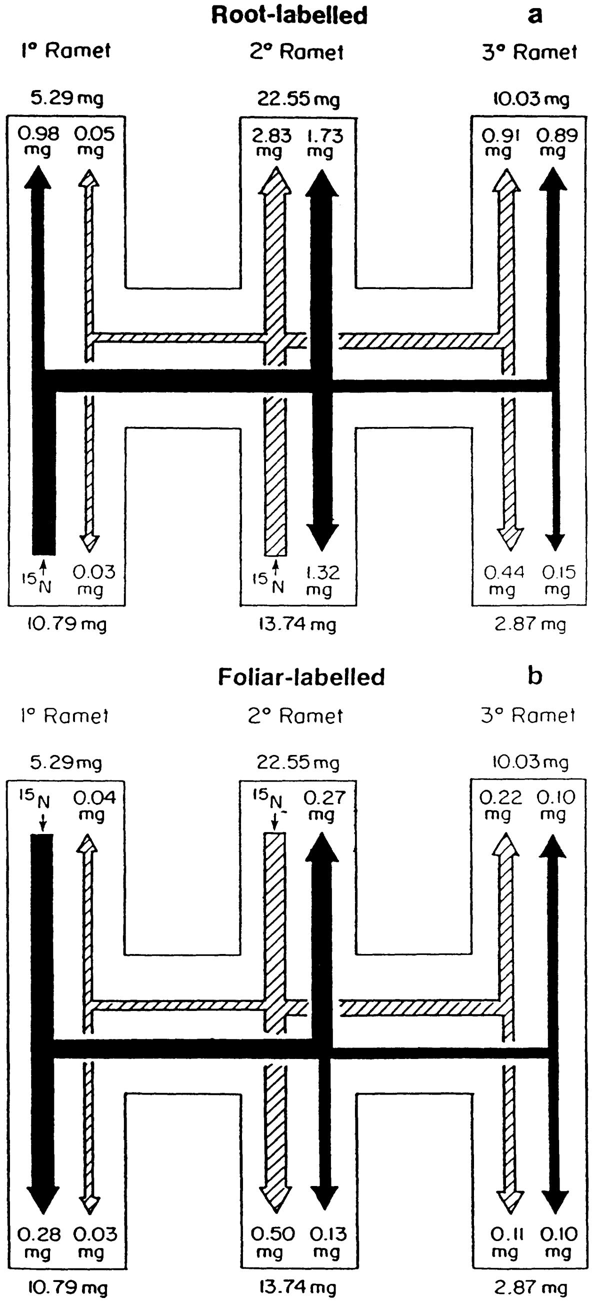

Fig. 2. Nitrogen allocation between roots and shoots of three connected ramet generations comprising the physiological individual in the caespitose graminoid *Schizachyrium scoparium.* Total nitrogen allocation was calculated from the product of the relative distribution of ^{15}N at 120 h following labelling and the total nitrogen pools (^{14}N + ^{15}N) of the respective organs. Solid arrows represent nitrogen allocation from the primary ramet generation and hatched arrows represent nitrogen allocation from the secondary ramet generation.

mets, was observed, but accounted for less than 1% of the ^{15}N mass in the ramet sequences at the end of the 5-d experiment.

The relative amount of ^{15}N allocated from a single labelled ramet sequence to associated ramet sequences within individual clones was significantly affected by the ramet generation through which ^{15}N was introduced (Welker et al. 1991b). Approximately, 7% of the total ^{15}N introduced into an individual labelled ramet sequence was allocated to other sequences within the clone following primary ramet labelling while only 2.4% of the ^{15}N was allocated to associated ramet sequences when the secondary ramet generation was labelled ($P < 0.01$). The vast majority of ^{15}N, 93 to 99%, remained within the ramet sequence into which it was initially introduced indicating a very limited capacity for complete integration within young clones possessing complete vascular continuity.

Magnitude of interramet resource allocation

Juvenile (tertiary) ramets imported a total of 2.9 mg of nitrogen from the primary and secondary ramet generations within the three generation ramet sequence of *S. scoparium* (Fig. 2). Seventy-three percent of the total, i.e. 2.1 mg, was incorporated into shoots while the remainder, 0.8 mg, was allocated to roots of juvenile ramets. These amounts represent 21 and 28% of the total nitrogen pool within the shoots and roots of the juvenile ramets, respectively.

