Oecologia (Berl) (1981) 49:272–278

Oecologia

Growth, Morphology and Gas Exchange of Mycorrhizal and Nonmycorrhizal *Panicum coloratum* L., a C_4 Grass Species, under Different Clipping and Fertilization Regimes

L.L. Wallace

Syracuse University, Department of Biology, Biological Research Labs, 130 College Place, Syracuse, NY 13210, USA

Summary. Root samples collected in grasslands of the Serengeti ecosystem, Tanzania, were found to be mycorrhizal and infection frequency was positively correlated with grazing intensity across sites. To examine the role of mycorrhizae in a grazing ecosystem, I analyzed the growth, morphology and gas exchange of mycorrhizal and nonmycorrhizal plants of *Panicum coloratum* L. under different fertilization and clipping regimes. Both severe clipping and high nitrogen promoted more prostrate shoot growth but inhibited root growth. However, mycorrhizal infection promoted a prostrate shoot morphology and enhanced root growth. Photosynthesis was inhibited by clipping, however; at the most severe clipping and nitrogen regime, photosynthesis of the mycorrhizal plants was not affected whereas the largest inhibition of photosynthesis occurred in similarly treated nonmycorrhizal plants. Discussion of the putative roles of mycorrhizae in intensely grazed ecosystems is presented.

Introduction

Mycorrhizal fungi affect their host's growth via several mechanisms, most prominently by improving the nutrient relations of the host plant (Harley 1969; Reid and Brown 1979). In turn, the host provides carbon to the fungus, frequently acting as the fungi's sole carbon supply (Christie et al. 1978). In a grazing ecosystem, grazer removal of above ground tissue may be deleterious to below ground growth (Troughton 1977). If the plant is mycorrhizal, the fungal response to loss of carbon due to grazing could be either 1) the fungus behaves more as a parasite than as a symbiont or 2) the infection frequency could be less.

The grazing environment in which I worked was the Serengeti ecosystem in NW Tanazania and SW Kenya which supports the largest biomass of grazing ungulates in the world (Hillborn and Sinclair 1979). Grazing is intense and plants have been found to compensate somewhat for herbage removal (McNaughton 1979). This may lead to a depletion of root reserves which could affect the plant-fungus symbiosis adversely. In such a heavily grazed environment are plants able to maintain carbon flows to both above ground consumers and mycorrhizal fungi? If so, what benefit does the plant accrue by doing this, i.e., what is the role of mycorrhizae in a grazing ecosystem? I considered this question in two ways. First, are plants in the grazing environment mycorrhizal and is there any relationship between infection frequency and grazing intensity? Second, what effect does mycorrhizal infection have on growth rate, morphology and gas exchange of grasses under different clipping and fertilization regimes imposed in the laboratory?

Methods

1) Field Studies

Root samples were collected in the Serengeti region of NW Tanzania and SW Kenya from 10 sites. Grazing intesity at each site had been determined previously (McNaughton 1979). Roots were washed, stored in formalin-acetic acid-alcohol (Christie et al. 1978) and returned to the laboratory for analysis. Infection frequency was determined by staining roots using a method modified from Phillips and Hayman (1971) and counting the number of 1 cm long sections infected out of a total sample of 30 sections. I examined the correlation between infection frequency and grazing intensity using least squares regression techniques.

2) Laboratory Studies

Twenty four plants of *Panicum coloratum* L., a C_4 mid-grass species in the Serengeti, were grown in an unbalanced factorial treatment design of mycorrhizal presence, clipping height and nitrogen availability. Nonmycorrhizal plants were obtained by rooting cuttings in distilled water and then placing them in sterile sand in surface sterilized 15 cm plastic pots. Mycorrhizal plants were obtained from our laboratory stock populations and were grown similarly in nonsterile, washed sand in a PGV-36 high-light intensity Conviron (Conviron, Pembina, ND, U.S.A.) plant growth chamber. Temperature and relative humidity were programmed to simulate field conditions of a 12 h photoperiod with the maximum day temperature of 30° C, the minimum night temperature of 14° C. Temperature and relative humidity were changed hourly to mimic the field diurnal cycle. Light intensity measured with a LI-190S quantum sensor (Licor, Inc., Lincoln, NB, U.S.A.) averaged 116 nE cm^{-2} s^{-1} at plant height.

