Rev. Fac. Agron. (LUZ): 1997, 14: 625-639

Acclimation of *Panicum maximum* to different light regimes. Effect of subsequent defoliation

Aclimatación de *Panicum maximum* a diferentes regimenes lumínicos. Efecto de defoliaciones sucesivas

Alejandra Páez[1]
Maria E. González O.[1]
Jose J. Villasmil[2]

Abstract

Plant performance depends directly on the available light, and defoliation may change plant structure by altering light interception. These two factors, irradiance and defoliation, together may cause important effects on growth patterns. The present research was conducted to evaluate growth and biomass allocation of guineagrass (*Panicum maximum* Jacq.), a C4 shade-tolerant plant, after acclimation to three light regimes, and to establish the effect of defoliation. After seedling emergence, plant height and the number of leaves and culms were recorded daily for 60 d. Harvests were made at 33 d and 63 d after planting. Other plants were clipped at 20 or 40 cm or left undefoliated (controls). Guineagrass was taller in the shade, with fewer leaves and culms than in full sunlight. In partial shade, leaf area and dry biomass were reduced less than in deep shade. Leaf area ratio (LAR) increased with decreasing irradiance due mainly to increases in specific leaf area (SLA), although leaf weight ratio (LWR) contributed to this effect. The biomass response to clipping was fairly similar in all irradiances, but there was a significant interaction of height of clipping and irradiance on root/shoot ratio (R/S). Root/Shoot ratio decreased with clipping in deep shade and full sunlight. The reduction was greatest under full sunlight conditions. The increases in LAR induced by shading may have adaptive significance in guineagrass. LWR was more affected by clipping than other biomass parameters, because it increased with more intense clipping, regardless of the irradience regime. Changes in irradiance affected LAR and SLA, whereas the effect of clipping was significantly greatest on LWR. Generally, biomass allocation of guineagrass was affected by clipping and irradiance, and growth depended on the irradience received.

Key words: *Panicum*, irradiance, clipping, biomass allocation.

Recibido el 26-05-1997 • Aceptado el 09-06-1997

1. Corresponding author. Laboratorio de Ecofisiología. Departamento de Biología, Facultad de Ciencias, La Universidad del Zulia, Maracaibo ZU 4005, Venezuela.
2. Facultad de Agronomía, La Universidad del Zulia, Maracaibo ZU 4005, Venezuela.

Resumen

El comportamiento de las plantas depende directamente de la luz disponible, y la defoliación puede cambiar la estructura de la misma mediante alteraciones en la intercepción lumínica. Estos dos factores juntos, irradiación y defoliación, pueden causar efectos importantes en los patrones de crecimiento vegetal. La presente investigación fue realizada para evaluar el crecimiento y distribución de biomasa de plantas de guinea (*Panicum maximum* Jacq.), planta C4 tolerante a la sombra, después de aclimatarse a tres regimenes lumínicos, y para establecer el efecto de la defoliación sobre dichos parámetros. Después de la emergencia de las plántulas, se determinó la altura de la planta y el número de hojas durante 60 d. Se realizaron cosechas a los 33 y a los 63 días después de la siembra. Otras plantas fueron cortadas a 20 o 40 cm de altura o dejadas sin corte como control. El pasto guinea fue más alto en la sombra, y con menos hojas y culmos que en luz solar total. En la sombra parcial, el área foliar y la biomasa disminuyeron menos que en sombra profunda. La relación de área foliar (RAF) aumentó con la disminución de la irradiación debido principaimente a aumentos en el área foliar específica (AFE), aún cuando la relación de peso foliar (RPF) contribuyó a este efecto. La respuesta de la biomasa al corte fue bastante similar en todas las irradiaciones, pero hubo una interacción significativa de la altura de corte y la irradiación sobre la relación raiz/vástago (R/V). La relación raíz/vástago disminuyó con el corte en la sombra profunda y luz solar total. La reducción fue mayor bajo condiciones de luz solar total. Los cambios en la irradiación afectaron a RAF y AFE, mientras que el corte alteró principalmente a la RPF. En general el efecto del corte sobre el crecimiento y distribución de biomasa del pasto guinea dependen de la irradiación recibida durante el crecimiento de la planta.

Palabras claves: Irradiación, corte, distribución de biomasa.

Introduction

Light provides the energy needed for photosynthesis, and canopy shading from trees may influence plant productivity and seedling survival. Irradiance (quantum flux density) is a key factor in the field which varies seasonally, diurnally and spatially (2).

Guineagrass, as well as other grasses are a very important component of tropical pastures. The effects of light on some physiological responses of guineagrass have been investigated (7, 13). Previous work with guineagrass has focused on the effects of defoliation frequency and intensity (31) and the interaction of defoliation with water stress (17, 18). Little Information is available concerning the combined effects of light and defoliation on plant responses in general, and on guineagrass specifically (19, 29, 30).