Parental (secondary generation) ramets contributed 1.1 mg of nitrogen to the shoots, but only 0.5 mg to the roots of juvenile ramets (Fig. 2). This represents 11.3 and 18.8% of the total nitrogen within the juvenile ramet shoots and roots, respectively. Primary ramets displayed similar allocation patterns contributing 1.0 and 0.25 mg of nitrogen to the shoots and roots of juvenile ramets, respectively. This represents 9.9 and 8.7% of the respective nitrogen pools in the tertiary ramet generation. Basipetal nitrogen allocation from secondary generation ramets accounted for 1.7 and 0.5% of the total nitrogen pools in shoots and roots of primary ramets, respectively.

Significance of physiological integration to productivity

Severing vascular connections between various ramet generations within a ramet sequence to create a series of potential physiological individuals significantly affected biomass accumulation within the experimental ramet sequences of *S. scoparium* (Williams and Briske 1991). Total biomass of the isolated two-generation (parent-juvenile) sequence was 58% less than the combined mass of similar ramets within non-severed sequences 24 d following severing ($P < 0.05$). Restricted growth of

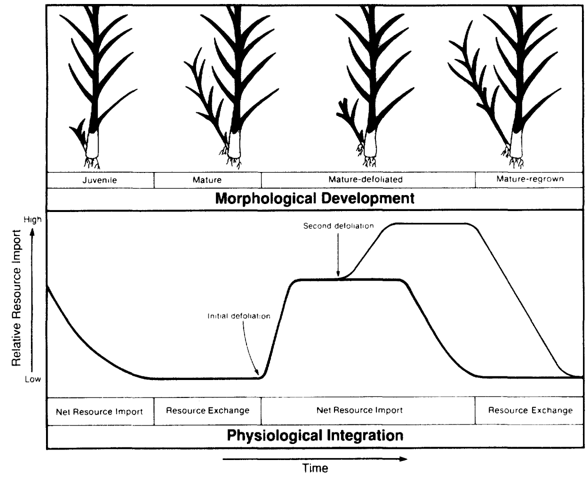

Fig. 3. Schematic representation of resource import by a secondary generation ramet connected to a parental ramet within a caespitose graminoid. The juvenile ramet is a net resource importer from initiation until substantial shoot and root development has occurred at which time resource import decreases to a low level of reciprocal exchange. Partial ramet defoliation rapidly reestablishes net resource import and subsequent defoliation of regrowth tissue further increases resource import. Resource import again diminishes to a low level of resource exchange following reestablishment of ramet leaf area.

parental ramets accounted for the entire mass reduction within the two-generation sequences while mass of the juvenile (tertiary) ramets was unaffected. Total sequence weights were not statistically different between the severed and non-severed three-generation sequences despite a two-fold increase in juvenile ramet mass within the three-generation sequences severed from the remainder of the clone. Mean juvenile ramet biomass in the severed three-generation sequences was 112% greater than that in severed two-generation sequences and 151% greater than in non-severed three-generation sequences 24 d following severing ($P < 0.01$). Increased juvenile ramet mass resulted from a release of resource competition following severance of vascular connections between the primary ramet and the remainder of clone.

Ramet demography

Demographic variables of juvenile ramets were also significantly affected by severing during an 80-d observation period in the field. Reproductive development was observed in a significantly greater number of juvenile ramets within non-severed sequences when compared to juvenile ramets within severed ramet sequences (Williams and Briske 1991). Reproductive development occurred in 13 of 16, 7 of 16 and 7 of 13 juvenile ramets in the non-severed sequence, two-generation sequence and isolated juvenile ramet, respectively ($P < 0.05$). Juvenile ramets in non-severed sequences also exhibited greater rates of leaf recruitment ($P < 0.01$). The mean cumulative number of leaves produced by juvenile ramets during the 80-d observation period was 5.0 ± 0.04, 3.9 ± 0.52, and 3.5 ± 0.45 for the non-severed sequences, two-generation sequences and isolated juvenile ramets, respectively. Juvenile ramets attached to the clone initiated a significantly greater number of ramets when compared to juvenile ramets severed from the clone ($P < 0.05$). The mean cumulative number of ramets recruited per parental tertiary ramet was 0.81±0.37, 0.75±0.31 and 0.15±0.01 for non-severed, two-generation and isolated tertiary ramet treatments, respectively.