Clipping height was either unclipped, 5 cm, or 10 cm with plants clipped every 6 days. Fertilization with 30 ml Hoagland's #2 was every four days with nitrogen at either 13 mM or 1 mM. Plants were watered with 30 ml distilled water every day except the day of fertilization. These treatments were chosen based on field observations of grazing height and frequency and soil nitrogen levels (McNaughton 1976, 1979; deWit 1978).

These conditions were maintained for nine weeks, after which I measured gas exchange rates and harvested the plants. Growth form and growth rate parameters were collected on the harvest date as well as immediately before harvest when it was determined that the plants had reached a steady state of growth. Growth parameters measured prior to harvest were leaf angle, shoot angle, canopy height, leaf elongation rate, number of leaves in the clipping zone and dry weight removed with each clipping (offtake). Following harvest, plants were separated into leaves, sheaths, crown, roots, litter and flowers. Each component was dried and weighed. Mean leaf length and width were determined along with crown area (cm^2), leaf area (cm^2), specific leaf weight (mg cm^{-2}), total number of tillers and total number of flowers. The total biomass of the plant when it was harvested was termed terminal weight. This value was added to the amount of offtake

0029-8549/81/0049/0272/$01.40

to obtain total weight. Comparable biomass values were obtained for living tissue by subtracting the weight of litter from each total weight or terminal weight term. A subsample of roots was taken and mycorrhizal infection frequency was determined as for the field root samples. Nitrogen content was determined using a micro-kjeldahl procedure.

Gas exchange was measured in a standard, open gas exchange system described previously (Wallace et al. in prep.). Light, temperature and CO_2 response curves were measured as was dark respiration at the end of the photoperiod. The light response curves were obtained at incident light intensities of 8, 38 and 116 nE cm^{-2} s^{-1} and a leaf temperature of 35° C. Temperature response curves were measured at 116 nE cm^{-2} s^{-1} and leaf temperatures of 25, 30, 35 and 40° C. Ingoing CO_2 and relative humidity were maintained at 330 ppm and 20%, respectively. The CO_2 response curves were measured at the highest light intensity and 35° C leaf temperature using external CO_2 concentrations of 330, 80 and 0 ppm. Internal CO_2 concentrations were calculated and the CO_2 response curve was plotted using those values. The slope between the lower two points of this curve was the inverse of intracellular resistance. Dark respiration was measured at the mean nighttime leaf temperature of 19.6° C, with an ingoing CO_2 concentration of 330 ppm and a relative humidity of 20%. All data were analyzed using an unbalanced factorial ANOVA (Barr et al. 1976; Helvig 1977) and by multiple regression techniques.

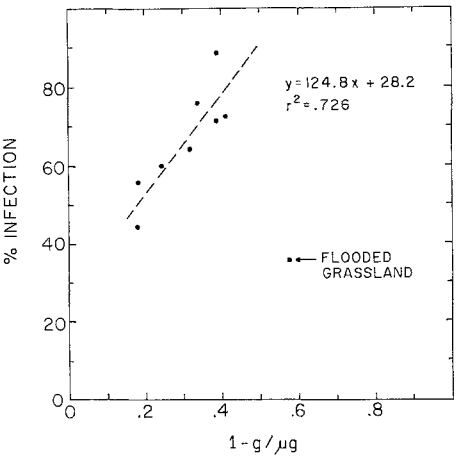

Fig. 1. The relationship between mycorrhizal infection frequency and grazing intensity (1–g/μg) at each of nine sites in the Serengeti ecosystem, Tanzania. The equation resulting from least squares regression analysis and the resulting line are given, excluding the data collected from one site which is occasionally flooded

Results

1) Field Studies

One field sample could not be used since the root cortex was lost during the staining process. Of the remaining nine samples, all were mycorrhizal, ranging in infection frequency from 36% in an occasionally flooded grassland, to 88% in a patch of annual grasses. Infection frequency was positively and significantly correlated with grazing intensity (Fig. 1). Excluding the flooded grassland, since mycorrhizae generally do not flourish in anaerobic conditions (Tansy 1977), a linear relationship defined 73% of the variance in mycorrhizal infection frequency. At site 2, a mid-grass area with a mean grazing intensity of 0.184 (McNaughton, 1979), two collections were made, one in an ungrazed patch (approximately 36 m^2) and one in a grazed patch (approximately 30 m^2). Infection frequenzy was higher in the grazed area (56% vs 44%) even though both areas had similar floristic compositions.

