NOTE

Ramet spacing of *Elymus lanceolatus* (thickspike wheatgrass) in response to neighbour density

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Abstract: Many plants exploit patchy resources through clonal foraging. Plants established in field plots were used to determine if *Elymus lanceolatus* ssp. *lanceolatus* (Scribner et J.G. Smith) Gould (thickspike wheatgrass) showed a clonal foraging response to neighbour densities, as it had previously shown to patchy soil nutrients. Neighbours consisted of the rhizomatous *E. lanceolatus* ssp. *lanceolatus* and the bunchgrass *Elymus lanceolatus* ssp. *wawawaiensis* (Scribner et Gould) J.R. Carlson et D.R. Dewey (proposed name), which are both native to the semiarid western U.S.A., and their ratios as well as total densities varied. Rather than an increase in spacing of exploratory ramets at high densities, as expected with clonal foraging, there was a decrease in spacing in both years of the experiment. Fewer target plants produced exploratory ramets at higher densities only in the second year. These reductions in exploratory clonal growth at higher neighbour densities, which were opposite to *E. lanceolatus* ssp. *lanceolatus*' response to low-resource patches, occurred perhaps because soil resource levels were too low overall to support rhizome production, and this condition was more pronounced in the second year. Physical resistance from neighbour roots perhaps also reduced rhizome production. However, rhizome growth may not be beneficial in such cases, and plants may be adapted to produce exploratory rhizomes only when some high-resource patches are encountered by the clone.

Key words: clonal growth, competition, *Elymus lanceolatus*, plasticity, resource levels, rhizomes.

Résumé : Plusieurs espèces de plantes exploitent les ressources inégales par avance clonale. Les auteurs ont utilisé des plantes établies en parcelles, sur le terrain, pour déterminer si l'*Elymus lanceolatus* ssp. *lanceolatus* (Scribner et J.G. Smith) Gould (élyme à gros épis) réagit par avance clonale à la densité des voisins, comme il l'a déjà été démontré pour l'inégalité des nutriments du sol. Les plantes voisines comportaient l' *E. lanceolatus* ssp. *lanceolatus* rhizomateux et l' élyme en touffes, *Elymus lanceolatus* ssp *wawawaiensis* (Scribner et Gould) J.R. Carlson et D.R. Dewey, toutes deux natives de l'ouest américain semi-aride; leurs rapports ainsi que leurs densités variaient. Plutôt que d'observer, à haute densité, une augmentation de l'espacement des ramettes exploratoires comme on l'attendrait d'avances clonales, on perçoit une diminution de l'espacement, au cours des deux années d'expérimentation. Moins de plantes cibles ont produit des ramettes exploratoires aux densités les plus élevées, seulement la deuxième année. Ces réductions de la croissance clonale exploratoire en présence de plus fortes densités de plantes voisines, une réaction opposée à celle de l'*E. lanceolatus* spp *lanceolatus* observée en présence de surfaces faibles en ressource, ont peut-être eu lieu parce que les teneurs en nutriments du sol étaient trop faibles en général pour supporter la production de rhizomes, cette condition étant plus marquée la deuxième année. La résistance physique de la part des racines des plantes voisines a peut-être également réduit la production de rhizomes. Cependant, la croissance des rhizomes pourrait ne pas être bénéfique dans ces cas, et les plantes pourraient être adaptées à produire des rhizomes exploratoires seulement lorsqu'elles rencontrent des surfaces riches en ressources.

Mots clés : croissance clonale, compétition, *Elymus lanceolatus*, plasticité, teneurs en ressources, rhizomes.

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Introduction

Many plants forage, i.e., exploit resource-rich patches and explore their surroundings for other patches, by morphological plasticity (de Kroon and Hutchings 1995). Along with plastic responses of roots and shoots (de Kroon and Hutchings 1995), a major form of foraging is selective placement of ramets in resource-rich patches through decreased lengths of spacers (i.e., rhizomes or stolons) between parent and daughter ramets and increased spacer branching in resource-rich patches, while long exploratory spacers are produced in resource-poor patches (Salzman

1985; Slade and Hutchings 1987). This ramet placement plasticity is referred to herein as clonal foraging. Higher branching in resource-rich patches may be a direct result of greater growth with greater resource availability and, as such, would exist regardless of any fitness advantages branching might confer. However, the spacer length response is an active response that is contrary to the direct effect of resource level on spacer growth (Cain 1994; de Kroon and Hutchings 1995; Cain et al. 1996).