Ramet recruitment within undisturbed clones of *S. scoparium* was primarily restricted to spring and autumn when a mean of 3.0 and 4.5 ramets, respectively, were initiated from ten permanently marked ramets per clone (Briske and Butler 1989). Ramet recruitment occurred from axillary buds of all four parental ramet categories monitored including live vegetative, senescent vegetative, live reproductive and senescent reproductive. However, the greatest number of ramets were recruited from the live, vegetative parental category. Approximately 70% of the total recruitment occurred from parental ramets on the clone periphery, rather than the interior ($P < 0.01$).

Ramet populations of *S. scoparium* in central Texas were under density-dependent regulation imposed by both interclonal and intraclonal interference. This was shown by reducing either interclonal or intraclonal interference which extended the seasonality of ramet recruitment and increased total recruitment by 57 and 71% respectively, during the two growing seasons the populations were monitored ($P < 0.05$, Briske and Butler 1989). However, a reduction in interference did not affect ramet survivorship or reproductive development in comparison with ramets in undisturbed clones. Reproductive development was initiated in July and a maximum of 40% of the total ramet population flowered in October. Only 5% of the permanently marked ramets survived throughout the 16-month investigation and the half-lives of cohorts recruited during the investigation ranged between 3 and 9 months. Maximum ramet mortality occurred in mid-winter regardless of interference from associated clones or ramets within the population.

Discussion

Implications for clonal biology

Data from these physiological and demographic investigations provide a basis from which we can draw inferences concerning the organization and function of the temperate, caespitose, graminoid growth form. Juvenile ramets are entirely dependent upon imported resources for growth immediately following initiation, but the amount decreases to low levels of continuous import as the root and shoot systems develop (Colvill and Marshall 1981, Welker et al. 1985, Welker et al. 1987, Marshall 1990, Fig. 3). However, a low level of continuous resource import does not necessarily constitute net resource import, but may merely represent reciprocal exchange between ramet generations. Consequently, carbon independence defined as the complete cessation of import may not occur and reintegration may represent accelerated levels of import rather than a resumption of import by previously independent ramets.

Rates of resource import increase in response to shading or partial ramet defoliation with multiple defoliations of an individual ramet further increasing the rate of resource import (Gifford and Marshall 1973, Welker et al. 1985, Fig. 1). However, an increased rate of import may not necessarily represent an absolute increase in resource accumulation because defoliation reduces shoot mass and subsequent sink strength (Welker et al. 1987). A large reduction in ramet mass following defoliation may reduce the absolute resource requirement to a greater extent than can be offset by an increase in the rate of resource import. Resource import again decreases to a low level with the reestablishment of photosynthetic surfaces or an increase in irradiance following shading (Gifford and Marshall 1973, Welker et al. 1985, Welker et al. 1987). The capacity for continuous resource integration may be a prerequisite for the occurrence of rapid shifts in resource allocation among ramets subjected to modified source-sink relations.

Increased rates of resource allocation to defoliated ramets provides a potential mechanism of herbivory tolerance by facilitating ramet survival and the reestablishment of photosynthetic tissue. Accelerated import is most likely the result of higher levels of photosynthesis and nutrient uptake by adjacent, nondefoliated tissue and the preferential allocation of these resources to damaged tissue (Gifford and Marshall 1973, Painter and Detling 1981, Welker et al. 1985). Consequently, the regrowth of defoliated ramets (Matches 1966) can be attributed to increased rates of allocation from nondefoliated to defoliated ramets which is made possible by higher rates of resource assimilation by nondefoliated portions of the plant (Watson and Ward 1970, Mattheis et al. 1976, Archer and Tieszen 1986, Jónsdóttir and Callaghan 1989).

Although inter-ramet resource allocation is an important attribute of growth in caespitose graminoids, increasing evidence indicates that not all ramets within caespitose clones are physiologically integrated. Isotopic tracers incorporated into individual ramets are not distributed throughout all ramets within the clone (Dodd and Van Amburg 1970, Colvill and Marshall 1981). Both tracer and severing experiments demonstrate that physiological integration in the caespitose graminoid *S. scoparium* is restricted to individual ramet sequences consisting of three connected ramet generations (Welker et al. 1991b, Williams and Briske 1991, Fig. 3). The propensity for acropetal resource allocation to juvenile ramets within a ramet sequence appears to be the predominant factor limiting resource allocation among ramet sequences within clones possessing complete vascular continuity. Death of the seminal ramet, within approximately 16 months, provides a more decisive morphological constraint to complete clonal integration when vascular connections among ramet sequences disintegrate.

