Revista Verde de Agroecologia e Desenvolvimento Sustentável
V.12, Nº 4, p. 641-647, 2017
Pombal, PB, Grupo Verde de Agroecologia e Abelhas
http://www.gvaa.com.br/revista/index.php/RVADS
DOI: http://dx.doi.org/10.18378/rvads.v12i4.5010

ARTIGO CIENTÍFICO

Phenotypic plasticity of leaves and yield of pineapple grown under shade conditions

Plasticidade fenotípica de folhas e produtividade do abacaxi sob condições de sombreamento

Irene Ferro da Silva[1]; Aldenice Santos de Lima Souza[2]; Sebastião Elviro de Araújo Neto[3]; Paulo Cesar Poeta Fermino Junior[4]; Roberto Aparecido Custódio[5]; Rafaella Georgia Lima Damasceno[6]

Abstract: The high temperature and solar radiation of the tropical regions can burn and reduce the fruits size of the pineapple. An alternative to the farmers of this crop is the shading of the plants, providing the climatic conditioning. Therefore, the objective was to evaluate the different shade conditions in the chlorophyll content and morpho-anatomy of pineapple leaves on fruit production. shading on the chlorophyll content, leaf morphology and anatomy, and pineapple productivity. The experiment was conducted in field and was of a randomized block design with four replicates of five treatments comprising 0% shading (pineapples grown in full sunlight), 45.0% shading (provided by adjacent cassava plants), 48.3% shading (provided by adjacent jack bean plants), and 30 and 50% shading (provided by shade netting). The anatomical, histological and biochemical characteristics of the leaves, along with the yield and percentage of sunburned fruits, were determined 16 months after planting the pineapples. Pineapples grown under natural shade provided by cassava or jack bean plants exhibited phenotypic plasticity with "D" leaves presenting trichomes of decreased length and vessel elements of reduced diameter. Under cassava shading, the thicknesses of the abaxial epidermis and chlorophyll parenchyma and stomatal density were increased, while the thickness of the aquiferous hypodermis and the percentage of sunburned fruits were reduced. Under jack bean shading, the thicknesses of the mesophyll, chlorophyll parenchyma and leaf blade were reduced. No significant differences in the yield of pineapple fruit were detected between treatments, although netting and shading by cassava produced significant reductions of sunburned fruit.

Key words: *Ananas comosus;* Photoinhibition; Anatomy.

Resumo: A alta temperatura e radiação solar das regiões tropicais podem queimar e reduzir o tamanho dos frutos do abacaxizeiro. Uma alternativa aos produtores dessa cultura é o sombreamento das plantas, proporcionando o condicionamento climático. Assim sendo, objetivou-se avaliar os efeitos do sombreamento sobre os teores de clorofilas, a morfologia e anatomia foliar e a produtividade do abacaxizeiro. O experimento foi realizado em condições de campo, em delineamento de blocos casualizados, com quatro repetições e cinco tratamentos de sombreamento: 0% (abacaxizeiro a pleno sol); 45,0% (cobertura com plantas de mandioca); 48,3% (cobertura com plantas de feijão-de-porco); 30 e 50% (cobertura com tela de sombreamento). As características anatômicas, histológicas e bioquímicas das folhas, juntamente com a produtividade e percentagem de abacaxis queimados, foram determinadas 16 meses após o plantio. Abacaxizeiros cultivados sob a sombra de feijão-de-porco ou mandioca mostraram plasticidade fenotípica, com as folhas "D" apresentando tricomas com menor comprimento e elementos de vasos com menor diâmetro. Sob a sombra da mandioca ocorreu aumento da espessura da epiderme abaxial, do parênquima clorofilado e densidade estomática e, enquanto que a espessura da hipoderme aquífera e a porcentagem de frutos queimados pelo sol foram reduzidas. Sob a sombra do feijão-de-porco, as espessuras do parênquima clorofilado, do mesofilo e da folha foram reduzidas. Não houve diferença significativa entre os tratamentos no que se refere à produtividade dos abacaxis, embora o sombreamento com tela e mandioca tenha produzido redução significativa de frutos queimados.

Palavras-chave: *Ananas comossus*; Fotoinibição; Anatomia.