2) Laboratory Studies

a) Growth and Yield

All 3 environmental treatments affected plant growth, as indicated by differences in terminal weight, terminal living biomass, total weight, and total living biomass (Table 1). The presence of mycorrhizae and the high nitrogen treatment both stimulated all yield measurements. Mycorrhizae, on average, stimulated plant yield over 20%, and the high nitrogen treatment increased yield an average of 30% over the low nitrogen treatment. Clipping, in contrast, had a deleterious affect on yield that increased with the severity of defoliation. Both total weight and total biomass, which included weights of tissues removed due to clipping, were less than half control values at the 5 cm clip height.

Differences in whole plant weights resulting from environmental factors were a consequence of different treatment effects on different plant parts (Table 2). Mycorrhizae stimulated root growth substantially, with the weight of roots of mycorrhizae-infected plants averaging over 60% greater than root yields of mycorrhizae-free plants. Increased nitrogen availability tended to have opposite effects on different components of plant yield. Therefore, the nitrogen treatment effects on whole plant biomass averages were not significant (Table 1). High nitrogen promoted leaf production substantially, while litter production was reduced at the high nitrogen treatment, suggesting leaf longevity was substantially greater when higher nitrogen levels were supplied. Clipping had deleterious effects on 5 plant components, reducing leaf blade, crown, leaf sheath, root and flower weight, with the proportional reduction greatest for the latter component.

Plant biomass accumulation can be viewed as plant output to various ecosystem trophic levels. Offtake by clipping is the

Table 1. Whole plant biomass averages (g DW) for the three clipping regimes, and the two mycorrhizal and nitrogen regimes. Terminal weight is the plant weight harvested at the end of the experiment, terminal living biomass is terminal weight less litter, total weight is terminal weight plus offtake, total living biomass is total weight less litter. Significance tests are the result of three way ANOVA's performed on whole plant biomass

	Mycorrhizae				Clipping					Nitrogen			
	Present	Absent	F	*p*	Unclipped	10 cm	5 cm	F	*p*	High	Low	F	*p*
Terminal weight	9.4	7.8	4.8	0.05	12.4	9.1	4.0	17.2	0.0003	9.5	7.7	0.4	0.54
Terminal living biomass	8.0	6.4	6.2	0.03	10.3	7.7	3.4	18.0	0.0002	8.2	6.2	1.8	0.21
Total weight	10.5	8.6	4.9	0.05	12.4	10.5	5.6	9.6	0.003	10.8	8.3	1.1	0.32
Total living biomass	9.0	7.2	6.0	0.03	10.3	9.1	4.9	8.7	0.005	9.4	6.8	3.0	0.11

Table 2. Significant treatment effects and interactions on the average biomass accumulation (g DW) of each morphological component of the plants as they were harvested. Significance was determined using an unbalanced ANOVA

a) Leaf

Clipping	Nitrogen		
	High	Low	Mean
Unclipped	1.9	1.5	1.7
10 cm	1.7	0.6	1.1
5 cm	0.6	0.5	0.55
Mean	1.4	0.8	

Interaction $F=5.07$ $p=0.0254$; $F_{nit}=22.4$, $p=0.0005$; $F_{clip}=30.4$, $p<0.0001$

b) Sheath

Clipping		
Unclipped	10 cm	5 cm
1.2	0.9	0.3

$F_{clip}=12.8$, $p=0.0011$

c) Crown

Clipping		
Unclipped	10 cm	5 cm
3.2	2.4	1.2

$F_{clip}=7.4$, $p=0.0081$

d) Root

Clipping	Mycorrhizae		
	Present	Absent	Mean
Unclipped	4.9	3.3	4.1
10 cm	3.8	1.8	2.8
5 cm	1.4	1.1	1.3
Mean	3.4	2.1	