These data indicate that the physiological individual in the caespitose graminoid *S. scoparium* may be smaller than generally assumed (Watson and Casper 1984, De Kroon and Van Groenendael 1990) and that they are substantially smaller than those observed in rhizomatous or stoloniferous graminoids (e. g. Jónsdóttir and Callaghan 1989, Carlsson et al. 1990). Both the primary and secondary (parental) ramet generations allocate resources to juvenile ramets within the physiological individual to promote both vegetative growth and sexual reproduction. Basipetal resource allocation from ontogenetically older to younger ramet generations also occurs, but in such minimal quantities that the ecological consequences of this phenomenon appear limited.

The survival value conferred by a clonal architecture composed of an assemblage of autonomous physiological individuals growing within close proximity requires further evaluation. Presumably, if the survival value derived from this clonal architecture was insufficient to offset the intense intraclonal competition experienced (i.e., competition among physiological individuals, i.e., James and Hutto 1972, Briske and Butler 1989), the caespitose graminoid growth form would not have diversified to such a large number of taxa or come to dominate such a diverse array of habitats (e. g., Mogie and Hutchings 1990). The survival advantage may be partially conferred by the ability of temperate, caespitose graminoids to sequester and concentrate nutrients within the immediate proximity of the clone (Heal et al. 1989). For example, soils beneath clones of *Bouteloua gracilis,* a caespitose graminoid of the Central Plains of North America, contain nitrogen and carbon concentrations 1.5 and 1.2 times greater, respectively, than soils in interstitial areas (Hook et al. 1991). Microscale soil heterogeneity resulting from site occupation by clones would minimize the benefits of resource foraging conferred by rhizomes and stolons if clones dominated patches containing the highest nutrient concentrations (i.e., Slade and Hutchings 1987a, b, De Kroon and Van Groenendael 1990).

Implications for climate change

The impact of climate change on the caespitose graminoid growth form is difficult to anticipate for several reasons. First, relatively little is known about the clonal biology and population ecology of this growth form with the exception of several forage species and intensively studied native species. Second, caespitose graminoids consists of both C_3 and C_4 species which will contribute additional complexity to the response of this growth form (Gould 1975, Waller and Lewis 1979, Curtis et al. 1989, Ziska et al. 1990). Third, modular construction of the growth form determines that responses at several levels of organization including the ramet, clone, and population will collectively influence community structure and function (White 1979, Briske 1991). The potential for disproportionate responses among the various organizational levels and the potential modification of responses at lower levels by processes and interactions at higher levels will make interpretation more difficult than in nonclonal plants (i.e., Allen and Star 1982).

Caespitose graminoids appear to possess much smaller physiological individuals than rhizomatous graminoids because individual ramets possess shorter life expectancies. Maximum ramet longevities of most temperate, caespitose graminoids do not exceed 2 yr (Langer 1956, Briske and Butler 1989), while ramets of high latitude rhizomatous graminoids frequently survive 4–6 yr (Mattheis et al. 1976, Callaghan 1984). Physiological individuals composed of only several ramet generations may be more susceptible to environmental variation because of a greater meristematic limitation to subsequent ramet recruitment (i.e., Watson and Casper 1984). If climatic variability singly or in combination with biotic agents, restricts recruitment of one or more successive ramet generations, clone and population persistence would be jeopardized by the depletion of available meristems. In contrast, axillary buds remain viable in the rhizomatous, tundra graminoid *Carex bigelowii* for several years and bud dormancy is alleviated by mechanical disturbance to the rhizome (Jónsdóttir and Callaghan 1989). However, field experiments on the caespitose sedge, *Eriophorum vaginatum* show that this species increases ramet production at high levels of enhanced CO_2 (Tissue and Oechel 1987).

Conclusion

Clonal biology of caespitose graminoids merits additional research emphasis because of the large area they occupy and their anticipated responsiveness to climate change. The modular construction of the growth form determines that research should be designed to simultaneously evaluate ramet, clone and population responses to effectively determine the impacts of climate change. Experimental approaches might include neighbourhood designs for assessing competitive interactions (Goldberg 1990, Welker et al. 1991c) and the evaluation of plant responses to multiple stress factors (Chapin et al. 1987, Toft et al. 1987, Welker and Menke 1990). Climate-induced modifications to the structure and function of caespitose graminoid communities will most likely effect ecosystem function (i.e, primary productivity, i.e., Hall and Scurlock 1991) and potentially feedback to effect atmospheric composition (i.e., CO_2 sequestration and emission, Anderson 1991).