Previous paper showed that plants shaded by other trees produced larger, thinner and wider leaves, with no damage, and higher LAR, LWR and SLA, lower allocation to the roots and a fourfold decrease in net photosynthesis and stomatal conductance (19). The changes in the distribution pattern caused by the lower irradience were not altered by clipping intensity. In turn, intense clipping produced more changes in assimilation patterns. The more intensively clipped plants showed the greater photosynthetic rate and stomatal conductance specially under full sunlight (19). Very high irradiance and intense clipping may alter grass performance in some areas depending on the season.

An enhancement in photosynthesis as a result of clipping was observed in guineagrass (18). This effect could lead to increased growth. The objective of this research was to acclimate guineagrass to different light regimes, evaluating its response, followed by different clipping treatments after acclimation to each irradiance, to determine if the effect of clipping on growth and biomass allocation depended on the irradiance received during growth. It was assumed that shading attenuated the clipping effect.

Materials and methods

Seedlings were germinated in 50 kg plastic pots filled with a soil mixture taken from the field. The soil pH was 6.2 to 6.4, conductivity was 80.3 μMhos, P was ≈5 g kg^{-1}, K was ≈50 to 100 g kg^{-1}, and organic matter was 1.34 %. The methods used for P, K, and organic matter determinations as well as other environmental variables are the same as described by Paez et al. (17). Plants were grown under three treatments: full sunlight (100 % of ambient light), partial shade (30 % of ambient light) and deep shade (10 % of ambient light). Partial and deep shade treatments were achieved by placing the plants under one or two layers of neutral density shade cloth, respectively. The full sunlight treatment was in an adjacent unshaded area. The mean daily photosynthetic photon flux densities (PPFD) received in each light treatment during measurement days with clear skies were 150, 400 and 2 000 μE m^{-2} S^{-1} for the 10, 30 and 100 % sunlight treatments, respectively.

Treatments were replicated two times. After seedlings reached 10 cm in height, the population in each pot was thinned gradually to leave one plant per pot. There were a total of 50 plants per light treatment. At 33 and 63 days after planting (DAP), two groups of five replicate plants from each of the three light treatments were harvested. They were selected at random since the begining of the experiment. The plants harvested at 63 DAP were previously used to record the number of leaves, number of culms and heights every two or three days.

At each harvest, plants were separated into leaves, culms and roots. Leaf area was measured with a LI-3100 leaf area meter (Li-Cor, Lincoln, NE). Roots were washed to remove soil. Leaves, culms and roots were placed in individual bags, dried at 65 °C for 3 d, and weighed to obtain dry biomass. The remaining 30 plants in each light treatment were divided into three series at the begining of the experiments. In the first series, two groups of five randomly selected plants were clipped at 20 cm from the soil surface. In the second series, two groups of five plants were clipped at 40 cm from the soil surface. In the third series two groups of five plants were left uncapped as controls. Clippings were performed with a 4-wk interval between each other. A final harvest was determined at the end of the experiment.

Using dry biomass and leaf area data, mathematical growth analysis techniques were applied (19) to calculate LAR, LWR, SLA and R/S. The experiment was a 3 -factorial arrangement in a completely randomized design. This arrangement was used to test for the effect of the two factors. irradiance and clipping height. Analysis of variance was applied to determine main effects and their interactions (23) on plant growth and biomass allocation. Tukey's test was applied for mean separation of the dependent variables at a 5 % probability level.

Results

Effect of irradiance. Plants grown in full sunlight showed a linear increase in height with time. Plant height was greatest under partial shade (figure 1). The number of leaves (figure 2) and culms (figure 3), however, increased with increasing irradiance.

At 33 DAP, plants grown in full sun had significantly greater leaf area and total dry biomass than those grown under partial -and deep- shade (table 1). In partial shade, leaf area was reduced 17 % at 33 DAP, and 21 % at 63 DAP. In deep shade, the reduction in leaf area was 93.5 % and 95 %, respectively. In addition, dry biomass was reduced 55 and 72 % under partial shade, and 97 % and 99 % under deep shade (table 1).

Components of dry biomass (leaves, culms and roots) were significantly greater under full irradiance than under partial and deep shade. Similarly, guineagrass plants grown under partial shade produced more leaf, culm and root biomass than those grown in deep shade (table 1).

Significantly LAR increased with decreasing light treatment (table 2). This effect was due mainly to increases in SLA both at 33 and 63 DAP. Leaf weight ratio (LWR) was greater in deep and partial shade than in full sun at 33 DAP. Root-to-shoot ratio was higher in deep shade than in partial shade and full sun at 33 DAP, at the second harvest, 63 DAP, R/S ratio was lower in deep shade (table 2).

