Colegio de Postgraduados

Influence of photoselective covers on the growth and stomatal anatomy of *Agave durangensis* Gentry under protected conditions

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ABSTRACT

Objective: To study the effect of light modification using photoselective covers on the growth and stomatal traits of agave cenizo (*Agave durangensis* Gentry) seedlings.

Design/methodology/approach: Seedlings were grown for eight months under different types of cover: 1) no cover (outdoor), 2) greenhouse, 3) blue net, 4) black net, 5) red net, and 6) green net. Height, rosette diameter, core diameter, number of expanded leaves, °Brix, biomass of the different components (root, cone, leaf), leaf area (LA), specific leaf area (SLA), and leaf succulence (LS), as well as different stomatal traits were evaluated.

Results: Seedlings under black and green nets had the lower development in height (7.6 and 8.2 cm) and diameter (2.0 and 2.2 cm), but increased SLA (100 and 89.7 cm^2 g^{-1}) and biomass allocation to leaves. Seedlings grown under red net, outdoors, and in the greenhouse showed the greatest growth in height (9.7, 8.8 and 8.5 cm) and diameter (2.5, 2.3 and 2.4 cm), and an increased biomass allocation to leaves, but with the lowest SLA values ($<$75 cm^2 g^{-1}). In addition, the red net condition marginally increased the increase in stomatal density (2500 and 1100 cm^{-2}, in the adaxial and abaxial surfaces, respectively). In general, the dimensions of the stomatal characters were smaller in the greenhouse condition, while they were favored in the blue net condition.

Limitations on study/implications: In addition to the practical implications for the seedling production in nurseries, the results contribute to understanding the species' capacity to acclimatize to heterogeneous light environments.

Findings/conclusions: Due to its heliophilous nature, *A. durangensis* seedlings have better development in conditions of greater luminosity (outdoors). However, photoselective covers, such as red and blue nets, improve some stomatal characteristics, which can contribute to the physiological performance of the plants.

Keywords: agave cenizo, light environment, biomass, stomatal density.

Citation: García-Rodríguez, J. L., Sigala-Rodríguez, J. A., Sarmiento-López, H., Basave-Villalobos, E., Monárrez-González, J. C., & Rodríguez-Reyes, J. U. (2025). Influence of photoselective covers on the growth and stomatal anatomy of *Agave durangensis* Gentry under protected conditions. *Agro Productividad*. https://doi.org/10.32854/qxtqkh76

Academic Editor: Jorge Cadena Iñiguez
Associate Editor: Dra. Lucero del Mar Ruiz Posadas
Guest Editor: Daniel Alejandro Cadena Zamudio

Received: August 15, 2025.
Accepted: November 14, 2025.
Published on-line: December XX, 2025.

Agro Productividad, 18(11). November. 2025. pp: 117-128.

INTRODUCTION

The cenizo agave (*Agave durangensis* Gentry) is a strategic resource for the regional mezcal industry in northern Mexico, particularly in the state of Durango. In this region, there is a growing demand for raw material for mezcal production and agave-derived products.

Consequently, this situation may pose a threat to natural populations of *A. durangensis* (López-Serrano *et al.*, 2021). Therefore, it is essential to develop and implement nursery-based plant production programs aimed at establishing commercial plantations to meet the mid-term demand for raw material.

The nursery cultivation of *A. durangensis* has been adapted from the production system used for forest tree species. This system involves the use of commercial substrate mixtures, forest containers, controlled-release fertilizers (CRF), water-soluble nutrients, and the regulation of environmental production conditions. Several aspects of this system have been refined and tailored to the specific needs of the species (García-Rodríguez *et al.*, 2023). However, among other factors, the most suitable light environment for agave growth under protected conditions remains unknown.

In protected agriculture, plastic covers are used to maintain optimal environmental conditions according to the crop's requirements and the region's climatic factors (Juárez *et al.*, 2011). One of the key features of these covers is their ability to transmit, block, or reflect specific wavelengths while still allowing sufficient photosynthetically active radiation (PAR) to ensure proper plant growth (Díaz *et al.*, 2001; Ombódi *et al.*, 2015). In warm and dry environments, plastic shade nets are commonly used, as they not only reduce radiation but also help prevent plant stress due to high temperatures during peak heat periods (Valera *et al.*, 2001). Additionally, they reduce the incidence of pests and diseases (Shahak *et al.*, 2008) and provide protection from physical damage caused by wind, hail, and birds (Ben-Yakir *et al.*, 2012).