Interaction $F=1.79$ $p=0.2092$; $F_{myc}=11.1$, $p=0.006$; $F_{clip}=17.8$, $p=0.0003$

e) Litter

Clipping	Nitrogen		
	High	Low	Mean
Unclipped	1.3	3.0	2.1
10 cm	1.4	1.0	1.2
5 cm	0.5	0.7	0.6
Mean	1.1	1.6	

Interaction $F=3.74$ $p=0.0546$; $F_{clip}=7.1$, $p=0.0093$; $F_{nit}=2.3$, $p=0.154$

Table 2 (continued)

f) Flower (mg DW)

Clipping		
Unclipped	10 cm	5 cm
106	19	1.3

$F_{clip}=20.1$, $p<0.0001$

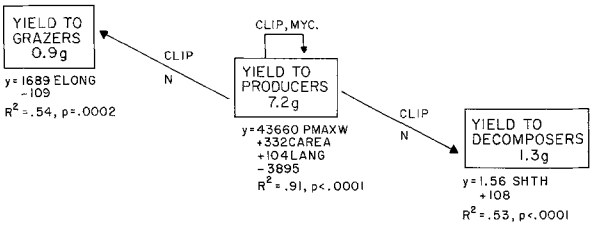

Fig. 2. Three plant biomass components viewed as outputs to various trophic levels in the ecosystem. Significant treatment effects ($p<0.05$) are shown on the arrows representing carbon flows between components with the average dry weight (g DW) listed inside each box. Correlations of the biomass allocation to each yield with various physiological and morphological parameters were determined using multiple regression analysis. The independent variables given in the equations are leaf elongation rate (ELONG, cm day^{-1}), maximum light saturated photosynthesis (PMAXW, mg CO_2 g^{-1} h^{-1}), crown area (CAREA, cm^2), leaf angle (LANG) and sheath biomass (SHTH, mg DW)

equivalent of yield to grazers, while litter production is yield to decomposers. The remaining live plant biomass is a yield to the producers. The production of litter, the amount available to grazers and the amount remaining in the plant system were all affected by different treatments (Fig. 2). These treatments are signified by the labels on the arrows symbolizing carbon flows between trophic yields in Fig. 2. The mechanism of the treatment effect on each yield was ascertained by determing the correlation between the dry weight allocation of that yield and various morphological and physiological parameters using multiple regression techniques.

Clipping and nitrogen acted on litter production primarily through their effects on sheath production and senescence. Both intense clipping and high nitrogen reduced the rate of senescence of above ground tissue. Offtake, or yield to grazers, was enhanced by high nitrogen and by clipping via their effects on leaf elongation (Table 3). The more rapidly elongating leaves grew into the clipping zone, the higher was the yield to grazers. On average, clipping removed only 10.6% of the total plant biomass. Yield to producers, the residual living plant biomass, was higher in mycorrhizal plants and was lowest in the severe clipping regime. The mechanisms involved were both physiological, since clipping inhibited photosynthesis, and morphological (crown area and leaf angle), both of which will be discussed in more detail below.

b) Morphology

In a grazing evironment, plants may assume prostrate growth forms and thereby escape from herbivores (Youngner 1972). Several components of plant morphology interact to yield the final three-dimensional placement of leaves and stems. One of the most important of these is crown area since this dictates the number of meristems or potential stems. Only one treatment,

Table 3. Significant treatment effects on leaf elongation rate (cm day^{-1}) and the average amount of biomass removed (g DW). Significance was determined using an unbalanced ANOVA

Elongation rate

Clipping	Nitrogen		
	High	Low	Mean
Unclipped	0.27	0.23	0.25
10 cm	1.07	0.56	0.81
5 cm	1.12	0.64	0.88
Mean	0.82	0.84	

Interaction $F=3.15$ $p=0.0795$; $F_{clip}=22.2$, $p<0.0001$; $F_{nit}=16.4$, $p=0.0016$

Offtake

Clipping	Nitrogen		
	High	Low	Mean
Unclipped	0.0	0.0	0.0
10 cm	1.8	0.6	1.2
5 cm	1.8	1.1	1.4
Mean	1.2	0.5	