Interaction of irradiance with defoliation. The response to clipping was consistent with the light conditions. In deep (figure 4) and partial (figure 5) shade, clipping the plants at 40 cm height reduced dry biomass relative to the controls. But in full sunlight, there were no differences between the 40 cm treatment and the unclipped controls (figure 6).

In deep (figure 4) and partial (figure 5) shade, root, culm, leaf, and panicle biomass increased with less

Table 1. Total leaf area per plant and dry biomass of leaves, culms, roots and total biomass of guineagrass plants grown under full sun, partial and deep shade (100, 30 and 10 % of ambient light) at 33 and 63 DAP. n = 10*.

Treatment	Leaf area	Leaf	Culm and sheath	Root	Total
First harvest 33 DAP					
%	dm^2	g $plant^{-1}$			
10	0.55^a	0.11^a	0.04^a	0.03^a	0.16^a
30	7.04^b	1.52^b	0.78^b	0.21^b	2.52^b
100	8.43^c	3.05^c	1.98^c	0.52^c	5.54^c
Second harvest 63 DAP					
%	dm^2	g $plant^{-1}$			
10	0.89^a	0.25^a	0.04^a	0.06^a	0.29^a
30	14.85^b	3.76^b	2.60^b	2.36^b	6.56^b
100	18.75^c	8.76^c	8.26^c	6.36^c	23.40^c

*different letters following means on the same column are significantly different at the 5 % level of probability.

intense clipping. Therefore, the undefoliated controls produced more biomass than plants clipped at 40 cm and 20 cm. Biomass production was, in fact, similarly affected by clipping height. In full sunlight, root, leaf and panicle biomass increased with less intense clipping, but culm biomass was greatest in the plants clipped at 40 cm (figure 6). This result suggests that leaf senescence had taken place in the undefoliated controls. The dry biomass of green leaves was similar, and dry leaves increased in the controls (figure 6). In this full light regime, the plants clipped at 20 cm produced the least root, culm and leaf biomass.

Shaded leaves had a greater LAR and SLA than leaves produced in full sun (figure 7 and 8). More clipping increased LAR in partial shade and full sunlight, and increased SLA in both shading treatments (figure 7 and 8).

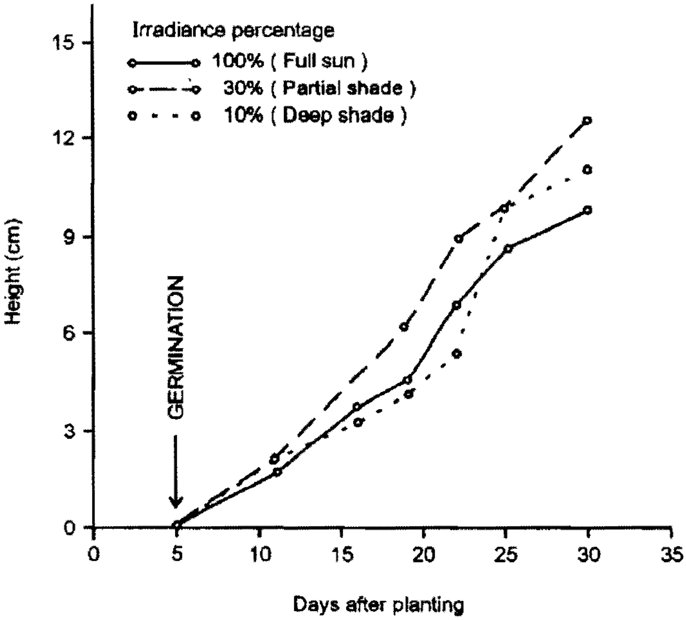

Figure 1. Height of guineagrass plants grown from seeds under full sun, partial and deep shade (100, 30 and 10 % of ambient light). n = 10.

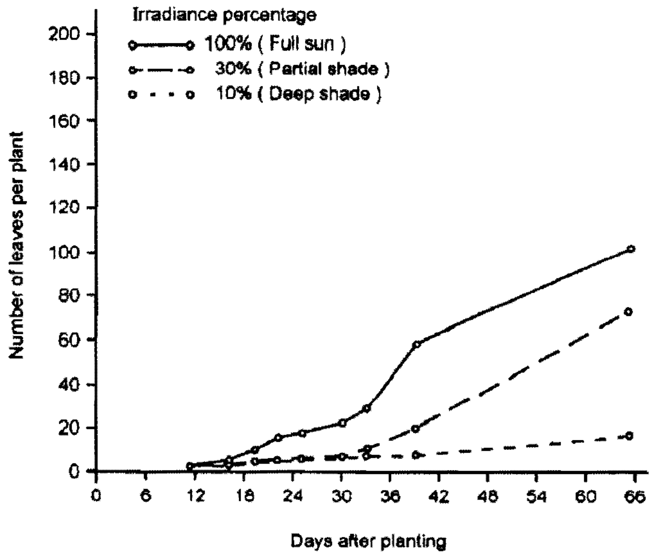

Figure 2. The number of leaves of guineagrass grown from seeds under full sun, partial and deep shade (100, 30 and 10 % of ambient light). n = 10.