*Autor para correspondência
Recebido para publicação em 02/08/2017; aprovado em 30/09/2017
[1]Engenheira Agronôma. Mestre em Produção vegetal, Universidade Federal do Acre. E-mail. dairene@hotmail.com
[2]Engenheira Agronôma., Universidade Federal do Acre. E-mail. aldenicelima_flor@hotmail.com
[3]Professor Doutor da Universidade Federal do Acre, BR 364, km04 – Distrito Industrial; CEP:69.920-900. E-mail:selviro2000@yahoo.com.br
[4]Biólogo Professor Doutor da Universidade de Santa Catarina, poetabio@hotmail.com
[5]Engenheiro Agronômo. Mestre em Produção vegetal, Universidade Federal do Acre. E-mail. robcustodio@hotmail.com
[6]Biólogoa, Mestre, Universidade Federal do Acre. E-mail:rafaelagd@gmail.com

INTRODUCTION

Pineapple (*Ananas comosus* L. Merrill) grows well in most tropical climate regions around the world, but the top producing countries, principally Brazil, China, Costa Rica, the Philippines and Thailand, account for more than a half of the total global production. The wide agronomical potential of the species is associated with its environmental adaptability, hardiness, facile propagation and high consumer acceptability of the fruit (CUNHA; HAROLDO, 2008; CRESTANI et al., 2010). In Brazil, the production of pineapple occurs all the year round, although the market value of the fruit fluctuates considerably, increasing by up to 19.3% in the non-peak season (January to April) and falling by as much as 10.1% during the peak harvesting period (AGRIANUAL, 2012). In the northern state of Acre, the out of season price per fruit can attain R$ 3.25 (US$ 1.50 approximately) or more depending on the size and quality of the fruit (AGRIANUAL, 2012; BAYMA et al., 2012). In this region, fruit mass may be up to 24.4% lower in full sun cultivation than fruit under shade (CUSTÓDIO et al., 2016).

A key issue concerning the cultivation of pineapple in regions with high levels of solar radiation can burn the fruit, giving rise to a loss in yield or an increase in production costs (by up to 11.7%) if the crop has to be protected through the provision of artificial shade (AGRIANUAL, 2012). However, the use of natural shade provided by a mixed culture system involving, for example, pineapple and cassava [*Manihot esculenta* Crantz] or jack bean [feijão-de-porco; *Canavalia ensiformis* (L.) DC.] represents an accessible and low-cost alternative to net shading. Such intercropping systems offer ecological and economical advantages since they enhance biodiversity, increase land-use efficiency, improve soil covering and biomass recycling, and enable the commercialization of additional products. These factors serve to improve the food security and economical stability of family farmers (LUDEWIGS; BRONDIZIO, 2009; ARAÚJO NETO et al., 2014; CUSTÓDIO et al., 2016).

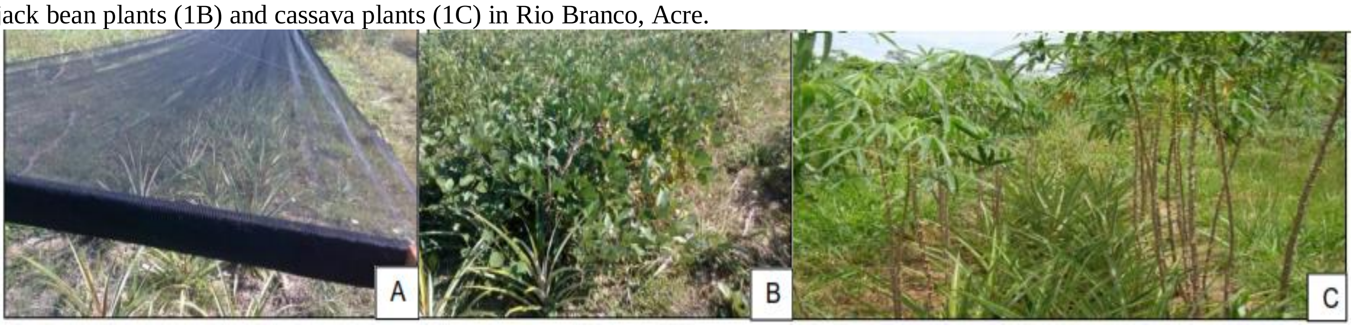
Under shade conditions, the growth and survival of a plant is closely associated with its ability to intercept light efficiently (KIM et al., 2011). Some species exhibit phenotypic plasticity, in that they can modify their shape and structure in response to changes in luminosity in order to improve photosynthetic efficiency (KIM et al, 2005; RIBEIRO et al., 2012), and various researchers have sought to understand this phenomenon by investigating the light-induced alterations in biochemical, anatomical and physiological variables (AOYAMA; SAJO, 2003; BARBOZA et al., 2006; ROZENDAAL et al., 2006; VOLTOLINI; SANTOS, 2011). In this context, the aim of the present study was to evaluate the different shade conditions in the chlorophyll content and morpho-anatomy of pineapple leaves on fruit production.