Neighbouring plants in high densities usually deplete belowground resources or preempt light. Do plants with clonal foraging respond to high densities in the same way they respond to resource-poor patches, i.e., with less branching and longer spacers? The stoloniferous *Prunella vulgaris* L. (Schmid 1986) and *Glechoma hederacea* L. (Price and Hutchings 1996) did respond to neighbours in this way. However, *Hieracium pilosella* L. did not increase stolon length (Bishop and Davy 1985), and *Trifolium repens* L. reduced stolon length (Bülow-Olsen et al. 1984). The rhizomatous species *Aster lanceolatus* Willd. and three *Solidago* species (Schmid and Bazzaz 1992), *Calamagrostis canadensis* (Michx.) Beauv. (Macdonald and Lieffers 1993), and *Amphibromus scabrivalvis* Trin. Swallen (Cheplick 1997) all reduced rhizome length in response to competitors (*Aster* and *Solidago* spp. also increased rather than reduced branching). Foraging responses in stoloniferous species can be mediated by changes in the red/far-red light ratio caused by shading from neighbours (Ballaré et al. 1990). Clonal foraging could occur in rhizomatous species in response to nutrient depletion by neighbours through hormonally mediated responses to nutrient uptake (Salisbury and Marinos 1985; Voesenek and Blom 1996). However, clonal foraging may not be an advantage under some high-density conditions. Under uniformly high densities, plants with closely spaced ramets were superior to plants with long rhizomes, even though the plants with long rhizomes were superior competitors at low densities (Schmid and Harper 1985; Winkler and Schmid 1995).

We investigated whether a rhizomatous perennial native to the western United States, *Elymus lanceolatus* ssp. *lanceolatus* (Scribner et J.G. Smith) Gould (thickspike wheatgrass), which showed a clonal foraging response to experimentally created high- and low-nutrient patches (Humphrey and Pyke 1997), showed the same response to varying neighbour densities. We addressed only the active response of spacer length plasticity, which is considered a valid test that foraging exists, whereas branching intensity can be merely a direct consequence of greater growth (Cain 1994; de Kroon and Hutchings 1995). To do this we examined the spacing from parent to daughter ramets for those ramets located around the periphery of the genet (i.e., the exploratory ramets of the genet). If high neighbour densities constitute poor-quality microsites, the clonal foraging response should result in greater spacing of these ramets under higher densities.

Methods

Neighbours consisted of *E. lanceolatus* ssp. *lanceolatus* and a closely related bunchgrass, *Elymus lanceolatus* ssp. *wawawaiensis* (Scribner et Gould) J.R. Carlson et D.R. Dewey (proposed name). Both occur in sagebrush (*Artemisia*) steppe, but ssp. *lanceolatus* typically occurs on sandy soils and ssp. *wawawaiensis* on medium-textured soils (Jones and Nielson
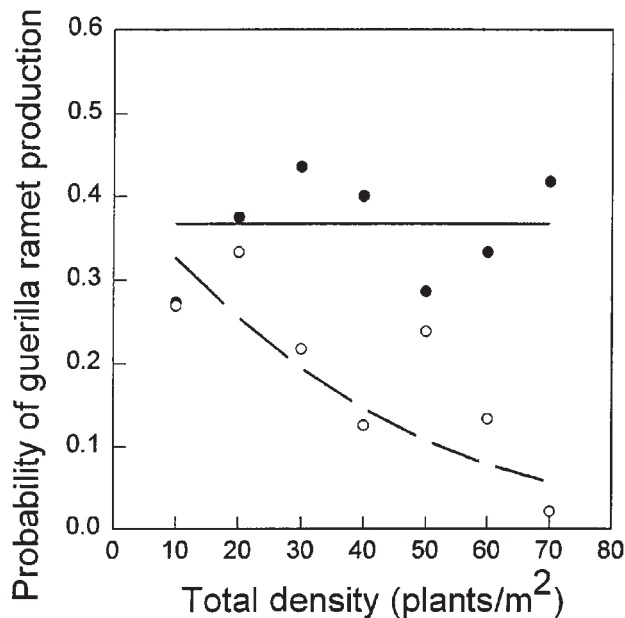
1993). Seeds of the two taxa were obtained from U.S. Natural Resources Conservation Service Plant Materials Centers in Aberdeen, Idaho, for ssp. *lanceolatus*, accession No. T-21076, and in Pullman, Washington for ssp. *wawawaiensis*, accession Secar. Accession No. T-21076 is from a population near The Dalles, Oregon, and Secar is from near Lewiston, Idaho. Seedlings were grown outdoors in partitioned styrofoam seedling flats and transplanted to plots at the Utah State University, Ecology Center's Green Canyon Complex in Logan, Utah (41°45′N, 111°48′W, 1460 m elevation) in May and June 1989. Plots were watered during spring and summer to enhance establishment. Native vegetation of this site is sagebrush steppe, similar to the natural habitat of the two taxa. Soils are Mollisols. The normal annual precipitation is 471 mm, most of which occurs in the winter as snow.