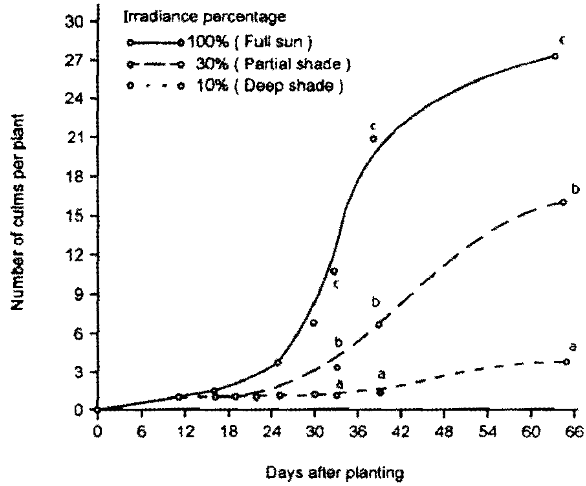

Figure 3. The number of culms of guineagrass plants grown under full sun, partial and deep shade (100, 30 and 10 % of ambient light). n= 10.

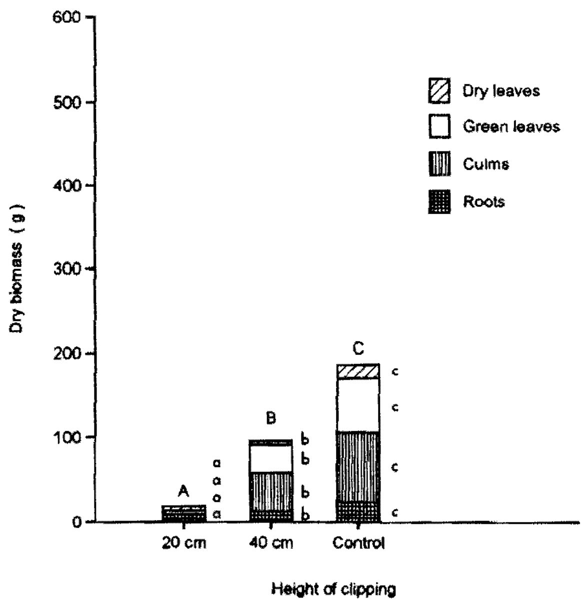

Figure 4. Dry biomass (g) of roots, culms, green leaves, dry leaves and panicles of guineagrass plants grown from seeds under deep shade (10 % of ambient light) and clipped at 20- and 40-cm from the soil surface. Unclipped controls are also presented. Different letters for the same plant organ indicate significant differences at the 0.05 level. n= 10.

Table 2. Leaf area ratio (LAR), leaf weight ratio (LWR), specific leaf area (SLA) and root-shoot ratio (R/S) of guineagrass plants grown under full sun, partial and deep shade (100, 30 and 10% of ambient light) at 33 and 63 DAP. n = 10.

First harvest 33 DAP				
Treatment %	LAR dm^2g^{-1}	LWR $g\,g^{-1}$,	SLA dm^2g^{-1}	R/S $g\,g^{-1}$,
10	3.39^c	0.62^b	5.50^c	0.19^b
30	2.80^b	0.60^b	4.64^b	0.09^a
100	1.53^a	0.55^a	2.77^a	0.10^a
Second harvest 63 DAP				
Treatment %	LAR dm^2g^{-1}	LWR $g\,g^{-1}$,	SLA dm^2g^{-1}	R/S $g\,g^{-1}$,
10	2.64^c	0.70^b	3.85^b	0.22^a
30	2.04^b	0.42^a	4.65^b	0.36^b
100	0.79^a	0.42^a	2.16^a	0.33^b

*different letters following means on the some column are significantly different at the 5 % level of probability.

Height of clipping did not affect SLA of plants grown in full sun. Leaf weight ratio, or the distribution of plant biomass as leaf weight increased with clipping in all light conditions (figure 9). Plants clipped at 20 cm had higher LWR at all light treatments: controls showed the smallest values. These data suggested that increases in LAR due to intense clipping (figure 7) resulted in partially shaded plants from the increases in SLA (figure 8) and LWR (figure 9). In full sunlight, however, the increases in LAR due to intense clipping (figure 7) were due primarily to increases in LWR (figure 9).

There was a significant interaction of height of clipping and irradiance on R/S due to the increase of R/S in the uncapped controls grown at full sunlight (figure 10). Root-to-shoot ratio decreased linearly with height of clipping in deep shade and remained almost constant and slightly higher in the clipped plants relative to unclipped controls under partial shade (figure 10).