Acknowledgements – Portions of this research were supported by the Texas Agricultural Experiment Station, U.S. Department of Agriculture (82-CSRS2-1040), National Science Foundation (DEB-22165), U.S. Department of Energy (DEA-101-81ER60012) and National Science Foundation (DEB-80-21312) support to the Duke University Phytotron. This manuscript is published with approval of the Experiment Station as technical publication 30267. We wish to thank T. V. Callaghan, B. Å. Carlsson, B. Schmid and C. Marshall for their constructive contributions to an earlier version of the manuscript.

References

Allen, T. F. H. and Star, T. B. 1982. Hierarchy: perspective for ecological complexity. – Univ. Chicago Press, Chicago.

Anderson, J. M. 1991. The effects of climate change on decomposition processes in grassland and coniferous forest. – Ecol. Appl. 1: 326–347.

Archer, S. R. and Tieszen, L. L. 1986. Plant response to defoliation: Hierarchical considerations. – In: Gudmundsson, O. (ed.), Grazing research at northern latitudes. Plenum, pp. 45–59.

Bell, A. D. 1976. The vascular pattern of Italian ryegrass (*Lolium multiflorum* Lam.) 3. The leaf trace system, and tiller insertion in the adult. – Ann. Bot. 40: 241–250.

Bradshaw, A. D. and McNeilly, T. 1991. Evolutionary responses to global climate change. – Ann. Bot. 67: 5–14.

Bremner, J. M. 1965. Isotope ratio analysis of nitrogen in ^{15}N tracer investigations. – In: Black, C. A. (ed.), Methods of soil analysis. American Society of Agronomy, Madison, WI, pp. 1256–1286.

Briske, D. D. 1991. Developmental morphology and physiology of grasses. – In: Heitschmidt, R. K. and Stuth, J. W. (eds), Grazing management: an ecological perspective. Timber Press, Portland, OR, pp 70–95.

– and Butler, J. L. 1989. Density-dependent regulation of ramet populations within the bunchgrass *Schizachyrium scoparium:* Interclonal versus intraclonal interference. – J. Ecol. 77: 963–974.

Callaghan, T. V. 1984. Growth and translocation in a clonal southern hemisphere sedge: *Uncinia meridensis.* – J. Ecol. 72: 529–546.

Carlsson, B. Å., Jónsdóttir, I. S., Svensson, B. M. and Callaghan, T. V. 1990. Aspects of clonality in the Arctic: a comparison between *Lycopodium annotinum* and *Carex bigelowii.* – In: Van Groenendael, J. and De Kroon, H. (eds), Clonal growth in plants: regulation and function. SPB Academic Press, The Hague, pp. 131–152.

Chapin, F. S., Bloom, A. J., Field, C. B. and Waring R. H. 1987. Plant responses to multiple environmental factors. – Bioscience 37: 49–57.

Cook, R. E. 1983. Clonal plant populations. – Am. Sci. 71: 244–253.

Covill, K. E. and Marshall, C. 1981. The patterns of growth, assimilation of $^{14}CO_2$ and distribution of ^{14}C-assimilate within vegetative plants of *Lolium perenne* at low and high density. – Ann. Appl. Biol. 99: 179–190.

Curtis, P. S., Drake, B. G., Leadley, P. W., Arp, W. J. and Whigham, D. F. 1989. Growth and senescence in plant communities exposed to elevated CO_2 concentrations on an estuarine marsh. – Oecologia 78: 20–26.

De Kroon, H. and Van Groenendael, J. 1990. Regulation and function of clonal growth in plants: an evaluation. – In: Van Groenendael, J. and De Kroon, H. (eds), Clonal growth in plants: regulation and function. SPB Academic Press, The Hague, pp. 177–186.

Dodd, J. D. and Van Amburg, G. L. 1970. Distribution of ^{134}Cs in *Andropogon scoparius* Michx. clones in two native habits. – Ecology 51: 685–689.