MATERIAL AND METHODS

The experimental area used for pasture was under five years fallow, at the Sítio Ecológico Seridó, Rio Branco, Acre, Brazil, located in latitude 9º53’16’’ S and longitude 67º49’11’’ W the 170 m in altitude. The experimente during the period January 2011 to October 2012. According to the Köppen classification, the tropical monsoon climate is of type Am, with a mean temperature of 24.5 ºC, a mean relative humidity of 84% and annual precipitation in the range 1,700 to 2,400 mm. According to the Brazilian Soil Classification System, the soil is yellow clay with plinthite (EMBRAPA, 2006) and revealed the following characteristics in the horizon A (0 – 0.20 m): base saturation 29%; pH 5.1; P 2 mg dm^{-3}; organic matter 17 g dm^{-3}; Ca 19 $mmol_c$ dm^{-3}; K 1.8 $mmol_c$ dm^{-3}; Al 8 $mmol_c$ dm^{-3}; Mg 9 $mmol_c$ dm^{-3}; H 64 $mmol_c$ dm^{-3}; Cu 1.6 mg dm^{-3}; Fe 530 mg dm^{-3}; Zn 2.6 mg dm^{-3}, B 0.17 mg dm^{-3} and Mn 99 mg dm^{-3}.

The plant material comprised pineapple propagules (30 – 45 cm long; Smooth Cayenne, cv. Rio-Branco 1), cassava stems (local genotype “Manteiguinha”) and jack bean seeds. The experiment was of a randomized block design with four replicates of five treatments each encompassing three rows of pineapple cultivated in direct sunlight (T1) or with shading provided by two rows of cassava (45% shade, T2) or two rows of jack bean (48.3% shade, T3) or net coverings (30% shade, T4; 50% shade, T5) (Figure 1).

Figure 1. Experiment of pineapple cv. Rio Branco-1 (RBR-1) established by shaded plants with 30% and 50% (1A) screens, jack bean plants (1B) and cassava plants (1C) in Rio Branco, Acre.



Source: Authors (2017)

The experimental field was ploughed and tilled with a disc harrow, but no fertilizer or soil correctives were applied. The pineapple were planted in plots containing three rows (0.25 m apart) of plants spaced at 0.80 m with those in the center row being offset by 0.40 m to afford a triangular arrangement. Each treatment plot contained 34 pineapple plants, with only 10 plants was considered the applicable plot.

Cassava cuttings and jack bean seeds were planted at 1.00 m and 0.50 m between plants and at 0.20 m from the external lines of pineapple, respectively. Artificial shading was provided by black shading nets with shading factors of 30 or 50%, installed 1.10 m above the soil. Cassava plants and shade nets were present throughout the entire experiment, while the jack bean plants remained for 12 months, following which the senescent plants were replaced by new plants. The level of shade was measured using a portable light meter on five alternate days, during which the weather was sunny with very low cloud cover.

Manual weeding was performed regularly as spontaneous weeds developed. Control of the fruit borer was performed by application of a *Bacillus thuringiensis*-based insecticide (500 g ha^{-1}; Dipel®) every 15 days from flowering to fruit maturation. Flowering of pineapple was induced 12 months after planting through application of 1 g of dry calcium carbide granules to the whorl of each plant.

"D" leaves from four previously identified 16 month-old pineapple plants were collected from each treatment and transported to the Tissue Culture Laboratory of the Federal University of Acre for morpho-anatomical analysis. Temporary and semi-permanent slides of paradermal and cross sections of fresh leaves were prepared, and 10 fields-of-view for each treatment were analyzed with the aid of an Olympus model CH030 light microscope. The images of the leaf sections were projected onto white paper using a Zeiss Opton camera attached to the microscope, and measurements were made using a Carl Zeiss micrometer scale. Measurements of leaf thickness were restricted to intercostal zones. In order to present measurements in µm, the thickness of the epidermal layer was determined at 40 X magnification while those of the chlorophyll parenchyma and aquiferous hypodermis the were determined at 10 X magnification. Measurements of the diameters of the metaxylem vessel elements and the lengths of the tector trichomes were performed at 40 X magnification.

Temporary slides of the paradermal sections of leaves were prepared according to a technique adapted from Barboza et al. (2006) to allow the examination of frontal views of the epidermal surfaces and to determine the dimensions of guard cells and stomatal pores and stomatal densities at 40 X magnification. Images of known areas (200 x 200 µm) were projected as described above, and the number of stoma counted and expressed as stoma per mm^2. The widths (transversal axis at the mid portion of the cell) and lengths (longitudinal axis between the poles) of the guard cells were measured, and the dimensions of the stomatal pores evaluated.

Fresh "D" leaves were collected from three randomly selected pineapple plants in each of the treatment plots and the chlorophylls extracted into 80% acetone. Quantitative determinations of chlorophylls a and b (Chl*a* and Chl*b*, respectively), total chlorophyll (Chl_{total}) and the Chl*a*/Chl*b* ratio were performed according to an adaptation of the method of Arnon (1949) and Vieira et al. (2010).

Chlorophyll a (mg g^{-1}) = (12.7 x A663 - 2.69 x A645) x V / 1000W;

Chlorophyll b (mg g^{-1}) = (22.9 x A645 - 4.68 x A663) x V / 1000W;

Chlorophyll a / b ratio (mg g^{-1}) = (4.70 x A663-A645 / 4.87 x A645-A663) x 0.574

Total chlorophyll a + b (mg g^{-1}).