Interaction $F=1.87$ $p=0.1964$; $F_{clip}=13.5$, $p=0.0008$; $F_{nit}=6.5$, $p=0.026$

Table 4. Significant treatment effects on morphological parameters as determined using an unbalanced ANOVA. Values shown are averages for each treatment

a) Tiller number

Mycorrhizae	Nitrogen		
	High	Low	Mean
Present	26.8	18.8	22.8
Absent	18.5	13.7	16.1
Mean	22.6	16.2	

Interaction $F=0.79$ $p=0.3930$; $F_{myc}=7.7$, $p=0.017$; $F_{nit}=7.1$, $p=0.021$

b) Crown area (cm^2)

Mychorrhizae	
Present	Absent
16.4	11.8

$F_{myc}=5.2$, $p=0.042$

c) Tiller density ($\#cm^{-2}$)

Clipping		
Unclipped	10 cm	5 cm
1.5	1.2	1.7

$F_{clip}=3.6$, $p=0.061$

Table 4 (continued)

d) Shoot angle

Clipping	Nitrogen		
	High	Low	Mean
Unclipped	60	77	68
10 cm	61	67	64
5 cm	46	62	54
Mean	56	69	

Interaction $F=0.056$ $p=0.5904$; $F_{clip}=4.64$, $p=0.0375$; $F_{nit}=6.56$, $p=0.0284$

e) Leaf angle

Nitrogen	
High	Low
47	60

$F_{nit}=19.0$, $p=0.0014$

f) Canopy height (cm)

Clipping	Nitrogen		
	High	Low	Mean
Unclipped	11.0	18.0	14.5
10 cm	9.6	9.0	9.3
5 cm	8.8	5.5	7.2
Mean	9.8	10.8	

Interaction $F=16.88$ $p=0.0009$; $F_{clip}=26.1$, $p<0.0001$; $F_{nit}=0.49$, $p=0.498$

mycorrhizal infection, significantly increased crown area ble 4). The number of tillers actually produced was stimulated by mycorrhizal infection and by high nitrogen fertilization. When more tillers are produced on a given crown area, many of the tillers will be produced on the edge of the crown. Instead of being oriented vertically, these buds are oriented more horizontally, yielding a lower shoot angle. Clipping, although not stimulating tillering per se, increased tiller density (Table 4). This led to the severely clipped plants having a greater number of tillers produced from the edge of the crown where there is less crowding and, therefore, having a lower shoot angle or more prostrate growth.

Mycorrhizal plants have an average tiller density of 1.7 cm^{-2} compared with the nonmycorrhizal density of 1.9 cm^{-2}. Shoot angle measured as degrees from horizontal was significantly lower in mycorrhizal plants, though (58° vs 66°, $p>0.02$, paired t-test), making it appear that mycorrhizal plants are able either to stimulate tillering on the edge of the crown or have lower shoot angles regardless of where the shoot is produced. The large crown area of mycorrhizal plants is the product of tiller growth on the edge, therefore making the latter possibility less likely.

High nitrogen also resulted in lower shoot angles (Table 4). Since high nitrogen stimulated tillering, the same explanation given for the other treatments would hold. Nitrogen fertilization resulted in a more horizontal leaf display as well.

Table 5. Significant treatment effects and interactions on gas exchange parameters as determined using an unbalanced factorial ANOVA. Values shown are means for each treatment combination. F values and their associated p values are given for both the interactions and the main effects

a) Photosynthesis (mg CO_2 dm^{-2} h^{-1})

1) Under low nitrogen

Clipping	Mycorrhizae		
	Present	Absent	Mean
Unclipped	33.5	75.1	54.3
10 cm	16.1	47.3	31.7
5 cm	25.9	13.2	35.6
Mean	25.2	45.2	

Interaction $F=5.67$ $p=0.04$, $F_{clip}=8.5$ $p=0.02$, $F_{myc}=8.2$ $p=0.03$

2) Under high nitrogen

Clipping	Mycorrhizae		
	Present	Absent	Mean
Unclipped	55.7	36.2	46.0
10 cm	26.8	42.8	34.8
5 cm	37.5	23.0	30.3
Mean	40.0	34.0	