Each plot contained seven target plants (i.e., plants from which data were obtained) of ssp. *lanceolatus,* each at the centre of a neighbourhood consisting of 18 plants arranged in two concentric hexagons with equal spacing among all plants; plants were positioned at midpoints of the sides as well as at points of the outer hexagon. Four levels of total density, 12, 36, 58, and 84 genets/m^2, were planted. These included densities higher than is typical of established stands to include densities typical of establishing stands prior to thinning. To obtain the four density levels, different spacings between plants (30, 18, 14, and 12 cm), applied to the same target-neighbourhood planting configuration, were used. Neighbour plants included ssp. *lanceolatus*, but to avoid uncertainty as to whether ramets were from the target plant or from ssp. *lanceolatus* neighbours, plots had high proportions of the bunchgrass, ssp. *wawawaiensis*. Two ratios of ssp. *wawawaiensis* to ssp. *lanceolatus*, 5:1 and 4:2, were crossed with the four density levels. This eight-plot set of density-ratio combinations was repeated in six blocked replicates. There was considerable mortality of plants shortly after they were transplanted, altering densities from the planting densities described above, but little mortality occurred later. Therefore, to better represent actual densities, densities of ssp. *lanceolatus* and ssp. *wawawaiensis* neighbours were quantified for each target plant's neighbourhood, yielding continuous variation in density. Target plants with ≥50% of neighbour plants dead were omitted. Several target plants were also omitted because guerilla ramets of the target plant could not be distinguished from ramets of neighbours. There were 251 target plants used.

Plants become dormant in July. Growth and ramet production resume in autumn. Autumn ramets overwinter and resume growth in spring. Plants first produce clumps of ramets from which exploratory rhizomes, often ≥10 cm long, later grow. Genets produced numerous ramets by 1990 (means of 149 and 54 for densities <10 and >70, respectively), and many plants flowered. Data were collected for the summer 1989 – summer 1990 and summer 1990 – summer 1991 growing seasons. In June 1990, any ramets that had emerged beyond the main clump were marked with colored wires. Distance from these ramets to the nearest ramet of the main clump represented spacing of guerilla ramets (sensu Lovett Doust 1981) produced from establishment of plots in June 1989 until June 1990. In July 1991, spacing was measured from any guerilla ramets that had emerged since summer 1990 to the nearest previously marked ramet or to the main clump. Rhizomes were not excavated to measure rhizome lengths because it was necessary to retain the plants intact, and excavation was impractical on these field sites. However, the aboveground measurements reflected the ecologically important result of plasticity in rhizome lengths: displacement of daughter ramets from the parent ramets or the main clump. When more than one guerilla ramet per target plant was produced over the sample period, the mean spacing of the ramets was used.

Spacing of guerilla ramets was analyzed as a response to total density of neighbours, ratio of ssp. *wawawaiensis* to ssp. *lanceolatus*, and year (i.e., 1989–1990 and 1990–1991 growing seasons). Because many target plants did not produce guerilla ramets, a

Fig. 1. Probability of *E. lanceolatus* ssp. *lanceolatus* producing guerilla ramets as a function of neighbour density in each year (1989–1990 and 1990–1991 growing seasons). In the first year, neither total density nor ratio was significant, and the intercept from the logistic regression is plotted (horizontal line). In the second year, total density (*D*) was significant (*P* < 0.001), and the probability based on the logistic regression, ln ($P/1 − P$) = −0.37 − 0.035*D*, where *P* is probability of producing guerilla ramets, is plotted. To provide a visual depiction of the data, along with the logistic regression results, actual proportions of plants producing guerilla ramets by density class are presented (circles). (The highest class, 70, includes all target plants with densities ≥70.) The solid line and solid circles show the 1989–1990 growing season, and broken line and open circles show the 1990–1991 growing season.

Fig. 2. Spacing of guerilla ramets as a function of neighbour density in each year (1989–1990 and 1990–1991). In individual regressions, total density was significant in both years (*P* < 0.001 and *P* < 0.05, respectively). Slopes for each year were not significantly different, but intercepts were (*P* < 0.05).