Where: A = absorbance (nm); Cl a = chlorophyll a; Cl b = chlorophyll b; V = final volume of the extract; W = fresh mass (mg).

The yield of pineapple (kg ha^{-1}) was estimated from the fresh masses (kg $fruit^{-1}$) of fruits collected on a weekly basis from a treatment plot. The percentage of sunburned pineapple fruits was established by counting those that exhibited yellow coloration between the base of the crown and the base of the stem on the side exposed to the sun.

The percentage of fruits exhibiting damage by sunlight under different shading conditions were analyzed using Friedman test at the 5% probability level. All other data were submitted to analysis of variance, and mean values were compared using the Scott-Knott testat the 5% probability level, with the software sisvar (FERREIRA, 2011).

RESULTS AND DISCUSSION

Although the pineapple plants responded to different shading conditions, there were no significant differences between the chlorophyll content of "D" leaves from pineapple plants that had been subjected to the different treatments (Table 1).

The anatomical characteristics of pineapple "D" leaves were similar in all plants, independent of the level of shading provided. In contrast, the aquiferous hypodermis of "D" leaves from pineapple plants exposed to direct sunlight (T1) was significantly thicker ($P < 0.05$) than those of plants subjected to shading treatments (Figure 2A and 2B; Table 2).

Table 1. Mean chlorophyll content of "D" leaves o the pineapple plants cultivated under different shade conditions.

Treatments[1]	Chl*a* (mg g^{-1})[2]	Chl*b* (mg g^{-1})[2]	Chl_{total} (mg g^{-1})[2]	Chl*a*/Chl*b* ratio[2]
T1	0.052a[3]	0.024a	0.077a	0.077a
T2	0.045a	0.022a	0.067a	1.645a
T3	0.048a	0.021a	0.069a	1.756a
T4	0.052a	0.026a	0.078a	1.899a
T5	0.057a	0.022a	0.079a	2.073a
CV (%)	0.051	0.023	0.074	1.857

[1]Treatments involved: 0% shade (direct sunlight; T1); 45% shade (cassava plants at 1.0 m spacing; T2); 48.3% shade (jack bean plants at 0.5 m spacing; T3); 30% shade (black shading net; T4) and 50% shade (black shading net; T5). [2]Mean values (n = 60) of variables within each column are not significantly different according to the Scott-Knott test ($P < 0.05$). Abbreviations: Chl, chlorophyll. CV, coefficient of variation.

Figure 2. Cross section of the leaf blade showing the difference in thickness of the aquiferous hypodermis (AH) formed under natural shade provided by cassava plants (T2, A) and under sunlight (T1, B). Paradermal sections showing stomata (ST) and stomatal pores (SP) arranged in parallel layers (C and H). Cross sections showing AH subjacent to the adaxial epidermis (ADE, D), chlorophyll parenchyma (CP) subjacent to the abaxial epidermis (ABE; E), tector trichomes (TT; A and F), metaxylem vessel elements (MX), vascular bundles (VB) and aerenchyma (AR) (G). Bars = 20 µm (A and B), 50 µm (D, E and H) and 200 µm (C, F and G).