Interaction $F=1.83$ $p=0.24$, $F_{clip}=1.31$ $p=0.34$, $F_{myc}=0.53$ $p=0.49$

b) Specific leaf weight (mg cm^{-2})

Clipping	Mycorrhizae		
	Present	Absent	Mean
Unclipped	5.49	5.70	5.60
10 cm	5.27	6.97	6.12
5 cm	6.46	5.08	5.77
Mean	5.74	5.92	

Interaction $F=2.81$ $p=0.09$, $F_{clip}=0.07$ $p=0.94$, $F_{myc}=0.05$ $p=0.83$

c) Intracellular resistance (s cm^{-1})

Nitrogen	Mycorrhizae		
	Present	Absent	Mean
High	3.45	5.79	4.62
Low	3.09	4.99	4.04
Mean	3.27	5.39	

Interaction $F=3.25$ $p=0.09$, $F_{nit}=0.39$ $p=0.54$, $F_{myc}=0.88$ $p=0.37$

d) Mean differences in rates of photosynthesis (mg CO_2 dm^{-2} h^{-1}), Unclipped mean – clipped value

1) Under low nitrogen

Clipping	Mycorrhizae		
	Present	Absent	Mean
10 cm	17.4	27.7	22.6
5 cm	7.6	61.9	34.8
Mean	12.5	44.8	

Interaction $F=5.99$ $p=0.07$, $F_{clip}=1.84$ $p=0.25$, $F_{myc}=2.97$ $p=0.02$

Table 5 (continued)

2) Under high nitrogen

Clipping	Mycorrhizae		
	Present	Absent	Mean
10 cm	28.9	−6.6	11.2
5 cm	18.3	13.3	15.8
Mean	23.6	3.4	

Interaction $F=1.68$ $p=0.26$, $F_{clip}=0.15$ $p=0.72$, $F_{myc}=2.97$ $p=0.16$

e) Leaf nitrogen content (%)

Nitrogen	Mycorrhizae		
	Present	Absent	Mean
High	2.81	2.27	2.55
Low	1.28	1.41	1.35
Mean	2.04	1.85	

Interaction $F=15.0$ $p=0.002$, $F_{nit}=201.4$ $p<0.0001$, $F_{myc}=5.29$ $p=0.04$

Although only clipping height had a significant effect on canopy height (Table 4), all of the factors discussed above (tiller density, shoot angle and leaf angle) interacted to produce the ultimate plant height in either clipped or unclipped regimes. More important than actual canopy height is the amount of biomass produced and maintained below the clipping zone. Those treatments that promoted prostrate growth maximized production of this biomass component (Fig. 2).

c) Gas Exchange Physiology

Photosynthesis was highest in the unclipped, nonmycorrhizal plants, averaging 42% greater than the rates of other treatments (Table 5a). Clipping was the only significant main effect on photosynthesis, reducing rates up to 50% in the most severely clipped regime. There were two significant interactions, mycorrhizae * nitrogen and mycorrhizae * clipping, accounting for 11% and 16% of the explained variance respectively. When the full model was decomposed by nitrogen, these interactions were found to be due to the effects of mycorrhizae under the low nitrogen regime. The inhibition of photosynthesis caused by clipping was much more severe in the low nitrogen regime when mycorrhizae were absent (Table 5d). However, when mycorrhizae were present, there was negligible inhibition caused by clipping in the low nitrogen regime.

In order to understand the mechanisms of this complex photosynthetic response, I performed multiple regression analysis with photosynthesis as the dependent variable. Photosynthesis (PMAXA) correlated more closely with intracellular conductance (CI) (1/resistance) than with stomatal conductance (CS), which indicates that photosynthesis was controlled more by intracellular conductance. A representative CO_2 response curve from which intracellular conductance was calculated is shown on Fig. 3C. The regression equantions and their associated significance tests were:

$PMAXA=21.9\ CS+25.4$, $R^2=0.07$, $F=1.54$, $p=0.23$,

$PMAXA=39.4\ CI+14.6$, $R^2=0.54$, $F=22.6$, $p>0.0001$.

