

ORIGINAL PAPER

G. Hartvigsen · S.J. McNaughton

Tradeoff between height and relative growth rate in a dominant grass from the Serengeti ecosystem

Received: 3 January 1995 / Accepted: 5 January 1995

Abstract We determined the relationship between plant height and whole-plant relative growth rate ($\text{g g}^{-1} \text{day}^{-1}$) for ten genotypes of *Sporobolus kentrophyllus* collected from an intensively grazed site on the Serengeti Plains, Tanzania. Plants were grown for 7 weeks in a greenhouse in Syracuse, N.Y., and harvested weekly. Plants that received simulated bovine urine showed a negative relationship between plant height and growth rate, suggesting a genetic tradeoff between competitive ability if ungrazed (height) and ability to recover from grazing (growth rate). There was no height-growth rate relationship under nitrogen addition rates similar to field mineralization rates. In addition, faster-growing, shorter plants tended to have relatively higher above-ground growth rates than slower-growing, taller plants. These results suggest that natural selection has maintained a gradient of morphologies within this species ranging from short, rapidly growing genotypes adapted to intense grazing conditions to tall, slow-growing, grazer-susceptible genotypes that are superior light competitors in absence of herbivory.

Key words Genotypic tradeoff · Plant height · Relative growth rate · Serengeti

Introduction

The ability of grasses to compensate for tissue removal, and thereby support large grazers, is intimately related to relative growth rate (RGR, in $\text{g g}^{-1} \text{day}^{-1}$) (Oosterheld and McNaughton 1988). Tradeoffs in plant morphology and physiological responses related to grazing have been found between plant height, tillering, leaf area per unit weight, assimilation rate, blade elongation, and other traits which affect RGR (Mooney 1972; Oosterheld and McNaughton 1988; Noy-Meir et al. 1989; Chapin 1991; Oosterheld and McNaughton 1991; Matches 1992). In

grasslands tall plants are generally favored in competition under low grazing intensities and often do not invest as heavily in leaf blade tissue, an investment that is crucial in allowing plants to attain an RGR necessary to assure rapid recovery from defoliation (McNaughton 1979; Oosterheld and McNaughton 1991). In addition, rapid growth in height places tissues in the spatial zone accessible to ungulates, making them more likely to be grazed (Arnold 1955; Koford 1958; McKinney and Fowler 1991; Painter et al. 1993). Thus, grazing tends to select for prostrate, low-growing ecotypes compared with the taller plants found in ungrazed or infrequently mowed habitats (Arnold 1955; Koford 1958; Bradshaw 1959; Hickey 1961; Westoby 1989; McKinney and Fowler 1991; Painter et al. 1993), and such selection has been demonstrated for Serengeti grasses (McNaughton 1979, 1984; Oosterheld and McNaughton 1991). Yet, we still do not know how prostrate stature of grazing adapted genotypes is related to RGR, a trait intimately related to grazing tolerance (Branson 1953; Ellison 1960; McKinney and Fowler 1991; Painter et al. 1993). In this paper we examine the relationship between grass height and RGR for ten genotypes of *Sporobolus kentrophyllus*, a dominant grass from an intensively grazed site in the Serengeti National Park, Tanzania (McNaughton 1983).

Materials and methods

Plants of ten genotypes of *S. kentrophyllus* were collected from the Serengeti National Park. Two genotypes were collected in 1977 and the remaining eight in 1991. Plants were selected non-randomly in a 20×20 area with the aim of collecting plants of different morphologies that would represent separate genotypes during both collections. These plants were propagated vegetatively in a greenhouse in Syracuse, N.Y. From each genotype we grew 16 plants in the greenhouse. Half the plants were treated with a synthetic bovine urine (Day and Detling 1990) at a rate of 40 g N m⁻² to simulate the effect of receiving a high nitrogen pulse early in the growing season. All plants were grown in 15 cm pots filled with calcined clay, watered to field capacity daily, and received Hoagland's complete nutrient solution weekly (0.58 g N m⁻² week⁻¹ for a total of 4.1 g N m⁻² over the length of the experiment). Plants were clipped to a height of 5 cm at weeks 0, 2, 4,

G. Hartvigsen (✉) · S.J. McNaughton
Biological Research Laboratories, Syracuse University,
130 College Place,
Syracuse, NY 13244-1220, USA

and 6. One plant from each treatment was harvested weekly for 7 weeks, for a total of eight plants per treatment. Plants were dried to a constant biomass at 60°C for 48 h. Clipped tissue was dried and treated as above-ground biomass. Plant height, determined as the tallest free-standing leaf above the clay substrate, was measured at 4 weeks, 2 weeks after clipping.