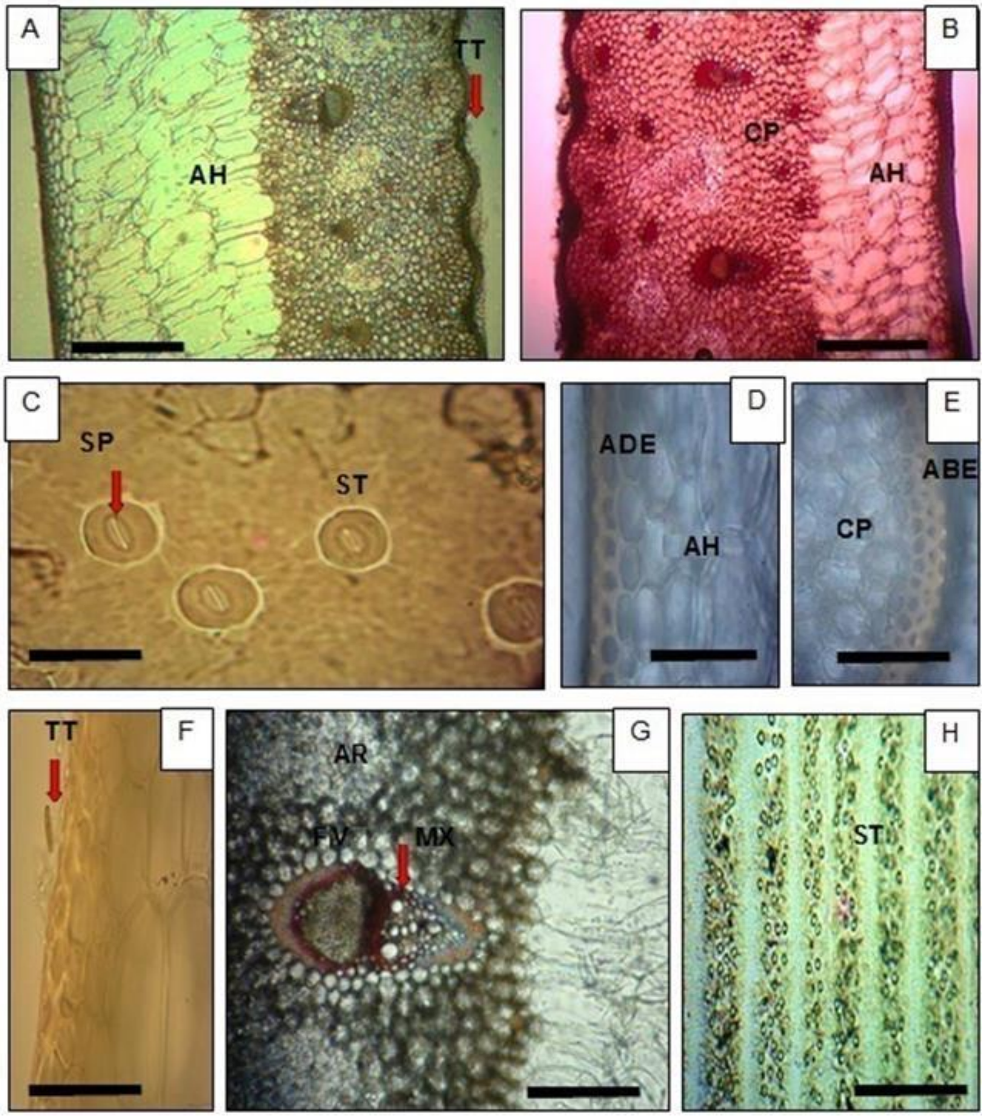


Table 2. Histological characteristics of "D" leaves from pineapple plants cultivated under different shade conditions.

Variable[2]	Treatments[1]					CV (%)
	T1	T2	T3	T4	T5	
Stomatal density (stoma mm^2)	109.10^b	125.00^a	99.60^b	105.20^b	103.50^b	8.23
Length of guard cells (µm)	25.00^b	24.80^b	33.80^a	33.50^a	34.00^a	5.71
Width of guard cells (µm)	11.75^a	9.75^b	12.75^a	12.50^a	12.25^a	9.54
Length of stomatal pore (µm)	13.80^a	13.00^a	12.00^a	13.30^a	12.50^a	7.52
Width of stomatal pore (µm)	1.85^a	2.19^a	1.93^a	1.98^a	1.91^a	12.14
Thickness of adaxial epidermis (µm)	12.60^b	16.40^a	16.50^a	16.80^a	15.50^a	4.74
Thickness of abaxial epidermis (µm)	10.00^c	12.50^b	12.50^b	15.00^a	14.80^a	6.98
Aquiferous hypodermis (µm)	4303.80^a	3220.80^c	3113.80^c	3744.50^b	2866.30^c	9.93
Thickness of chlorophyll parencyma µm	3067.80^b	4493.80^a	2680.00^b	2555.00^b	5175.80^a	13.73
Thickness of mesophyll (µm)	7349.00^a	7685.80^a	5765.00^b	6269.30^b	8010.30^a	6.72
Total thickness of the leaf blade µm	7371.50^a	7714.50^a	5793.80^b	6299.50^b	8042.00^a	6.70
Length of tector trichomes (µm)	643.50^a	511.50^b	584.50^c	621.80^a	394.30^c	11.32
Diameter of vessels elements (µm)	986.40^a	527.00^c	806.50^b	845.80^b	628.30^c	12.34

[1]Treatments involved: 0% shade (direct sunlight; T1); 45% shade (cassava plants at 1.0 m spacing; T2); 48.3% shade (jack bean plants at 0.5 m spacing; T3); 30% shade (black shading net; T4) and 50% shade (black shading net; T5). [2]Mean values (n = 120) of variables within each row bearing similar superscript lowercase letters are not significantly different according to the Scott-Knott test (P < 0.05).

Abbreviation: CV, coefficient of variation. Under normal light conditions, the rate of synthesis and degradation of chlorophylls is the same, but degradation can be accelerated by excess solar radiation (FERREIRA et al., 2012). The thicker aquiferous hypodermis detected in non-shaded plants might function as a filter to protect chlorophyllous tissue from intense radiation, thereby reducing the level of chlorophyll degradation (CUSTÓDIO et al., 2016). In addition, carotenoids serve as photoprotective agents and could function as safety valves by liberating excess light reaching the chloroplasts through rapid quenching of the excited states of chlorophyll (TAIZ; ZIEGER, 2006).