In forest nurseries, black shade nets are widely used (Bustos-Salazar & Zuñiga-Feest, 2019), mainly due to their low cost. However, they are not spectrally selective and reduce the transmission of both PAR and near-infrared radiation (Ayala-Tafoya *et al.*, 2018), potentially lowering photosynthetic rates and, consequently, crop performance. For this reason, modifications in net properties such as texture, pigmentation, density, and porosity can be implemented to enhance light transmission quality (Abdel-Ghany & Al-Helal, 2010). For instance, changing the net color alters the light spectrum filtered across the ultraviolet, visible, and far-red regions, and increases light scattering (diffuse light), which also influences the thermal component (infrared region) (Oren-Shamir *et al.*, 2001; Demotes-Mainard *et al.*, 2016). Alterations in light quality parameters have been shown to directly impact vegetative growth (Li *et al.*, 2012; Sergejeva *et al.*, 2018) and other physiological traits, such as photosynthetic pigment concentrations (Sergejeva *et al.*, 2018).

Plant responses to photo-selective covers are varied due to the complexity and variability of natural radiation. Therefore, predicting how light manipulation will affect specific vegetative responses is challenging particularly in heliophilous species, such as agaves from arid ecosystems (Novel, 1988). Specifically, little is known about how agaves respond to modified light environments at the leaf surface level, particularly in terms of epidermal and stomatal characteristics. In this context, the study of the cuticular membrane and stomatal apparatus components is relevant, as these structures serve as the interface between the plant and its environment (Monja-Mio *et al.*, 2015). This study aimed to evaluate the effect of different light conditions defined by the type and color of cover on the morphological attributes and stomatal anatomy of *Agave durangensis* plants grown in nursery conditions.

MATERIALS AND METHODS

The experiment was carried out at the forest nursery facilities of the Valle del Guadiana Experimental Station of the National Institute for Forestry, Agricultural and Livestock Research (INIFAP), Durango, located at coordinates 24° 01' N and 100° 44' W, at an altitude of 1806 m. *Agave durangensis* seedlings were obtained from direct sowing in expanded polystyrene containers with 77 cavities of 160 cm^3, using a substrate composed of peat moss (50%), perlite (25%), and vermiculite (25%). Two months after sowing, an experiment was established under a completely randomized design with six environmental conditions varying in the type and photoselectivity of the cover: 1) without cover (outdoors), 2) plastic cover (milky white polyethylene, 720 μm), 3) blue shade net, 4) black shade net, 5) red shade net, and 6) green shade net. For each condition, four replications were included (four trays with 77 plants), totaling 308 plants per treatment. In each type of cover, photosynthetically active radiation (PAR) was measured with a ceptometer (Model SF-80, Decagon, Pullman WA, USA), as well as transmittance (%) relative to the outdoor condition (Table 1).

Plants were grown under the different light conditions for eight months, from November 2022 to June 2023. Depending on water requirements, three irrigations per week were applied during the driest months, and one irrigation per week during winter. At each irrigation event, 30 to 50 mL of water per plant were applied. Additionally, fertilizations were performed twice a week using nutrient solutions at a dose of 0.71-0.36-0.28 g L^{-1} of N-P-K, plus 0.08 g L^{-1} of a micronutrient mix [Micromix® (Fe, Mn, Zn, S, B, Cu, Mo)]. Nitrogen (N) was applied as ammonium sulfate [$(NH_4)_2SO_4$], phosphorus (P) as single superphosphate [$Ca(H_2PO_4)_2$], and potassium (K) as potassium sulfate (K_2SO_4). At the end of the cultivation period, 40 plants were extracted per treatment (10 per tray). In each plant, the following morphological traits were measured: plant height (cm), from the surface of the root ball to the tip of the central spine; rosette diameter (RD, cm), taken as the average of two perpendicular distances from spine to spine of fully expanded leaves; number of expanded leaves (NEL), defined as leaves fully separated from the central meristem.

Table 1. Average values of internal photosynthetically active radiation (PAR) and transmittance in different light environments during the development of *Agave durangensis*.

Light Environment	Internal PAR (μmol m^{-2} s^{-1})	Transmittance (%)
Outdoor	1,898	100
Greenhouse	835	44
Blue shade net	532	28
Black shade net	497	26
Red shade net	658	35
Green shade net	467	25

After removing the substrate and carefully washing the root system, plants were dissected into parts (core, leaves, roots). Once dissected, core diameter (CD, mm) was measured using a digital caliper (HER-411, Steren®, China), and °Brix percentage was determined with a portable refractometer (Vee Gee®) using juice drops extracted from the core. Finally, samples were dried in a forced-air oven (FE-133, Felisa®, Mexico) at 60 °C for 120 hours, and biomass (g) per plant component was determined with an analytical balance (Ohaus Adventurer®, Ohaus, Mexico). Additionally, three fully expanded representative leaves were selected from each plant to determine leaf area (LA). For this, cardboard imprints were made for each leaf and photographed against a contrasting background. Photographs were analyzed using the digital image processing software ImageJ 1.49 (Wayne Rasband/National Institutes of Health [NIH], Bethesda, MD, USA) to determine the area of each imprint and the LA. Specific leaf area (SLA) was then calculated using the LA/DW ratio, where DW is the dry weight of the leaves. Leaf succulence (LS) was also determined following the method described by Mantovani (1999), using the formula:

$$LS=(FW-DW)/LA$$

where: FW is maximum fresh weight (g).

