INTERPRETING GUINEAGRASS BEHAVIOUR UNDER DIFFERENT CLIPPING, NITROGEN AND IRRADIANCE REGIMES

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ABSTRACT

An increase in the photosynthetic rate of the remaining tissues or regrowth has been proposed to explain compensatory growth after defoliation. In fact, we observed this effect in guineagrass, but it was not solely related to higher stomatal conductance. Nitrogen and irradiance may influence this response in the field, interacting with clipping. The objective of this research was to determine if these factors alter photosynthesis of intensively clipped well-watered guineagrass. Plants grown in a soil mixture were placed in the shade and in full sunlight. After establishment, some plants in each irradiance were clipped monthly at 20-cm, and the others left unclipped . Half of the plants in each irradiance and clipping regime were extra fertilized monthly using urea. With the clipped-off tissue, leaf area was measured, oven dried and weighed to obtain biomass. Samples were selected to analyze soluble sugar, starch, and total non-structural carbohydrates (TNC). A factorial 2^2x4 in a split plot completely randomized design was used. With the residual plants, photosynthesis and stomatal conductance were measured. In the final harvest biomass data was also obtained and a completely randomized 2^3 factorial arrangement was applied. In the clipped-off tissues significant differences were found for the biomass increments due to the nitrogen treatments, but not to irradiance regimes. Leaf area was more responsive to irradiance. In full sunlight, residual biomass was greatest using extra fertilization, both in unclipped and clipped plants. Clipped plants had higher photosynthesis than unclipped ones in the sun, and extra urea decreased this effect. Shaded guineagrass showing lower photosynthesis were not affected by clipping. Extra nitrogen applied in the shade alter only unclipped plants. When residual biomass and the clipped off tissues were added together, it was seen that clipping decreased total yield. In full sun, nitrogen fertilization reduced photosynthesis and stomatal conductance and increased chlorophyll both in clipped and unclipped plants. Higher photosynthesis in these well-watered plants was related with higher stomatal conductance, and higher yield with extra nitrogen.

KEYWORDS

Guineagrass, clipping, irradiance, fertilization, plant behaviour

INTRODUCTION

The enhancement in plant productivity observed as a result of grazing or clipping has been related to increased photosynthetic rates. This effect has been associated in some species with increased stomatal conductance (Painter and Detling, 1981; Detling and Painter, 1983; Wallace et al, 1984), but in other species no direct relationship has been found (Páez and González, 1995; Wallace, 1981), thus, other factors must have been involved. In previous research (Páez and González, 1995),the most closely clipped guineagrass plants exposed to water stress showed greater photosynthesis, but not increased stomatal conductance. Photosynthesis was also greater in the most frequently clipped plants. However, after reirrigation highest photosynthesis in closely clipped plants was associated with increased stomatal conductance. The increase in photosynthesis caused by close clipping is not fully related to higher stomatal conductance as previously reported, so other factors must be involved. This research was thus conducted in an attempt to understand the mechanism to explain the increase in photosynthesis caused by greater clipping focusing more specifically on the role of light and nitrogen in this response.