The two components of intracellular resistance (1/conductance) are transfer resistance and carboxylation resistance. An

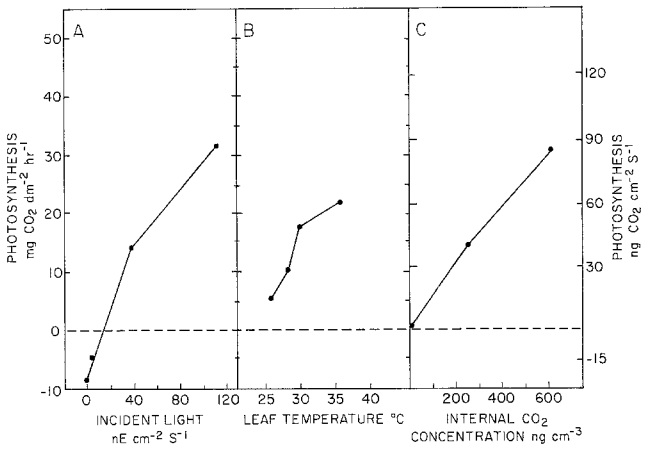

Fig. 3A–C. Representative photosynthetic response curves to incident light (**A**), leaf temperature (**B**) and internal CO_2 concentration (**C**). Note different axes on panel C. The plant whose responses are graphed here was unclipped, mycorrhizal and receiving low nitrogen fertilizer

indirect measure of transfer resistance is specific leaf weight, which, when high, indicates a low transfer resistance. The crude protein or nitrogen content of the leaf is an indication of the amount of protein available to make carboxylating enzymes and therefore a high leaf nitrogen or crude protein content may be associated with low carboxylation resistance. Specific leaf weight was lowest in the unclipped plants, which could mean that transfer resistance was high (Table 5b). Leaf nitrogen content also was lowest in the unclipped plants which would indicate that carboxylation resistance was high (Table 5e). A more direct measure of these resistance values is needed, such as measuring the A^{mes}/A ratio (Nobel 1977) or the carboxylating enzyme activity.

Photosynthetic responses to light and leaf temperature were unaffected by the treatments. The average light compensation point was 1.1 nE cm^{-2} s^{-1}. Since temperature control was not precise, the temperature optimum is that leaf temperature, out of the four used, that resulted in the highest measured photosynthetic rate and therefore does not represent an optimum in the truest sense. However, the mean temperature "optimum" was 34° C, a value in the range commonly reported for C_4 plants. Representative light and temperature response curves are shown on Fig. 3A and B.

Dark respiration also was unaffected by the treatment regimes. The mean values of dark respiration was 11.7 mg CO_2 dm^{-2} h^{-1}. On average, dark respiration was 22% of gross photosynthesis, much lower than values of 31 and 42% reported for C_3 grasses (Mogensen 1977). This indicates that *P. coloratum,* irrespective of its mycorrhizal, nutrient or grazing status, potentially has a very favorable carbon budget.

Discussion

A significant correlation between grazing intensity and mycorrhizal infection was found in the field. What may be the underlying mechanisms of this relationship? Contrary to field data, where grazing can stimulate production (McNaughton 1979), production was inhibited by clipping in the laboratory, similar to results obtained by Ackerson and Chilcote (1978). Mycorrhizal infection or fertilization can therefore affect plant growth only within the genetic limitations of that plant (Harley 1969). The plants used in this study were collected from an area of little grazing pressure. I feel, then, that the putative mechanisms of relationship between mycorrhizal infection and grazing discussed below must be considered as hypotheses for further work rather than as definitive statements of relation for the entire ecosystem.

A plant which is optimally adapted to withstand grazing pressure does so via prostrate, spreading growth (Hyder 1972) and maintenance of sufficient root biomass to supply above ground needs. In this study, clipping in itself and high nitrogen produced prostrate plants but did so while minimizing root production. However, mycorrhizae produced prostrate plants as well as enhanced root growth.

