Responses of an African tall-grass (*Hyparrhenia filipendula* stapf.) to defoliation and limitations of water and nitrogen

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Summary. *Hyparrhenia filipendula* stapf., a tall (1–1.5 m) perennial grass common in dry-subhumid African savannas, was collected from Serengeti National Park in Tanzania, propagated vegetatively, and grown in controlled environments simulating conditions in nature. Plants were subjected to a factorial experiment with combinations of watering frequency, nitrogen supply, clipping height (10 and 15 cm) and clipping frequency (7 and 14 d). Biomass yield and allocation to various tissue types, morphometric traits, and growth processes were measured.

Watering frequency affected leaf elongation rate while nitrogen affected tiller number. Clipped yield was strongly correlated with leaf elongation rate but not tiller number; therefore it was primarily controlled by the activities of intercalary rather than apical meristems. There was a negative exponential relationship between tillering and clipped yield per tiller. Plants that received both high nitrogen and high water closely followed a $-3/2$ power law in this trade-off. The fraction of total net photosynthate allocated to roots was not significantly related to any environmental treatment. Root and crown growths were not affected by defoliation treatment; leaf blade and stem growths were inhibited; and sheaths were inhibited only under low water.

Despite a tall stature, *H. filipendula* tolerated herbivory by increased photosynthetic rate (Wallace et al. 1984), through continued production of young tissues by intercalary meristems balanced against tiller number, and by a statistically constant proportional allocation to roots. Clipped yield increased only when both nitrogen and water were abundant, and then, proportional clipped yield did not surpass an upper asymptotic limit.

Simulation models suggest that African graminoids with a tall-statured morphology should respond more favorably to infrequent (>30 d) than frequent (<30 d) defoliation because of low tiller density and high yield per tiller, while shorter graminoids should exhibit the reverse tendencies (Coughenour et al. 1984a, 1984b; Coughenour 1984). Aboveground productivities of tall grasses should increase with cutting interval at intervals less than 30–45 d. Water stress should be lessened by defoliation, allowing greater photosynthesis and belowground tissue survival. While these models are relatively complex, they may nevertheless fail to capture the subtle complexities of combined morphological and physiological responses that might allow tall-grasses to withstand more frequent defoliation.

In the Serengeti ecosystem of Tanzania, *Hyparrhenia filipendula* is an important grass layer species of *Acacia* savannas which receive 900–1,100 mm rainfall annually (Sinclair 1977, McNaughton 1983). Those savannas represent the more mesic environments of the Serengeti as they occur in the wet half of a geographic rainfall gradient of 500 mm in the southeast to over 1,100 mm in the northwest (Norton-Griffiths et al. 1975). *Hyparrhenia filipendula* occurs predominantly on sandy ridge tops of the Park’s Northwest (Jager 1982; McNaughton 1983). It does not occur in the more arid Serengeti plains. The northern and western savannas are inhabited throughout the year by buffalo (*Syncerus caffer*), elephant (*Loxodonta africana*), topi (*Damaliscus korrigum*), gazelle (*Gazella granti*), and zebra (*Equus burchelli*). During the dry season, grasses are heavily grazed by migratory wildebeest (*Connochaetes taurinus*), zebra, and gazelle (Pennycuick 1975). Tall grass savannas are periodically burned.

*Hyparrhenia filipendula* is evidently best adapted to relatively light defoliation. In central Africa it is abundant only in the least heavily grazed plant communities (Whyte 1974). In a field in Zimbabwe *H. filipendula* was cut at a height of 4 or 12 cm every 2–16 weeks (Mufandaedza 1976a). Greater yields were attained with increasing intervals and greater cutting height. In pot trials with plants cut at 4 or 10 cm every 2–8 weeks, leaf yields were similar for all treatments but stem yields increased with cutting interval (Mufandaedza 1976b). Root, stubble, and total non-structural carbohydrates were higher in less frequent and less severe cutting regimes. However, in Ugandan grasslands where *H. filipendula* was cut monthly at a height of 5 and 20 cm, twice as much was harvested in the 5 cm treatment (Strugnell and Pigott 1978).

The experiment reported here is linked by a common methodology to experiments performed on short and mid-statured species from the Serengeti (McNaughton et al. 1983; Coughenour et al. 1985). Since water is more plentiful, and the growing season is longer, in the native environment of the tall-statured species, tall-statured species have a greater opportunity to accumulate leaf area and extend...
vertically upwards. However, tall stature may be maladaptive in environments dominated by grazing ungulates (Quinn and Miller 1967; Noy-Meir 1975; McNaughton 1979). In view of the differing selection pressures acting upon taller species, we expect them to exhibit differing responses to manifold variations in environmental defoliation, water and nitrogen treatments.

Materials and methods

*Hyparrhenia filipendula* clones were collected from the northern extension of Serengeti National Park and these were grown for almost 3 years in controlled environments. Plants were subdivided into equal sized ramets and transplanted to washed sand in polyvinyl-chloride tubes 3.7 cm inside diameter by 50 cm high. Photoperiod was 12 h with a light intensity of 116 nE cm⁻² s⁻¹. Plants were grown for 11 mo at 2⁴ combinations of clipping height (10 and 15 cm), clipping frequency (7 and 14d), watering frequency (30 ml every 1 or 2d), and nitrogen (1 and 13 mM) in 30 ml Hoaglands No. 2 nutrient solution supplied every 4 days. Control plants were unclipped at each of the 2⁴ nitrogen-water combinations. There were two replications for each of the 20 treatments, which yielded a total of 40 experimental plants.