METHODS

Guineagrass plants were grown from certified seeds in a sandy-clay soil mixture in 50-kg plastic pots. After seedling emergence the population was thinned to one plant per pot, and then allowed to establish during 6 weeks. Half of the plants were placed in the shade (35% full sunlight) since the start of the experiments, and the others in full sunlight. In each light regime, a group of plants were clipped at 20-cm from the soil surface and the others were left unclipped. All the plants were fertilized every 30 d at a rate of 100 kg N, 50 kg P, and 50 kg K ha^{-1}. But, half of the 20-cm clipped plants and half of the unclipped ones in each light regime were fertilized with extra nitrogen (urea). Clipping treatments were performed monthly. With the clipped off tissue, leaf area was measured using a LI-3100 leaf area meter (LiCor, Lincoln, NE) and these tissues were oven dried at 65°C for 3d to obtain dry biomass. A factorial 2^2x4 in a split plot completely randomized design was used, where Nitrogen and Irradiance were the main plot and the evaluation each month was the secundary plot. In the third clipping, samples were selected to make determinations of sugar, starch, and total non-structural carbohydrates (TNC). TNC was determined using the method of Tissue and Wright (1995). Plant material was dried in an oven, ground into a fine powder, and then extracted three times with 2 ml of a methanol:chloroform:water (12:5:3 v/v) solution to separate the soluble sugars from the pellet fraction containing starch. The pellet was treated with 5 ml of perchloric acid (35% v/v) for 1 h to hydrolyse the starch. Soluble sugar and starch concentration were determined colorimetrically using a phenol-sulfuric acid method. TNC was calculated as the sum of soluble sugar and starch. With the remaining plants, photosynthesis, and stomatal conductance, were measured. A final harvest was made using all the plants. Roots were washed, placed individually in paper bags and oven dried. Leaves and culms were also separated and dried to obtain biomass. A completely randomized 2^3 factorial arrangement was used. The data were analyzed by the general linear models procedure of the Statistical Analysis Sistem (SAS) followed by the Tukey test for mean separation.

RESULTS AND DISCUSSION

The comparison between sun clipped-plants with and without extra nitrogen indicates more photosynthesis and higher stomatal conductance without extra nitrogen. However, more total dry biomass due to increased shoot and root development is obtained with extra nitrogen (Table 1). The same trend is observed when comparing sun-unclipped guineagrass with and without extra nitrogen. With extra nitrogen there is more root, shoot and total biomass, but lower photosynthesis and conductance (Table 1). In the shade, however, clipped plants with and without nitrogen do not show differences in photosynthetic rates, root, shoot and total dry biomass. Similar results were obtained previously (Páez et al., 1994). The unclipped plants with extra nitrogen had lower photosynthesis and more shoot biomass, causing greater total biomass under this condition. The fact that photosynthesis and stomatal conductance were greater without extra nitrogen in the sun-clipped and -unclipped plants, and without extra nitrogen in the unclipped plants only in the shade (Table 1), evidences a significant interaction between nitrogen and clipping for photosynthesis. In the clipped plants, chlorophyll content was higher in the shade than in the sun. This result is in agreement with the higher chlorophyll content obtained previously in shaded guineagrass plants (Páez et al., 1984). Chlorophyll was also higher with extra nitrogen in the sun and without extra nitrogen in the shade (Table 1). In the clipped off material, the data were analyzed by intervals, that is, by the difference between two succesive clippings. The dry biomass increments between the second and the first clippings, between the third and the second, and between the fourth and the third clippings were significant due to the nitrogen treatment, but no differences were found in leaf area increments, except for the last interval (Table 2). The irradiance regime caused significant differences in the leaf area increments in the last two intervals. In the first interval, no difference in leaf area increment was caused by the light regime. There were no differences in biomass increment due to light either (Table 2). Therefore, leaf area was more responsive to irradiance and yield was more altered by nitrogen fertilization than by light. More leaf area was produced in the shade and extra nitrogen increased this effect (Table 2). McNaughton et al (1983), concluded that nitrogen level was the major variable affecting the amount and proportion of total yield that was clipped off in an African C4 sedge. More sugars, starch and TNC in the clipped off material

were obtained in full sunlight than in the shade. Sugars and TNC were more abundant without extra nitrogen in the shade (Table 2). When residual biomass and clipped-off tissues were added together, it could be concluded that total yield was decreased by clipping as compared with unclipping (Tables 1 and 2), supporting the previous research data which shows that active leaf biomass was reduced by the shortest clipping height, more frequent clippings and water stress (Páez et al., 1995). In full sunlight, nitrogen fertilization decreases photosynthesis and stomatal conductance and increases chlorophyll content in clipped and unclipped guineagrass plants. In conclussion Leaf area was more responsive to irradiance and total yield to nitrogen fertilization. Clipped plants had higher photosynthesis in the sun, and extra urea decreased this effect. Clipping decreased total yield. In full sun, nitrogen fertilization reduced photosynthesis and stomatal conductance and increased chlorophyll. Higher photosynthesis in these well-watered plants was related with higher stomatal conductance, and higher yield with extra nitrogen.