Whole-plant RGR was determined by sequentially testing cubic, quadratic, and linear functions for the relationship between \ln (biomass) versus number of days of the experiment (0–50 days at weekly intervals) (SAS 1990). For 18 of the 20 trials (ten genotypes each with and without urine) we found a very tight, significant linear relationship ($r^2 > 0.96$, $P < 0.001$), suggesting that RGR was constant for the duration of this experiment, and, therefore, was independent of plant size. The remaining two genotypes fit quadratic and cubic functions and occurred in the no-urine treatment. For these we determined instantaneous RGRs by differentiating and solving for time when plant height was measured (week 4). Though comparing plant RGR at a common time can be problematic when RGR is related to plant size (Coleman et al. 1994), this was not problematic in our case because: (1) RGR was independent of plant size for 18 of 20 cases and (2) our interpretation of the relationship between plant height and RGR was unchanged when we used a linear function for the two genotypes fitting quadratic and cubic functions (e.g., the r^2 value, for the genotype fitting a cubic function, decreased from 0.996 to 0.974 when fitted with a line, and this relationship remained significant at $P < 0.0001$). In addition, above- and below-ground RGRs were calculated using linear regression (r^2 ranged between 0.89 and 0.999, $P < 0.01$).

The difference between RGRs of genotypes for urine and non-urine treatments was tested using a t -test. Multiple comparisons of mean plant height among genotypes was performed using least-significant differences ($\alpha = 0.05$).

Results

Plant height was inversely related to mean whole-plant RGR during the 7-week experiment when treated with synthetic urine ($r^2 = 0.77$; $P < 0.001$; Fig. 1) but there

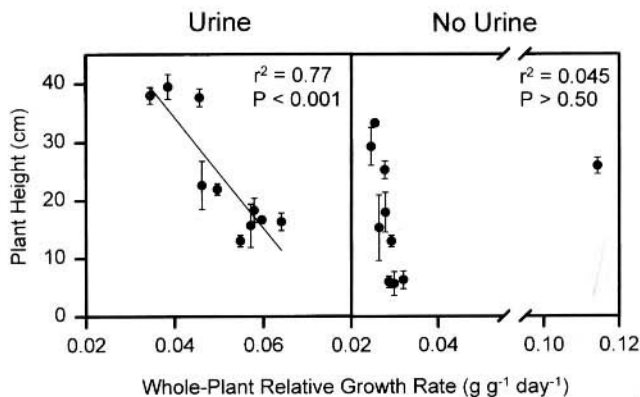


Fig. 1 Height from ten *Sporobolus kentrophyllus* genotypes at week 4 plotted against mean whole-plant relative growth rate (RGR) for each genotype determined over the 7-week experiment. Relative growth rates were determined using least-squares regression of \ln (total biomass) against day ($\text{g g}^{-1} \text{day}^{-1}$). Error bars for plant height are ± 1 SD. The outlier in the no-urine treatment is the genotype with a significant cubic relationship between \ln (total biomass) and day, with RGR determined at the time plant height was measured (week 4). If fitted with a linear function the point joins the cloud of other genotypes ($r^2 = 0.25$, $P = 0.14$)

was no relationship when plants were not treated with urine ($r^2 = 0.045$; $P > 0.50$; Fig. 1). In addition, seven of the ten genotypes showed a significant increase in height in response to urine addition, one showed a decrease in height, and two genotypes were not affected, resulting in a significant urine \times genotype interaction ($P < 0.0001$; Table 1). RGRs were significantly higher for urine treatments ($P < 0.0001$; mean ± 1 SE: 0.028 ± 0.00077 for non-urine treatment, 0.051 ± 0.00303 for urine treatment). Most genotypes, therefore, respond to urine application, a condition that generally indicates grazer presence, by modifying plant height and growth rate.