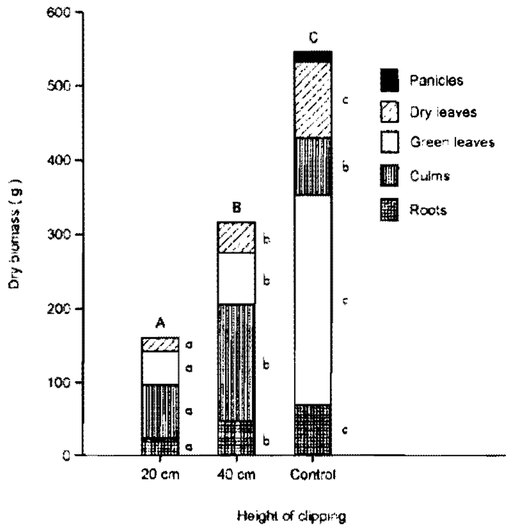

Figure 5. Dry biomass (g) of roots, culms, green leaves, dry leaves and panicles of guineagrass plants grown from seeds under partial shade (30 % of ambient light), and clipped at 20- and 40-cm from the soil surface. Unclipped controls are.also presented. Different letters for the same plant organ indicate significant differences at the 0.05 level. n = 10.

Discussion

Growth of crops may be inhibited by canopy shade (21). Although it is a shade-tolerant C4 grass, guineagrass is found in areas where canopy shading from trees may influence its growth and survival. In this study guineagrass growth was directly influenced by irradiance (figure 2 and 3).

Considerable information is available concerning plant response to irradiance (1, 3, 8, 15, 27). Irradiance is the main environmental factor to which the plants must adapt, and in a particular habitat, photosynthetic flux density varies seasonaly, diurnally and spatially (2).

Several reviews discuss plant adaptation to light (2, 3, 8) and other literature mentions individual growth responses of plants to irradiance (4, 5, 6, 11, 12, 14, 22, 24), little research has examined the combined effect of light and defoliation on plant responses (19, 29, 30). Plants growing in dense populations are often taller than those growing in ample ones, which has been attributed to the difference in irradiance intensity and quality (14) in partial and deep shade.

Shaded guineagrass plants showed increased stem elongation (figure 1) which is considered to be due to photosynthetic limitation under these treatments. Kephart *et al.* (11) found that increased stem elongation was associated with moderate reductions in

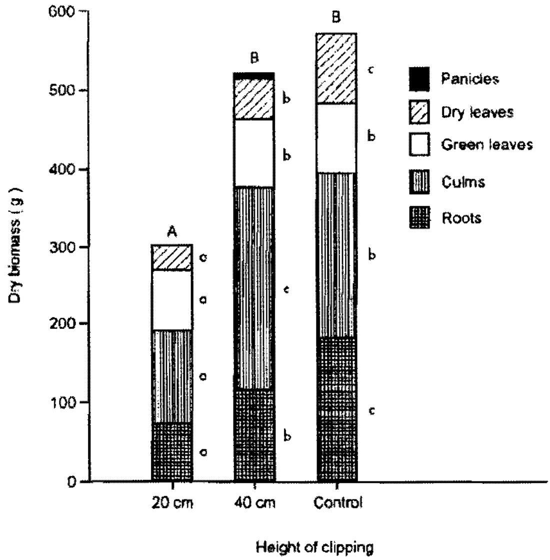

Figure 6. Dry biomass (g) of roots, culms, green leaves, dry leaves and panicles of guineagrass plants grown from seeds under f ull sunlight (100 % of ambient light), and clipped at 20- and 40-cm from the soil surface. Unclipped controls are also presented. Different letters for the values corresponding to the same plant organs indicate significant differences at the 0.05 level. n = 10.

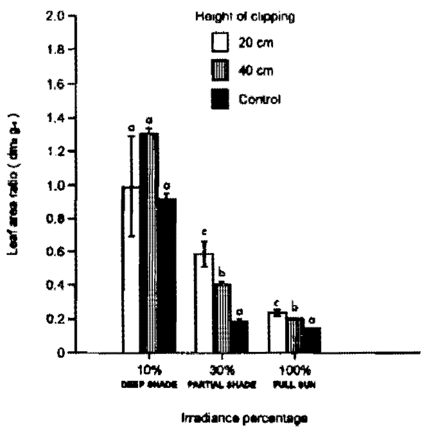

Figure 7. Leaf area ratio (LAR) of guineagrass grown under full sunlight, partial and deep shade, and clipped at 20- and 40-cm from the soil surface. Values for unclipped control plants are also given. For each irradiance regime, different letters represent significant differences at the 0.05 level. Bars represent standard errors of the means. n = 10.