Emanuel, W. R., Shugart, H. H. and Stevensohn, M. P. 1985. Climate change and the broad-scale distribution of terrestrial ecosystem complexes. – Climate Change 7: 29–43.

Gifford, R, M. and Marshall, C. 1973. Photosynthesis and assimilate distribution in *Lolium multiflorum* Lam. following differential tiller defoliation. – Aust. J. Biol. Sci. 26: 517–526.

Goldberg, D. E. 1990. Components of resource competition in plant communities. – In: Grace, J. B. and Tilman, D. (eds), Perspectives on plant communities, Academic Press, New York, pp. 27–50.

Gould, F. W. 1975. The grasses of Texas. – Texas A&M Univ. Press, College Station, TX.

Hall, D. O. and Scurlock, J. M. O. 1991. Climate change and productivity of natural grasslands. – Ann. Bot. 67: 49–55.

Heal, W. O., Callaghan, T. V. and Chapman, K. 1989. Can population and process ecology be combined to understand nutrient cycling? – In: Clarholm, M. and Bergstrom, L. (eds), Ecology of arable land. Kluwer Academic Publishers, The Netherlands, pp. 205–216.

Hitch, P. A. and Sharman, B. C. 1968. Initiation of procambial strands in axillary buds of *Dactylis glomerata* L., *Secale cereale* L., and *Lolium perenne* L. – Ann. Bot. 32: 667–676.

Hook, P. B., Burke, I. C. and Lauenroth, W. K. 1991. Heterogeneity of soil and plant N and C associated with individual plants and openings in North American shortgrass prairie. – Ecol. Soc. Am. Bull. 72: 144.

Houghton, J. T., Jenkins, G. J. and Ephraums, J. J. 1990. Introduction. – In: Houghton, J. T., Jenkins, G. J. and Ephraums, J. J. (eds), Climate change: The IPCC Scientific Assessment, Intergovernmental panel on climate change. Cambridge Univ. Press, Cambridge.

Huntley, B. 1991. How plants respond to climate change: migration rates, individualism and the consequences for plant communities. – Ann. Bot. 67: 15–27.

James D. B. and Hutto, J. M. 1972. Effects of tiller separation and root pruning on growth of *Lolium perenne* L. – Ann. Bot. 36: 485–495.

Jónsdóttir, I. S. and Callaghan, T. V. 1989. Localized defoliation stress and the movement of ^{14}C-photoassimilates between tillers of *Carex bigelowii*. – Oikos 54: 211–219.

Langer, R. H. M. 1956. Growth and nutrition of timothy (*Phleum pratense*). I. The life history of individual tillers. – Ann. Appl. Biol. 44: 166–187.

Leith, H. 1978. Primary productivity in ecosystems: Comparative analysis of global patterns. – In: Leith, H. F. H. (ed.), Patterns of primary production in the biosphere. Dowden, Hutchinson and Ross, Stroudberg, PA, pp. 300–321.

Magnuson, C. E., Fares, Y., Goeschl, J. D., Nelson, C. E., Strain, B. R., Jaeger, C. H. and Bilpuch E. G. 1982. An integrated tracer kinetics system for studying carbon uptake and allocation in plants using continuously produced $^{11}CO_2$. – Radiat. Environ. Biophys. 21: 51–65.

Manabe, S. and Wetherald, R. T. 1987. Large-scale changes in soil wetness induced by an increase in carbon-dioxide. – J. Atmos. Sci. 44: 1211–1235.

Marshall, C. 1990. Source-sink relations of interconnected ramets – In: Van Groenendael, J. and De Kroon, H. (eds), Clonal growth in plants: regulation and function. SPB Academic Press. The Hague, pp. 23–42.

Matches, A. G. 1966. Influence of intact tillers and height of stubble on growth responses of tall fescue (*Festuca arundinacea* Schreb.). – Crop Sci. 6: 484–487.

Mattheis, P. J., Tieszen, L. L. and Lewis, M. C. 1976. Responses of *Dupontia fischeri* to simulated lemming grazing in an Alaskan arctic tundra. – Ann. Bot. 40: 179–197.

Melillo, J. M., Callaghan, T. V., Woodward F. I. and Salati, E. 1990. Effects on Ecosystems. – In: Houghton, J. T., Jenkins, G. J. and Ephraums, J. J. (eds), Climate change: The IPCC Scientific Assessment: Intergovernmental panel on climate change. Cambridge Univ. Press, Cambridge, pp. 285–310.