In addition, we found that urine-treated plants had a positive slope for above- versus below-ground RGR ($m = 1.154$; $r^2 = 0.95$; $P < 0.0001$), though not significantly greater than 1.0 ($P = 0.149$; Fig. 2). We found no relationship between above- and below-ground RGR without urine ($r^2 = 0.01$; $P > 0.80$; Fig. 2). The finding that above-ground RGR was consistently higher than below-ground RGR (points above the equal above-ground:below-ground RGR line in Fig. 2) is consistent with the general trend in herbaceous plants, resulting in decreasing root:shoot ratios during growth (Wilson 1988a). These data, therefore, indicate that when treated

Table 1 Analysis of variance table for effect of urine and genotype on plant height. The urine \times genotype interaction suggests within-species plasticity in plant height in response to urine application. Seven genotypes increased height, one genotype decreased height, and two remained unchanged in response to urine application

Source	df	MS	F	P
Urine	1	483.4	78.0	<0.0001
Genotype	9	530.8	85.7	<0.0001
Urine * genotype	9	64.7	10.45	<0.0001

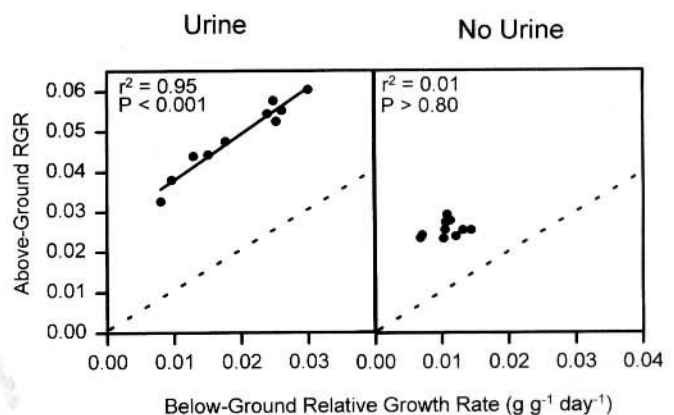


Fig. 2 Relationship between above- and below-ground relative growth rate (RGR) ($\text{g g}^{-1} \text{day}^{-1}$) for the ten *Sporobolus kentrophyllus* genotypes ($m = 1.154$; $r^2 = 0.95$; $P < 0.001$). Dashed lines represent equal above-ground:below-ground RGR ($m = 1.0$). Clones treated with urine show a slight but insignificant relative increase in above-ground to below-ground growth rate, compared to the line of equal above-ground:below-ground RGR ($P = 0.149$)

with urine, faster-growing plants have both relatively higher above-ground growth rates and are shorter in height.

Discussion

The relationship between plant height and growth rate determines a plant's ability to compete for light and tolerate herbivory. We have found for *S. kentrophyllus*, a dominant grass of the Serengeti Plains, that plant height and RGR were inversely related when plants received simulated bovine urine but were unrelated without urine addition. In addition, when treated with urine faster-growing, shorter plants tended to increase above-ground RGR relative to below-ground RGR. Previous attempts to link growth rate and morphology to competitive ability have been promising (Grime 1977; Gaudet and Keddy 1988; Lambers and Poorter 1992). Our results suggest that genetic variability and plasticity in growth rate and morphology allow this species to cope with the presence of grazing ungulates.

Competitive hierarchies between plants are not generally explained by RGR (Berendse and Elberse 1990; Lambers and Poorter 1992). Our results show that with urine addition plant height, an important morphological determinant of competitive ability (e.g., Wilson 1988b), is negatively related to RGR, suggesting that growth rate, in the absence of herbivory, is negatively related to competitive ability. This also suggests that the frequently observed positive relationship between plant size and reproductive output, particularly in vegetatively reproducing species, may need to be re-examined. The effect of herbivores on plant height variability has only recently been tested and found to increase variability, a response that may be important in other species as well (Weiner 1993). The observed height and RGR variability among genotypes of *S. kentrophyllus* in response to urine application, therefore, may be coupled to morphological responses to ungulate herbivory.

In the Serengeti Plains nutrient availability has been shown to be important in determining grazing animal movement patterns (McNaughton 1990). Simulated urine addition significantly increased growth rate and biomass accumulation in *S. kentrophyllus*, and has also been shown to be important for plants in a temperate grassland (Day and Detling 1990). The co-occurring genotypes from this study vary in their relationship between height and growth rate, suggesting that natural selection operates to maintain both plants that grow taller, a strategy likely to be competitively advantageous in the absence of herbivores, and plants which are shorter but grow faster in the presence of grazers.

Our results suggest a species-level tradeoff between plant height and growth rate when treated with urine, a factor that occurs when grazers are locally active. In absence of urine application, a condition that may signal plants of grazer absence, no tradeoff occurred between

plant height and growth rate. Spatial and temporal fluctuations in herbivore populations and the related grazing intensity may differentially confer an adaptive advantage to either tall or short genotypes. The coupling of plant height with growth rate may help to explain the coexistence of disparate growth strategies between genotypes within a species so that, in an evolutionary sense, species may hedge their bets between times which vary in the intensity of grazing pressure and urine deposition.