Clipped yields were accumulated over 47 weeks, when the experiment was terminated and plants were harvested, oven-dried, separated into components, and weighed. Leaf moisture was the difference between fresh and dry weight. Leaf elongation rates were determined once, over a 7 day period, after 14 weeks of growth. Tiller number, leaf number, leaf area, and crown area were determined at the end of the experiment. Plant tissues were separated into root, crown, stem, sheath, leaf (blade), litter (dead shoots), and clipped yield. “Residual live” was the sum of all green shoots, crowns, and roots at the end of the experiment. Total yield was the sum of residual live, clipped yield, and litter.

The data were analyzed by constructing general linear models with SAS (Helwig and Council 1979). The models included all main effects and two through four-way interaction terms. The models were unbalanced in the sense that there were half as many unclipped plants as clipped plants per nitrogen-water combination. Type 1 sums-of-squares were used for significance testing. The Duncan-Waller multiple range test was used to assess significant differences between three or more means. Least squares methods were used to examine associations between plant traits. All proportions were angularly transformed for statistical testing.

Results

Biomass production by *Hyparrhenia* was affected by clipping, nitrogen, water, and nitrogen-water interaction (Table 1). Significant effects of clipping height on stem, litter, clipped yield, and leaf masses reflected different responses of clipped and unclipped plants (Table 2). High nitrogen stimulated growths by a factor of 2–4 in frequently watered plants. Frequent watering increased leaf, sheath, stem, and root weights in high-nitrogen plants by 51%, 64%, 266%, and 78% respectively. Clipped yield was stimulated only with combined high-nitrogen and frequent watering. Clipping frequency affected only clipped yield, with 43% more yield under infrequent clipping.

Morphological responses to environmental treatments were similar to biomass responses (Tables 1 and 3). Nitrogen stimulated tiller number (102%), total leaf number (102%), leaf area (129%), leaf length (26%), and leaf width (39%). Frequent watering stimulated leaf area by 24%, leaf elongation rate by 47%, and total leaf number by 37%. Leaf length was 38% less, but leaf elongation rate was 84% grater in clipped plants than unclipped plants.

Any two components of total yield tended to be positively correlated. Correlation coefficients (r) ranged from 0.34 to 0.79 with the exceptions of the low correlation between stem and crown tissues (r = 0.23), and (among all plants) between clipped yield and leaf (r = 0.13), stem (r = 0.02) or crown (r = 0.02). Among clipped plants, clipped yield was correlated with everything except crown mass (r = 0.23). A positive correlation between root and clipped yields (r² = 0.62, P = 0.0001) indicated that increased removal of shoot tissues did not impair root growth.

There was nearly twice as much proportional allocation to litter in unclipped plants compared to clipped plants (Table 4). Frequent watering stimulated the proportion of litter in unclipped plants. Allocation of total yield was affected by nitrogen, clipping, and water. Surprisingly, there were no treatment effects on the total fraction of yield that was located above or belowground. However, a greater fraction was allocated to residual leaves and sheaths with high nitrogen. High nitrogen increased the fraction of crowns in plants clipped to 10 cm. Overall, plants clipped to 10 cm allocated a higher fraction of total yield to crowns, but a smaller fraction to residual leaf and stem biomass. A greater fraction was clipped off from 10 cm than from 15 cm clipped plants. Frequently watered plants had greater fractions of crown and clipped yields than infrequently watered plants. Among unclipped plants there was a greater fraction of litter with frequent watering. Root biomass as a fraction of total yield (31%) was unaffected by treatment.

As more shoot tissue grew into the clipping zone, the overall allocation pattern changed. The proportion of total yield that was clipped off increased but reached an asymptote (Fig. 1) indicating that plants with highest clipped yields allocated a constant, minimal fraction of their total photosynthetic to ungrazeable biomass while low-yield plants invested relatively more in ungrazeable biomass. There was a tendency for high-nitrogen plants to be below, and for low-nitrogen plants to be above, the regression line. Simultaneously the proportion of residual biomass consisting of root tissue remained constant as clipped yield increased (r² = 0.03, P = 0.34).

Five components of shoot growth might have determined clipped yield. The product of specific leaf weight, leaf width, and elongation rate is individual leaf growth rate (mass/leaf/time), while the product of tiller number and leaves per tiller is the total leaf number. Two of these, leaf elongation rate (r² = 0.37, P = 0.001) and specific leaf weight (r² = 0.25, P = 0.004), were correlated with clipped yield while leaf width, tiller number, and the number of leaves per tiller were not correlated with clipped yield. Thus, morphological controls over individual leaf growth affected clipped yield, while factors affecting total leaf number did not affect clipped yield. Thus, intercalary, rather than apical, meristems exerted primary control over clipped yield.

The effect of environmental treatments on clipped yield were the result of interactive effects of water and nitrogen on specific components of growth (Tables 1 and 3). Leaf