Inhibition of production resulting from grazing in many instances is due to carbon mobilization from roots to shoots reducing water and nutrient availability (Jameson 1963; Marshall 1977). Two treatments, clipping and high nitrogen, resulted in minimal root growth and minimal photosynthesis. Thus, the prostrate shoot growth seen in these regimes, although adaptive in minimizing herbivore offtake, occurred at the expense of the plant's ability to supply itself with water, nutrients and carbon. Eventually, the diminished supply of these factors would limit growth and the yields to all three ecosystem tropic levels. For example, reduced nitrogen availability has been shown to have immediate effects on plant growth slowing cell elongation and division (Charles-Edwards 1979; Dale and Wilson 1979). Chlorophyll synthesis also is diminished with a subsequent reduction in photosynthetic efficiency was seen here. As a result of changes in these processes, yield to decomposers (litter production) is enhanced by low nitrogen and the yield to grazers (offtake) is enhanced by high nitrogen.

One primary role of mycorrhizae in a grazing environment apparently is to confer grazing tolerance on plants by maximizing plant biomass production below the grazing zone via promotion of tillering and prostrate growth while maintaining root production. The mechanism for this may be hormonal since mycorrhizae have recently been found either to produce cytokinins themselves or to stimulate root production of cytokinins in the host plant over control levels (Allen et al. 1980). Cytokinins stimulate cell division thus overriding apical dominance, increase respiration rates of cells and thereby increase the power of that tissue as a nutrient and carbohydrate "sink" (Gross 1972; Miller 1979; Moore 1979). The main effects of mycorrhizae in this study may have been mediated via an increase in cytokinin content of the infected plants since tillering was greater in infected plants, indicative of weak apical dominance (Youngner 1972), and root biomass was higher in infected plants which could result from these roots constituting a larger respiratory sink than uninfected roots (Trappe and Fogel 1977).

Another major function of mycorrhizae could be to buffer the plant from environmental extremes, i.e., allowing normal plant processes to occur at environmental extremes that would normally inhibit or stop that process from occurring. Under the low nitrogen regime, photosynthesis of mycorrhizal plants was unaffected by severe clipping whereas that of the nonmycorrhizal plants was the most severely inhibited. In many areas of the Serengeti, this low nitrogen, intensely grazed environment is what the plants experience during the growing season (McNaughton 1976, 1979). In order to account for the high growth rates observed in the field (McNaughton 1979), some amelioration of the effects of these environmental extremes must occur within these plants that would allow photosynthesis to continue at a high rate. Some types of environmental buffering have been attributed to mycorrhizae, particularly in revegetated mine spoils (Allen and Allen 1980; Khan 1978; Lambert and Cole 1980) and other disturbed areas (Antibus et al. 1980; Zak 1971), but never to my knowledge has this been considered in an ecosystem with naturally-occurring, periodic perturbations.

The mechanisms by which mycorrhizae reduce the effects of severe clipping and low nitrogen are not known. Photosynthesis in this study was most closely controlled by intracellular resistance similar to the results of Ludlow and Wilson (1971) on *P. coloratum*. They attributed this to changes in the biochemical rather than biophysical resistances. This may be the case here, as well, since mycorrhizae are known to have substantial effects on plant nutrient status (Harley 1969; Ho and Trappe 1975).

The interaction between grazing and mycorrhizal infection is manifested on two levels of organization, the individual plant level and as an ecosystem property. On the plant level, mycorrhizae promoted prostrate growth, thus minimizing losses to herbivores and promoted root growth, assuring the plant of adequate supplies of water and nutrients so that photosynthesis could continue unabated. Thus mycorrhizal infection greatly enhances the fitness of a plant in a grazing ecosystem.

On an ecosystem level, the positive relationship between grazing intensity and mycorrhizal infection may result from any or all of several factors. Mycorrhizae have been shown to result in tighter nutrient cycles (Odum 1971) which could result in higher quality forage which would attract grazers. Grazers themselves could promote mycorrhizal infection by moving spores from place to place and by dung deposition. Since dung is usually relatively improverished in phosphorous (Brady 1974), this would provide the nutrient regime favoring mycorrhizal growth (Harley 1969). These putative mechanisms of relation on both the individual plant and ecosystem levels will be the object of further study.

Acknowledgements. This work was supported by National Science Foundation grants DEB 77 20360 and DEB 79 22991 to S.J. McNaughton. The excellent technical assistance of M.M. McNaughton is deeply appreciated.

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Received November 25, 1980