The “D” leaves from pineapple plants presented a hypostomatic structure with the stomata distributed in parallel layers (Figure 2C and 2H). Stomata were located at the same level as other epidermal cells suggesting the adoption of an adaptive strategy aimed at reducing or preventing excess losses through transpiration (PROENÇA; SAJO, 2007; RIBEIRO et al., 2012). The stomatal density was significantly higher (P < 0.05) in pineapple leaves shaded with cassava plants (T2) in comparison with all other treatments, although the lengths and widths of the stomatal pores were not influenced by the applied shading (Table 2). However, the different shading treatments did affect the dimensions of the guard cells, the lengths and widths of which were significantly greater (P < 0.05) in leaves of plants shaded with jack bean and plastic nets (T3 - T5) compared with those exposed to direct sunlight (T1) and cassava shading (T2) (Table 2). It has been reported that leaves exposed to direct sunlight may present stomata that are smaller and exhibit greater resistance to water diffusion, thereby improving hydraulic efficiency (BALTZER; THOMAS, 2005; BARBOZA et al., 2006). Moreover, Voltolini and Santos (2011) found that, under low levels of sunlight, the guard cells of the bromeliad *Aechmea lindenii* expand longitudinally, a characteristic that was also observed in pineapple leaves exposed to treatments T3 - T5.

The epidermal layers of both surfaces of the semi-perennial leaves of pineapple were unistratified and contained irregular rectangular cells. The abaxial surfaces of shade-grown plants exhibited epidermal cells with sinuous anticlinal walls (Figure 2D) and aquiferous hypodermis devoid of chloroplasts (Figure 2A and 2E). The mesophyll was of the dorsiventral type in which the chlorophyll parenchyma contained rounded cells (Figure 2B and 2E). Identical structures have been observed in the pineapple cultivar Pérola (BARBOZA et al., 2006) and in some other bromeliads (AOYAMA; SAJO, 2003; PROENÇA; SAJO, 2007; VOLTOLINI; SANTOS, 2011). Another feature that is common to the leaves of pineapple is the presence of aerenchyma intercalated with vascular bundles (Figure 2G) located adjacent to the chlorophyll parenchyma and connected with substomatic spaces. The aerenchyma not only permits the circulation of air in the inner tissues of the leaf blade but also confers greater leaf flexibility and resistance to wind (AOYAMA; SAJO, 2003).

In the present study, the thicknesses of the abaxial and adaxial epidermal layers increased significantly (P < 0.05) in plants grown under shade conditions (T2 - T5; Table 2). Typically, the epidermis of leaves exposed to direct sunlight is thicker than that of plants grown in a shaded environment, since this tissue acts as a protective filter against excessive solar radiation. However, it would appear that pineapple leaves acquire greater protection by investing in the enlargement of the aquiferous hypodermis, thereby confirming a high level of plasticity regarding sun/shade variations in the environment (KIM et al., 2005; ROZENDAAL et al., 2006). Markesteijn et al. (2007) also recorded increased epidermal thickness in leaves from tree species collected in a dry deciduous forest in Bolivia, and explained the phenomenon as an attempt to minimize the effect of the high levels of sunlight on sensitive mesophyll tissues.

The thickness of the chlorophyll parenchyma was increased significantly (P < 0.05; Table 2) in pineapple leaves exposed to treatments T2 and T5. Under such mild conditions, cells were less compacted and better able to retain water, thereby reducing the possibility of internal desiccation (ARAÚJO; DEMINICIS, 2009).

In the present study, the largest increases in total thickness of leaf blade were recorded in plants subjected to treatment T1, in which the overall expansion was mainly due to the enlargement of the aquiferous hypodermis and mesophyll cells, and in plants exposed to treatments T2 and T5, where the observed increase was due to the augmentation of the adaxial epidermis, chlorophyll parenchyma and mesophyll cells. The occurrence of thicker leaf blades in response to increased exposure to light has been reported by Lobo et al. (2013) for gravatá (*Dyckia brevifolia*; Bromeliaceae) and by Martins et al. (2009) for alfaca-cravo (*Ocimum gratissimum* L.; Lamiaceae).

Shading under treatments T2, T3 and T5 gave rise to significant (P < 0.05) reductions in length of the tector trichomes in pineapple leaves (Table 2; Figure 2F). Leaf trichomes fulfill various functions, of which the most important probably relates to the reduction of transpiration by reflectance (BARBOZA et al., 2006; PROENÇA; SAJO, 2007). It is believed that the layer of tector trichomes on the leaf blade can transform direct sunlight into diffuse light, thereby minimizing the effects of intense irradiance on the internal tissues (TAIZ; ZEIGER, 2006).

As shown in Table 2, the diameters of xylem vessel elements (Figure 2G) of leaves from plants grown under shade treatments T2 – T5 were significantly (P < 0.05) smaller than those of leaves that had been exposed to direct sunlight (T1), demonstrating the flow of sap diminishes under lower light conditions but increases under sunlight by virtue of higher transpiration.