FW was obtained after soaking the leaves in distilled water for 24 h prior to drying. Furthermore, three cuticle samples were taken from both the adaxial and abaxial sides of the leaves from one plant per replicate. These were used to prepare fixed slides to determine stomatal density (cm^2). The cuticle samples were mounted on glass slides using methylene blue as a mounting and contrast medium. A 1 cm^2 square was previously marked on the back of each slide, within which the number of stomata was counted using a 10x objective under bright-field in an OMAX® optical microscope with an OMAX® camera (model A3550S). In addition, stomatal complex morphology was characterized using a 40x objective, determining: stomatal complex area (SA, μm^2), diameter and length of subsidiary cells (SC, μm) and guard cells (GC, μm), diameter of epidermal cells (EC, μm), and lengths of the polar ledge (PL, μm) and cuticular polar ledge (CPL, μm) (Figure 1).

The effects of light condition on growth, foliar, and stomatal apparatus anatomical variables were analyzed using one-way ANOVA in R software. For each variable, the assumptions of normality and homogeneity of variance were verified using the Shapiro-Wilk and Levene tests, respectively. Variables that did not meet these assumptions were log-transformed. When significant differences were detected, a multiple means comparison was conducted using Tukey's adjustment ($\alpha=0.05$).

RESULTS AND DISCUSSION

Overall, plants grown outdoors exhibited greater height and core diameter (CD), although not significantly different from those grown under red and blue nets or in the greenhouse. Under these same conditions, plants developed smaller rosette diameters (Table 2). In contrast, plants grown under black and green nets showed reduced growth in height and CD. Specifically, under the black net, plants also developed fewer expanded leaves but had the largest rosette diameter.

On the other hand, the outdoor condition resulted in greater biomass production, in contrast to plants grown under black and green shade nets. Meanwhile, under greenhouse, blue, and red net conditions, plants showed intermediate values (Table 2).

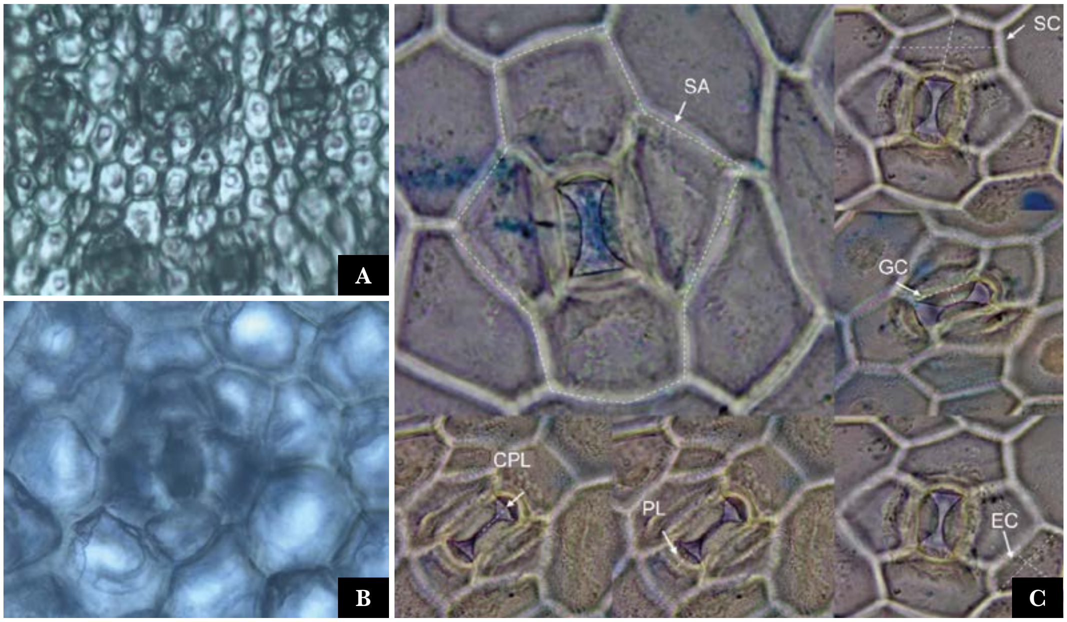

Figure 1. A) General view of the leaf adaxial cuticle of agave (10x), B) sunken stoma (40x), and C) cells and structures of the stomatal apparatus on the adaxial surface of expanded leaves of 10-month-old *Agave durangensis* (40x): SA=Stomatal apparatus area, SC=Subsidiary cells, GC=Guard cells, CPL=Cuticular polar ledge, PL=Polar ledge, EC=Epidermal cells.