Logistic regressions were run in PROC LOGISTIC, and the analysis of covariance was run in PROC GLM of SAS (SAS Institute Inc. 1990).

two-step approach was used in analyzing the data. In the first step, the effects of density and ratio on the binary response, producing guerilla ramets or not, were analyzed by logistic regression. The 2 years were analyzed separately, as measures were repeated on the same plants in each year. This response was potentially biased toward greater probability of producing guerilla ramets for larger plants because larger plants may produce both more phalanx and more guerilla ramets (Birch and Hutchings 1994). However, neighbour densities reduced numbers of ramets per genet on these plots (Humphrey and Pyke 1998), as well as potentially affecting rhizome lengths. Therefore, we also tested ramet numbers per genet as a covariate after fitting total density. In the second step, for those target plants that produced guerilla ramets, spacing of guerilla ramets as a function of density, ratio, and year was analyzed. As only 10% (9) of the target plants that produced guerilla ramets in the first year were among those that did so in the second year, the 2 years' ramet spacing data essentially do not represent repeated measures on the same plants. Thus, the factor, years, was analyzed along with the continuous variable (covariate), total density, in an analysis of covariance (ANCOVA). Although the total densities quantified for each target plant were continuous, distributions of proportion of those neighbours that were ssp. *wawawaiensis* were very bimodal. For both the logistic regression and ANCOVA data sets, the two ratio categories had means of 62% and 81% ssp. *wawawaienis* and standard deviations of only 4–5%. Thus, we included ratio as a categorical variable in both the ANCOVA and the logistic regressions.
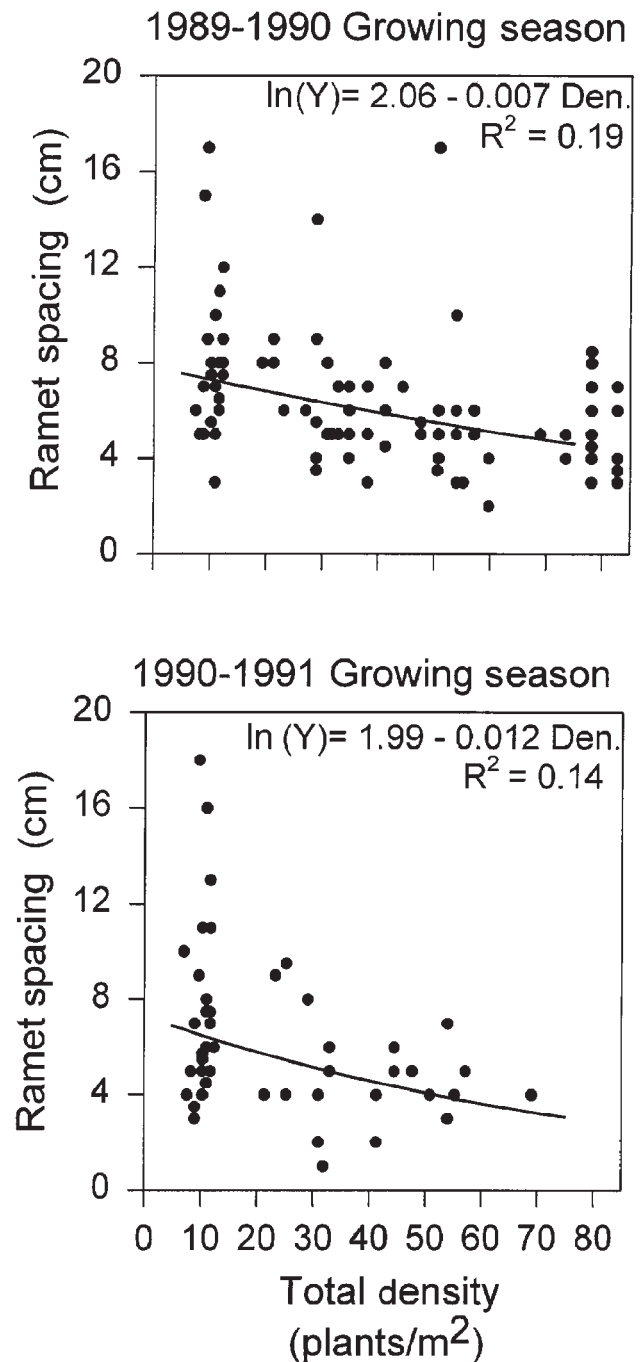
Results