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Table 1

Dry biomass, net photosynthesis, stomatal conductance and Chlorophyll content of guineagrass plants clipped at 20-cm from the soil surface or left unclipped, grown under two irradiance regimes, and fertilized with extra nitrogen (Extra N) or no extra nitrogen (No Extra N).

	DRY BIOMASS (g)			Photosynthesis	Conductance	Chlorophyll
	Root	Shoot	Total	($\mu molm^{-2}s^{-1}$)	($\mu molm^{-2}s^{-1}$)	(μmol/L)
SUN						
Clipped No extra N	70.4cd	98.8cd	169.2ef	40.24a	0.882a	22.80abc
Unclipped No Extra N	113.6cb	166.8c	280.4de	34.15b	0.769ab	14.52d
Clipped Extra N	150.8ab	266.8b	417.6bc	30.75c	0.619b	28.96ab
Unclipped Extra N	205.0a	392.0a	597.0a	26.76c	0.535bc	33.76bcd
SHADE						
Clipped No Extra N	33.8d	48.2d	82.0f	17.27d	0.505c	36.32a
Unclipped No Extra N	92.4bcd	263.4b	355.8dc	18.71d	0.317d	17.82cd
Clipped Extra N	7.4cd	118.6cd	166.0ef	16.14d	0.618b	33.16ab
Unclipped Extra N	99.6bcd	399.2a	498.8ab	17.51d	0.411cd	26.24abc

Means followed by different letters in the same column are significantly different at the 5% level of probability.

Table 2

Leaf area, dry biomass, sugar, starch and total non-structural carbohydrates (TNC) of the guineagrass clipped-off tissues from plants grown under two irradiance regimes, and fertilized with extra or no extra nitrogen.

	Leaf area (dm^2)	dry biomass (g)	% sugar by DW	% starch by DW	% TNC by DW	Difference in Biomass Significance		Difference in Leaf area Significance	
FIRST CLIPPING						Nitrogen	Light	Nitrogen	Light
SUN NO EXTRA N	5.12d	2.8c							
SUN EXTRA N	9.21c	4.8b							
SHADE NO EXTRA N	18.74b	10.0a							
SHADE EXTRA N	32.36a	11.2a							
SECOND CLIPPING						0.0159*	0.1112 NS	0.0819 NS	0.3180 NS
SUN NO EXTRA N	8.87d	4.8d							
SUN EXTRA N	14.51c	11.8c							
SHADE NO EXTRA N	25.54b	14.6b							
SHADE EXTRA N	30.85a	23.6a				0.0066**	0.3065 NS	0.2027 NS	0.0239*
THIRD CLIPPING									
SUN NO EXTRA N	15.92c	8.68c							
SUN EXTRA N	18.44b	12.19b							
SHADE NO EXTRA N	43.26a	18.80a							
SHADE EXTRA N	42.11a	19.77a				0.0014**	0.2474 NS	0.0001***	0.0113*
FORTH CLIPPING									
SUN NO EXTRA N	8.53c	4.75c	2.8a	5.7a	8.5a				
SUN EXTRA N	25.12b	14.46b	2.7a	5.6a	8.2ab				
SHADE NO EXTRA N	17.13b	11.13b	2.6a	4.5b	7.1bc				
SHADE EXTRA N	51.19a	21.07a	1.7b	4.5b	6.3c				

Means followed by different letters in the same column are significantly different at the 5% level of probability, significance for the increments of the clipped off dry biomass and leaf area between two successive intervals.