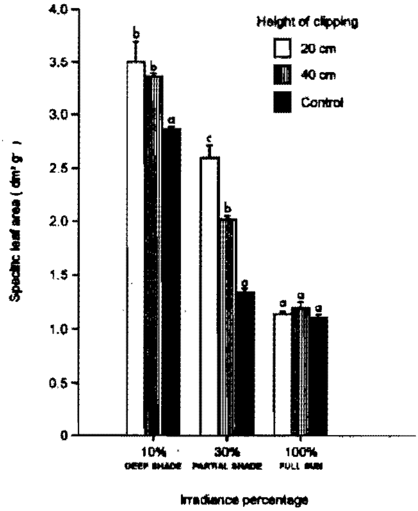

Figure 8. Specific leaf area (SLA) of guineagrass plants grown under full sun, partial and deep shade, and clipped at 20- and 40-cm from the soil surface. Values for unclipped control plants are also given. For each irradiance regime, different letters represent significant differences at the 0.05 level. Bars represent standard errors of the means. n = 10.

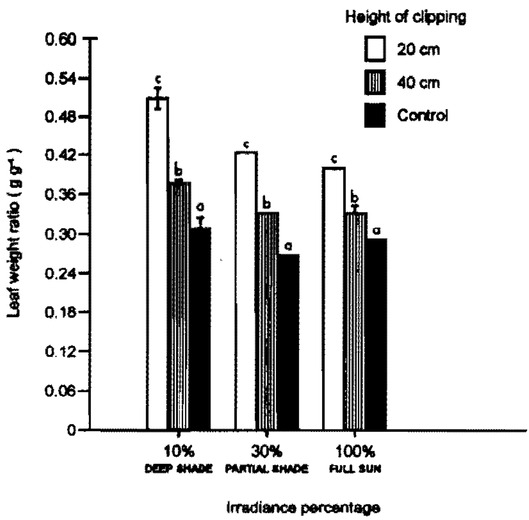

Figure 9. Leaf weight ratio (LWR) of guineagrass plants grown under full sun, partial and deep shade, and clipped at 20- and 40-cm from the soil surface. Values for unclipped controls are also given. For each irradiance regime, different letters represent significant differences at the 0.05 level. Bars represent standard errors of the means. n = 10.

irradiance, which is influenced by photosynthate availability and photosynthate partitioning into stem growth. Kephart *et al.* (11) observed that stem elongation may not occur when irradiance is reduced to a level where plant developmental processes become photosynthate limited.

Leaf, culm and root biomass increased proportionately with irradiance (table 1, figures 4-6). Total dry biomass was greater in the full sun treatment than the partial-(30 % sunlight) and deep-(10 % sunlight) shaded treatments (figure 6). In contrast with these findings, Wong and Wilson (30) found increased herbage yields for green panic gross (*Panicum maximum* var. trichoglume Eyles) grown under 40 and 60 % ambient sunlight and harvested at 8-wk intervals, as compared with plants grown in full sunlight. Shading, however, markedly reduced dry matter production of itchgrass (*Rottboellia exaltata*) and tended to decrease tiller production (20).

In guineagrass, shade resulted in thinner leaves in both harvests (table 2, figure 8), which was reflected in their greater SLA or area per unit leaf weight (table 2). Many plants develop smaller and thicker leaves in the sun and larger and thinner leaves in the shade (2, 3, 8, 14, 19). Therefore, specific leaf area decreased in full sun. The distribution of plant biomass as leaf weight (LWR) also increased significantly with lower irradiance (table 2). This effect was seen in the more intensively defoliated plants grown under all irradiances (figure 9). Both the increase in SLA with reductions in irradiance (table 2) and in LWR with more intense clipping (figure 9), resulted in increases in LAR as the irradiance decreased from 100 to 30 or 10 % (table 2) and clipping height decreased (figure 7) in partial shade and full sun.

These guineagrass data indicate that in full sunlight SLA (or its inverse, specific leaf weight (SLW)) does not vary with clipping height (figure 8). With shading, however, SLA increased with clipping (figure 8). Leaf weight ratio (LWR) increased significantly with clipping in all irradiance regimes (figure 8). It was reported in a previous paper (17) that increasing heights of clipping reduced the leafiness (LAR) of waterstressed plants and increased the dry matter in the leaves (SLW), whereas LAR and SLW of well-watered plants remained constant. In contrast, Wallace (25) observed a decrease in SLW (increase in SLA) with lower clipping height in *P. coloratum* plants without mycorrhizae. Oesterheld and McNaughton (16) found that *Themeda triandra* Forssk. plants compensated for the removal of leaf area by producing new leaves with lower specific weights.