No significant differences regarding yields or mean masses of pineapple fruits (Table 3) were detected between treatments. However, the percentages of sunburned fruits were significantly higher under treatments T1 and T3 in comparison with other treatments. In treatment T2, however, some of the cassava plants collapsed during the experiment exposing the rows of pineapples to direct sunlight, hence a small percentage of fruits were burned.

Table 3. Production of pineapple fruit cultivated under different shade conditions.

Treatments[1]	Sunburned fruit[2] (%)	Mean mass of fruit[3] (kg fruit^{-1})	Yield of fruit[3] (kg ha^{-1})
T1	34.2[a]	1.28[a]	19,156.73[a]
T2	8.8[b]	1.37[a]	20,540.20[a]
T3	43.6[a]	1.27[a]	18,950.88[a]
T4	0.0[c]	1.26[a]	18,894.58[a]
T5	0.0[c]	1.26[a]	18,843.03[a]
CV (%)	-	10.86	10.96

[1]Treatments involved: 0% shade (direct sunlight; T1); 45% shade (cassava plants at 1.0 m spacing; T2); 48.3% shade (jack bean plants at 0.5 m spacing; T3); 30% shade (black shading net; T4) and 50% shade (black shading net; T5). [2]Within the column, mean values bearing similar superscript lowercase letters are not significantly different according to the non-parametric Friedman test (P < 0.05). [3]Within a column, mean values bearing similar superscript lowercase letters are not significantly different according to the Scott-Knott test (P < 0.05). Abbreviation: CV, coefficient of variation

CONCLUSIONS

Pineapple plants grown under natural shade provided by cassava (T2) or jack bean (T3) showed phenotypic plasticity with the “D” leaves presenting trichomes of reduced length and vessel elements of smaller diameter in comparison with plants cultivated under sunlight. Under treatment T2, the stomatal density and the thicknesses of the abaxial epidermis and chlorophyll parenchyma were increased while the thickness of the aquiferous hypodermis and the percentage of sunburned fruits were reduced. When pineapple plants were exposed to T3, the thicknesses of the chlorophyll parenchyma, mesophyll and leaf blade were reduced. Net shading (treatments T4 and T5) prevented the loss of fruit by sunburn while maintaining a level of fruit production that was similar to that observed in the other treatments.

ACKNOWLEDGMENTS

The authors are grateful to the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) and the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for the award of grants.

REFERENCES

AGRIANUAL. Anuário da Agricultura Brasileira. 2012, p. 126-133.

AOYAMA, E. M.; SAJO, M. das G. Estrutura foliar de *Aechmea* Ruiz & Pav. subgênero *Lamprococcus* (Beer) Baker e espécies relacionadas (Bromeliaceae). Revista Brasileira de Botânica, Campinas, v. 26, n. 4, p. 461-473, 2003.

ARAÚJO, S. A. do C.; DEMINICIS, B. B. Fotoinibição da Fotossíntese. Revista Brasileira de Biociências, Porto Alegre, v.7, n. 4, p. 463-472, 2009.

ARAÚJO NETO, S. E. de; CAMPOS, P. A.; TAVELLA, L. B.; SOLINO, A. J. da S.; SILVA, I. F. Organic polyculture of passion fruit, pineapple, corn and cassava: the influence of green manure and distance between espaliers. Ciência e Agrotecnologia, Lavras, v. 38, n. 1, p. 1-5, 2014.

ARNON, D. I. Copper enzymes in isolated chloroplasts: polyphenoloxydase in *Beta vulgaris*. Plant Physiology, Maryland, v. 24, n. 1, p. 1-15, 1949.

BARBOZA, S. B. S. C.; GRACIANO-RIBEIRO, D.; TEIXEIRA, J. B. PORTES, T. A.; SOUZA, L. A. C. Anatomia foliar de plantas micropropagadas de abacaxi. Pesquisa Agropecuária Brasileira, Brasília, v.41, n. 2, p. 185-194, 2006.

BALTZER, J. L.; THOMAS, S. C. Leaf optical responses to light and soil nutrient availability in temperate deciduous trees. American Journal of Botany, St. Louis, v. 92, n. 2, p. 214–223, 2005.

BAYMA, M. A.; SÁ, C. P.; GONZAGA, D. de O. M.; KLEIN, M. A. Boletim de preços de produtos agropecuários e florestais do Estado do Acre. Boletim Embrapa Acre. 2012.

CRESTANI, M.; BARBIERI, R. L; HAWERROTH, F. J.; CARVALHO, F. I. F. de; OLIVEIRA, A. C. de. Das Américas para o Mundo origem, domesticação e dispersão do abacaxizeiro. Ciência Rural, Santa Maria, v. 40, n. 6, p. 1473-1483, 2010.

CUNHA, G. A. P. DA; HAROLDO, D. Cuidados para evitar queima solar no abacaxi**.** Revista Frutas e derivados, São Paulo, v. 3, n. 9, p. 9-17, 2008.