Acknowledgements We thank Terry Chapin, Jim Coleman, and an anonymous reviewer for helpful comments. Funding for this research was provided by the Syracuse University Graduate School (G.H.) and by NSF grant BSR-8817934 (S.J.M.).

References

- Arnold JF (1955) Plant life-form classification and its use in evaluating range conditions and trend. *J Range Manage* 8:175–181
- Berendse F, Elberse WT (1990) Competition and nutrient availability in heathland and grassland ecosystems. In: Grace JB, Tilman D (eds) *Perspectives on plant competition*. Academic Press, San Diego, pp 93–116
- Bradshaw AD (1959) Population differentiation in *Agnostis tenuis* Sibth. I. Morphological differentiation. *New Phytol* 58:208–227
- Branson FA (1953) Two new factors affecting resistance of grasses to grazing. *J Range Manage* 6:163–171
- Chapin FS III (1991) Integrated responses of plants to stress. *BioScience* 41:29–36
- Coleman JS, McConnaughay KDM, Ackerly DD (1994) Interpreting phenotypic variation in plants. *Trends Ecol Evol* 9:187–191
- Day TA, Detling JK (1990) Grassland patch dynamics and herbivore grazing preference following urine deposition. *Ecology* 71:180–188
- Ellison L (1960) The influence of grazing on plant succession. *Bot Rev* 26:1–78
- Gaudet CL, Keddy PA (1988) A comparative approach to predicting competitive ability from plant traits. *Nature* 334:242–243
- Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am Nat* 111:1169–1194
- Hickey WC (1961) Growth form of crested wheatgrass as affected by site and grazing. *Ecology* 42:173–176
- Koford CB (1958) Prairie dogs, whitefaces, and blue grama. *Wildl Monogr* 3, pp 1–78
- Lambers H, Poorter H (1992) Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. *Adv Ecol Res* 23:187–261
- Matches AG (1992) Plant response to grazing: a review. *J Prod Agric* 5:1–7
- McKinney KK, Fowler NL (1991) Genetic adaptations to grazing and mowing in the unpalatable grass *Cenchrus incertus*. *Oecologia* 88:238–242
- McNaughton SJ (1979) Grassland-herbivore dynamics. In: Sinclair ARE, Norton-Griffiths M (eds) *Serengeti: dynamics of an ecosystem*. Chicago University Press, Chicago, pp 46–81
- McNaughton SJ (1983) Serengeti grassland ecology: the role of composite environmental factors and contingency in community organization. *Ecol Monogr* 53:291–320
- McNaughton SJ (1984) Grazing lawns: animals in herds, plant form, and coevolution. *Am Nat* 124: 863–886
- McNaughton SJ (1990) Mineral nutrition and seasonal movements of African migratory ungulates. *Nature* 345:613–615
- Mooney HA (1972) The carbon balance of plants. *Annu Rev Ecol Syst* 3:315–346

- Noy-Meir I, Gutman M, Kaplan Y (1989) Responses of Mediterranean grassland plants to grazing and protection. *J Ecol* 77: 290–310
- Oosterheld M, McNaughton SJ (1988) Intraspecific variation in the response of *Themeda triandra* to defoliation: the effect of time of recovery and growth rates on compensatory growth. *Oecologia* 77:181–186
- Oosterheld M, McNaughton SJ (1991) Effect of stress and time for recovery on the amount of compensatory growth after grazing. *Oecologia* 85:305–313
- Painter EL, Detling JK, Steingraeber DA (1993) Plant morphology and grazing history – relationships between native grasses and herbivores. *Vegetatio* 106:37–62
- SAS Institute (1990) SAS/STAT User's Guide, version 6. SAS Institute Inc., Cary, NC
- Weiner J (1993) Competition, herbivory and plant size variability: *Hypochaeris radicata* grazed by snails (*Helix aspersa*). *Funct Ecol* 7:47–53
- Westoby M (1989) Selective forces exerted by vertebrate herbivores on plants. *Trends Ecol Evol* 4:115–117
- Wilson JB (1988a) A review of evidence on the control of shoot: root ratio, in relation to models. *Ann Bot* 61:433–449
- Wilson JB (1988b) The effect of initial advantage on the course of plant competition. *Oikos* 51:19–24