The increase in LAR may have adaptive significance in shade-grown guineagrass plants because it represents a greater investment of plant biomass in photosynthetic tissue (21). LWR was more affected by clipping than other biomass parameters, because it increased with more intense clipping, regardless of the irradiance regime. Likewise, this increase in LWR may have adaptive significance for plants subjected to defoliation. LAR, LWR and SLA decreased with increas-

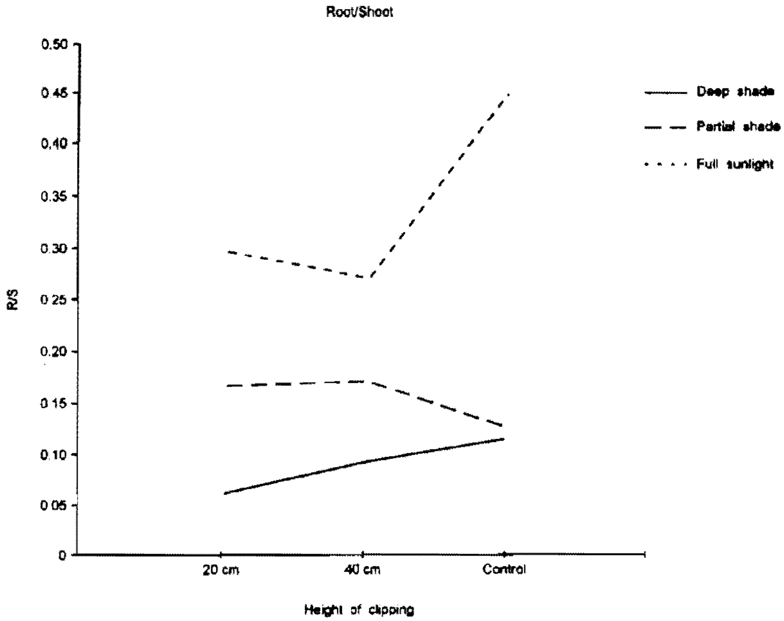

Figure 10. Effect of clipping height and irradiance level on R/S of guineagrass grown under full sunlight, partial and deep shade, and clipped at 20- and 40-cm from the soil surface or left unclipped. n = 10.

ing irradiance of itchgrass (20). Shading green panic pasture stimulated greater growth and higher nitrogen concentration compared with adjacent plots in full sunlight (28). The data reported here, and those of Boardman (3) and Jones (1985) support the conclusion that increases in LAR, SLA and stem length and decreases in plant dry biomass, leaf blade thickness, and root growth relative to shoot growth are common plant responses to low irradiance. However, it is important to note that changes in irradiance affected biomass distribution to leaf area; whereas clipping shifted biomass allocation to leaves.

The response of R/S to clipping after acclimation varied with light treatment. In full sun, R/S was highest and the increase in R/S was due to a much larger increment in root biomass (figure 10). Values of R/S decreased with clipping compared to unclipped controls under deep shade (figure 10), and were higher in clipped then uncapped plants in partial shade (figure 10). Although the increase in R/S with irradiance has been observed previously (26), in this research it was also found that R/S decreased with clipping in full sunlight and deep shade.

Acknowledgment

The authors wish to express their gratitude to CONDES (Consejo de Deserrollo Científico y Humanístico de LUZ) for financing this research, also to FUNDACITE-Zulia and CONDES for giving financial aid to present this paper in the Annual Meeting of the Ecological Society of America held in Hawaii.

Literature cited

1. Björkman, O. 1973. Comparative studies on photosynthesis in higher plants. pp 1-63.In: Giese A. (Ed.) Current Topics in Photobiology, Photochemistry and Photophysiology. Vol. 8. Academic Press, New York.

2. Björkman, O. 1981. Responses to different quantum flux densities. pp 57-107. In: O. L., Lange, P. S., Nobel, C. B. Osmond, and H. Ziegler, (eds). Encyclopedia of Plant Physiology New Series., vol. 12A, Physiol. Plant Ecology I. Springer Berlin Heidelberg New York.

3. Boardman, N.K. 1977- Comparative photosynthesis of sun and shade plants. Ann. Rev. Plant Physiol. 28: 355-377.

4. Chazdon, R. L., and R. W. Pearcy. 1906. Photosynthetic responses to light variation in rainforest species. I. Induction under constant and fluctuating light conditions. Oecologia 69: 517-523.

5. Eriksen, F. I., and A. S. Whitney. 1981. Effects of light intensity on growth of some tropical forage species. Interactions of light intensity and nitrogen fertilization on six forage grasses. Agron.J. 73: 427-433.

6. Fetcher, N., B. R. Strain, and S. F. Oberbauer. 1983. Effects of light regime on the growth, leaf morphology, and water relations of seedlings of two species of tropical trees. Oecologia 58:314-319.

7. Fladung, M., and J. Hesselbach. 1989. Effect of varying environments on photosynthetic parameters of C3, C3-C4 and C4 species of *Panicum*. Oecologia 79:168-173.