CUSTÓDIO, R. A.; ARAÚJO NETO, S. E.; FERMINO JUNIOR, P. C. P.; ANDRADE NETO, R. de C.; SILVA, I. F. Morpho-anatomy of leaves and yield of pineapple plant in intercropping with cassava. Bioscience Journal, Uberlândia, v. 32, n. 4, p. 839 - 848, 2016.

EMBRAPA - Empresa Brasileira de Pesquisa Agropecuária. Centro Nacional de Pesquisa do Solo. Sistema brasileiro de classificação de solos. (2. Ed.) Brasília: Embrapa, 2006. 306p.

FERREIRA, D. F. Sisvar: a computer statistical analysis system. Ciência e agrotecnologia. Lavras, v.35, n.6, p.1039-1042, 2011.

FERREIRA, W. N.; ZANDAVALLI, R. B.; BEZERRA, A. M. E.; MEDEIROS FILHO, S. Crescimento inicial de *Piptadenia stipulacea* (Benth.) Ducke (Mimosaceae) e *Anadenanthera colubrina* (Vell.) Brenan var. *cebil* (Griseb.) Altshul (Mimosaceae) sob diferentes níveis de sombreamento. Acta Botanica Brasilica, Feira de Santana,, v. 26, n. 2, p. 408-414, 2012.

KIM, G.; YANO, S.; KOZUKA, T.; TSUKAYA, H. Photomorphomogenesis of leaves: sahad-avoidance and differenciation of sun and shade leaves. Photochemetry, Photobiology and Science, Cambridge, v. 4, n. 5, p. 770-774, 2005.

KIM S. J.; YU D. J.; KIM T.C.; LEE H. J. Growth and photosynthetic characteristics of blueberry (*Vaccinium corymbosum* cv. Bluecrop) under various shade levels. Scientia Horticulturae, Cambridge, v. 129, n. 5, p. 486-492, 2011.

LUDEWIGS, T.; BRONDIZIO, E. S. Paths of diversification: land use, livelihood strategies and social learning along the aging of a land reform settlement in Acre, Brazil. Amazônica: Revista de Antropologia, Belém, v. 1, n. 2, p. 330-367, 2009.

LOBO, G. M.; SOUZA, T. V. DE; VOLTOLINI, C. H.; REIS, A.; SANTOS, M. Leaf Epidermis of the Rheophyte *Dyckia brevifolia* Baker (Bromeliaceae). The Scientific World Journal, London,, v. 2013, n. 1, p. 1-7, 2013.

MARKESTEIJN, L.; POOTER, L.; BONGERS, F. Light-dependent leaf taint variation in 43 tropical dry forest tree species. American Journal of Botany, St. Louis, v. 94, n. 4, p. 515-525, 2007.

MARTINS, J. R.; ALVARENGA, A. A.; CASTRO, E. M. de.; SILVA, A. P. O. da.; OLIVEIRA, C.; ALVES, E. Anatomia foliar de plantas de alfavaca-cravo cultivadas sob malhas coloridas. Ciência Rural, Santa Maria, v. 39, n. 1, p. 82-87, 2009.

PROENÇA, S. L.; SAJO, M. das G. Anatomia foliar de bromélias ocorrentes em áreas de cerrado do Estado de São Paulo, Brasil. Acta Botânica Brasílica, Belo Horizonte, v. 21, n. 3, p. 657-673, 2007.

RIBEIRO, M. de N. O.; CARVALHO, S. P. de; PEREIRA, F. J.; CASTRO, E. M. de. Anatomia foliar de mandioca em função do potencial para tolerância à diferentes condições ambientais. Revista Ciência Agronômica, Fortaleza, v. 43, n. 2, p. 354-361, 2012.

ROZENDAAL, D. M. A.; HURTADO, V. H.; POORTER, L. Plasticity in leaf traits of 38 tropical tree species in response to light; relationships with light demand and adult stature. Functional Ecology, London, v. 20, n. 2, p. 207-216, 2006.

TAIZ, L.; ZEIGER, E. Fisiologia vegetal. 3 ed. Tradução Eliane Romanato Santarém. Porto Alegre: Artmed, 2006. 722 p.

VIEIRA, D. A. de P.; PORTES, T. de A.; STACCIARINI-SERAPHIN, E.; TEIXEIRA, J. B. Fluorescência e teores de clorofilas em abacaxizeiro cv. pérola submetido a diferentes concentrações de sulfato de amônio. Revista Brasileira de Fruticultura, Jaboticabal, v. 32, n. 2, p. 360-368, 2010.

VOLTOLINI, C. H.; SANTOS, M. Variações na morfoanatomia foliar de *Aechmea lindenii* (E. Morren) Baker var. *lindenii* (Bromeliaceae) sob distintas condições ambientais. Acta Botanica Brasilica, Belo Horizonte, v. 25, n. 1, p. 2-10, 2011.