Mogie, M. and Hutchings, M. J. 1990. Phylogeny, ontogeny and clonal growth in vascular plants. – In: Van Groenendael, J. and De Kroon, H. (eds), Clonal growth in plants: regulation and function. SPB Academic Press, The Hague, pp. 3–22.

Painter, E. L. and Detling, J. K. 1981. Effects of defoliation on net photosynthesis and regrowth of western wheatgrass. – J. Range Manage. 34: 68–71.

Schneider, S. H. 1989. The greenhouse effect: Science and policy. – Science 243: 771–781.

Slade, A. J. and Hutchings, M. J. 1987a. Clonal integration and plasticity in foraging behavior in *Glechoma hederacea*. – J. Ecol. 75: 1023–1036.

– and Hutchings, M. J. 1987b. An analysis of the influence of clone size and stolon connections between ramets on the growth of *Glechoma hederacea* L. – New Phytol. 106: 759–771.

Tiffney, B. H. and Niklas, K. J. 1985. Clonal growth in land plants: A palaeobotanical perspective. – In: Jackson, J. B. C., Buss, L. W. and Cook, R. E. (eds), The population biology and evolution of clonal organisms. Yale Univ. Press, New Haven, CT, pp. 35–66.

Tissue, D. T. and Oechel, W. C. 1987. Response of *Eriophorum vaginatum* to elevated CO_2 and temperature in the Alaskan tussock tundra. – Ecology. 68: 401–410.

Toft, N. L., McNaughton, S. J. and Georgiadis, N. J. 1987. Effects of water stress and simulated grazing on leaf elongation and water relations of an east African grass, *Eustachys paspaloids*. – Aust. J. Plant Physiol. 14: 211–226.

Waller, S. S. and Lewis, J. K. 1979. Occurrence of C_3 and C_4 photosynthetic pathways in North American grasses. – J. Range Manage. 32: 12–28.

Walter, H. 1979. Vegetation of the Earth and ecological systems of the geobiosphere. – Springer, New York.

Watson, M. A. and Casper, B. B. 1984. Morphogenetic constraints on patterns of carbon distribution in plants. – Annu. Rev. Ecol. Syst. 15: 233–258.

Watson, V. H. and Ward, C. Y. 1970. Influence of intact tillers and height of cut on regrowth and carbohydrate reserves of Dallisgrass (*Paspalum dilatatum* Poir.). – Crop Sci. 10: 474–476.

Welker, J. M. and Menke, J. W. 1990. The influence of simulated browsing on tissue water relations, growth and survival of *Quercus douglasii* (Hook and Arn.) seedlings under slow and rapid rates of soil drought. – Funct. Ecol 4: 807–817.

– , Rykiel, E. J., Briske, D. D. and Goeschl, J. D. 1985. Carbon import among vegetative tillers within two bunchgrasses: Assessemnt with carbon-11 labelling. – Oecologia 65: 209–212.

– , Briske, D. D. and Weaver, R. W. 1987. Nitrogen-15 partitioning within a three generation tiller sequence of the bunchgrass *Schizachyrium scoparium:* response to selective defoliation. – Oecologia 24: 330–334.

– , McClelland, S. and Weaver, T. 1991a. Soil water retention after natural and simulated rainfall on a temperate grassland. – Theor. Appl. Climatol. 44: 229–237.

– , Briske, D. D. and Weaver, R. W. 1991b. Intraclonal nitrogen allocation in the bunchgrass *Schizachyrium scoparium:* An assessment of the physiological individual. – Funct. Ecol 5: 433–440.

– , Gordon, D. R. and Rice, K. J. 1991c. Capture and allocation of nitrogen by *Quercus douglasii* seedlings in competition with annual and perennial grasses. – Oecologia 87: 459–468.

White, J. 1979. The plant as a metapopulation. – Annu. Rev. Ecol. Syst. 10: 109–145.

Williams, D. G. and Briske D. D. 1991 Size and ecological significance of the physiological individual in the bunchgrass *Schizachyrium scoparium*. – Oikos 62: 41–47.

Ziska, L. H., Drake, B. G. and Chamberlain, S. 1990. Long-term photosynthetic response in single leaves of a C_3 and C_4 salt marsh species grown at elevated atmospheric CO_2 *in situ*. – Oecologia 83: 469–472.