8. Givnish, T.J. 1988. Adaptation of sun and shade: A whole plant perspective. Aust. J. Plant Physiol. 15:63-92.

9. Jones, C.A. 1985. C4 grasses and cereals. Growth, development, and stress response. John Wi ley & Sons, New York.

10. Kvet, J., J. P. Ondok, J. Necas, and P. G. Jarvis. 1971. Methods of growth analysis. p. 343-391. In Z. Sestak, *et al.* (Ed.). Plant Photosynthetic Production: Manual of methods. W. Junk, The Hague.

11. Kephart, K. D., D. R. Buxton and S. E. Taylor. 1902. Growth of C3 and C4 perennial grasses under reduced irrediance. Crop Sci. 32:1033-1038.

12. Leverenz, J. W., and P. G. Jarvis. 1980. Photosynthesis in sitka spruce (*Picea sitchensis* (Bong.) Carr.) X. Acclimation to quantum flux density within and between trees. J. Appl. Ecology 17: 697-708.

13. Ludlow, M. M., and G. L. Wilson. 1971. Photosynthesis of tropical pasture plants. I. Illuminance, carbon dioxide concentration, leaf temperature, and leaf-air vapour pressure difference. Aust. J. Biol. Sci. 24: 449-470.

14. Nobel, P. S. 1976. Photosynthetic rates of sun versus shade leaves of *Hyptis emoryi* Torr. Plant Physiol. 58: 218-223.

15. Osmond, C. B., O. Bjorkman, and D. J. Anderson. 1980. Physiological processes in plant ecology. Springer, Berlin-Heidelberg, New York.

16. Oesterheld, M. and, S. J. McNaughton. 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.

17. Páez, A., M. E. González O., X. Yrausquin, A. Salazar, and A. Casanova. 1995. Water-stress and clipping management effects on guineagrass: I. Growth and biomass allocation. Agron. J. 87: 698-706.

18. Páez, A., and M. E. González. 1995. Water stress and clipping management effects on Guineagrass: II. Photosynthesis and water relations. Agron. J. 87: 706-711.

19. Páez, A., M. E. González, y N. Pereira. 1994. Comportamiento de *Panicum maximum* en condiciones de sombreado y de luz solar total. Efecto de la intensided de corte. Rev. Fac. Agron. (LUZ). 11: 25-42.

20. Patterson, D. T. 1979. The effects of shading on the growth and photosynthetic capacity of itchgrass (*Rottboellia exaltata*). Weed Sci. 27: 549-553.

21. Patterson, D. T. 1982. Shading responses of purple and yellow nutsedges (*Ciperus rotundus* and *C. esculentus*). Weed Sci. 30: 25-30.

22. Patterson, D. T., S. O. Duke, and R. E. Hoagland. 1978. Effects of irradiance during growth on adaptive photosynthetic characteristics of velvetleaf and cotton. Plant Physiol. 61: 402-405.

23. SAS Institute. 1982. SAS User's guide: Statistics. SAS Inc. Cary, NC.

24. Sims, D. A., and R. W. Pearcy. 1989. Photosynthetic characteristics of a tropical forest understory herb, *Alocasia macrorrhiza*, and a related crop species, *Colocasia esculenta* grown in contrasting light environments. Oecologia 79:53-59.

25. Wallace, L. L. 198 1. Growth, morphology and gas exchange of mycorrhizal *Panicum coloratum* L., a C4 grass species, under different clipping and fertilization regimes. Oecologia 49: 272-278.

26. Wareing, P. F., M. M. Khalifa, and K. J. Treherne. 1968. Rate limiting processes in photosynthesis at saturating light intensities. Nature 120: 453-458.

27. Wild, A. 1979. Physiologie der photosynthese hoherer pflanzen. die anpossung an lichtbedingungen. Ber Disch Bot. Ges. 92: 341-364.

28. Wilson, J. R. V. R. Catchpoole, and K. L. Weier. 1986. Stimulation of growth and nitrogen uptake by shading a rundown green panic pasture on brigalow clay soil. Trop. Grasslands 20:134-143.

29. Woledge, J. 1977. The effects of shading and cutting treatments on the photosynthetic rate of ryegrass leaves. Ann. Bot. 41: 1279-1286

30. Wong, C. C. and J. R. Wilson. 1980. The effect of shading on the growth and nitrogen content of green panic and Siratro in pure and mixed swards defoliated at two frequencies. Aust. J. Agric. Res. 31: 269-285.

31. Yrausquin, X., A. Páez, J. J. Villasmil y M. Urdaneta. 1995. Comportamiento fisiológico del pasto guinea (*Panicum maximum* Jacq.) sometido a diferentes frecuencias y alturas de corte. 1. Distribución de biomasa y análisis de crecimiento. Rev. Fac. Agron. (LUZ). 12: 313-323.