In each year, most ssp. *lanceolatus* genets (>60%) did not produce guerilla ramets. Logistic regression indicated that the probability of ssp. *lanceolatus* producing guerilla ramets was

unaffected by densities in the first year but significantly reduced by higher neighbour densities in the second year ($P < 0.001$; Fig. 1). Ratio was not significant in either year. Fewer ssp. *lanceolatus* plants produced guerilla ramets in the second year than in the first (Fig. 1). Larger plants may be more likely to produce guerilla ramets simply because they produce more total ramets. However, ramet numbers per genet had no effect on probability of a genet producing exploratory rhizomes independent of density in the second year when density was significant and, also, had no effect the first year when densities had no effect. Ramet spacing in the ANCOVA was also unaffected by ramet numbers.

Parent–daughter ramet spacing of the guerilla ramets that were produced was less at higher densities in both years ($P < 0.001$ and $P < 0.05$, respectively; Fig. 2). Ratio, density–ratio interaction, and replicate were not significant. In the ANCOVA, effects of density did not differ between years, but intercepts for the 2 years differed ($P < 0.05$). Low R^2 indicated that densities explained only a small portion of the variation in spacing of guerilla ramets (Fig. 2).

Discussion

Guerilla ramets of ssp. *lanceolatus* reduced spacing at higher densities, opposite to the response expected with clonal foraging (sensu Salzman 1985; Slade and Hutchings 1987), although ssp. *lanceolatus* did show a clonal foraging response to patchy nutrients (Humphrey and Pyke 1997), and some stoloniferous plants have shown such a response to neighbours (Schmid 1986; Price and Hutchings 1996).

Ramet spacing was reduced by densities in both years, but fewer plants produced guerilla ramets at higher densities only in the second year. Lower aboveground biomass on the plots overall in the second growing season (Humphrey and Pyke 1998) indicated that plant growth had more greatly reduced resources in the second year. Weather conditions were not responsible for the decline, since precipitation in January–July 1990 and 1991 was 23.1 and 26.4 cm, respectively.

The reduced spacing of exploratory rhizomes at high densities may have occurred because availability of unexploited soil patches was too low to provide sufficient resources for the production of exploratory rhizomes. The reduction in the probability of producing exploratory rhizomes at high densities in the second year indicates greater effect in that year when resource availability was still lower. *Trifolium repens* showed a clonal foraging response to mild shading, with increased stolon internode lengths relative to no shading; however, with deep shading where growth was greatly reduced, this response was no longer shown, and only short internodes were produced (Thompson 1993). Rhizomes are costly structures, and allocation of resources to them is likely to be reduced during resource shortages (Fitter 1986; Dong and de Kroon 1994), and other species have shown enhanced increase in stolon lengths in unfavorable patches when more resources were available from other parts of the genet (Turkington and Klein 1991; Evans 1992).

In addition to nutrient limitation, mechanical resistance to rhizome growth from dense mats of roots may also reduce rhizome lengths at higher neighbour densities (Schmid and Bazzaz 1992). Huber-Sannwald et al. (1998) found that dense roots reduced clonal growth of *E. lanceolatus* ssp.

lanceolatus. McConnaughay and Bazzaz (1992) found that the presence of artificial neighbour root systems reduced plant growth. Thus, resource limitation and mechanical constraints at high neighbour densities may prevent a plastic rhizome length response, that may be adaptive under some patchy-nutrient conditions, from being expressed.

However, at very high densities, in addition to being a direct result of resource limitation, reduced rhizome growth might confer selective advantage. Even under considerable resource reduction, plants can maintain increased spacer lengths by shifts in allocation and by altering traits such as tissue mass-density and thickness of spacers (Price and Hutchings 1996; Ryser and Eek 2000). However, when resources are greatly depleted, resource patches remaining may be too small to be exploited effectively by rhizome growth (e.g., Wijesinghe and Hutchings 1997). Guerilla-rhizomatous genotypes were affected by competition more adversely than phalanxlike genotypes (Cheplick 1997), suggesting that production of guerilla rhizomes resulted in a net cost under these conditions. The guerilla-rhizomatous *Prunella vulgaris* was a superior competitor to the phalanx species *Bellis perennis* L. at low densities, but under high densities the competitive advantage shifted to the phalanx species (Schmid and Harper 1985; Winkler and Schmid 1995). If a phalanx growth form is the more fit under high densities, then an active response of ceasing production of guerilla rhizomes under such conditions, or making no allocation or anatomical adjustments to maintain it, would be beneficial.

Acknowledgements

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