Table 2. Morphological characteristics of *Agave durangensis* plants grown under different light environments in a nursery.

Light Environment	Height (cm)	RD (cm)	CD (cm)	NEL	Biomass per Component (g)		
					Leaves	Core	Roots
Outdoor	9.7±0.3a	8.1±0.2c	2.5±0.1a	7.2±0.2ab	5.2±0.3a	2.1±0.2a	2.0±0.1a
Greenhouse	8.8±0.3ab	10.8±0.4b	2.3±0.1ab	7.2±0.2ab	4.4±0.3ab	1.6±0.1a	1.3±0.1b
Blue shade net	8.5±0.4ab	12.5±0.5ab	2.5±0.1a	7.1±0.2ab	3.8±0.3b	1.6±0.1a	1.2±0.1b
Black shade net	7.6±0.3b	12.1±0.3a	2.0±0.1c	6.4±0.2b	2.4±0.2c	0.7±0.1b	0.4±0.1d
Red shade net	8.5±0.2ab	11.0±0.4b	2.4±0.1a	7.4±0.2a	4.3±0.3ab	1.7±0.2a	1.1±0.1b
Green shade net	8.2±0.4b	11.7±0.4b	2.2±0.1bc	7.2±0.2ab	2.9±0.3c	0.9±0.1b	0.7±0.1c

RD=Rosette diameter; CD=Core diameter; NEL=Number of expanded leaves.
Within the same variable, means with different letters indicate statistically significant differences ($p<0.05$).

Additionally, biomass allocation patterns particularly for leaf and root biomass were affected by the light environment. It was observed that plants grown under black, red, and green nets allocated proportionally more biomass to leaves and less to roots compared to those grown outdoors, in the greenhouse, or under the blue net. Agaves are ecophysiologically considered heliophilous plants, meaning they require high light intensity for optimal growth. Their rosette-shaped leaf arrangement is regarded as an adaptation that maximizes interception of photosynthetically active radiation (PAR) (Stewar, 2015). This may explain why plants exposed to direct sunlight exhibited better growth performance. In contrast, plants grown under the black net showed the least growth, as this type of net is minimally photoselective and reduces PAR transmission, thereby affecting photosynthetic activity (Ayala-Tafoya *et al.*, 2011) and the production of photoassimilates (*i.e.*, sugars) (Wang *et al.*, 2014). This latter effect was also evident in the °Brix results, which showed that plants cultivated under the black net had the lowest values compared to those in higher-light environments (Figure 2). Likewise, in the black net environment, plants allocated more biomass to leaves than to roots. In this regard, Poorter *et al.* (2011) noted that under low-light conditions, plants tend to allocate a proportionally greater share of resources to shoot growth as a shade acclimation or escape strategy.

Under blue and red net conditions, intermediate growth was generally observed, which was contrary to expectations, since blue and red light are essential for photosynthesis (Snowden *et al.*, 2016; Li *et al.*, 2012). Nevertheless, the biomass distribution of plants under the blue net was similar to those grown in the greenhouse or outdoors, even though transmittance levels were comparable to those of the other tested nets. In this regard, studies have shown that the red to far-red (R/FR) light ratio transmitted by blue nets resembles that of natural light (Oren-Shamir *et al.*, 2001). In fact, the reduction in R/FR caused by shade nets can result in increased shoot growth as a shade avoidance mechanism (Arthurs *et al.*, 2013), a typical phytochrome-mediated response (Baraldi *et al.*, 1994). Therefore, it is possible that *Agave durangensis* plants grown under the blue net were not exposed to sufficiently low R/FR ratios to trigger greater biomass allocation to leaves.

Moreover, the modification of the light environment also significantly affected leaf area and succulence. The black and green nets induced a significant increase in specific leaf area (SLA) compared to the other treatments (Figure 3A). This change in leaf area could be explained as an acclimation mechanism involving morphogenetic control of leaf development to enhance light interception (Puglielli *et al.*, 2017). Similarly, the black and green nets resulted in the lowest leaf succulence (LS), whereas plants grown outdoors

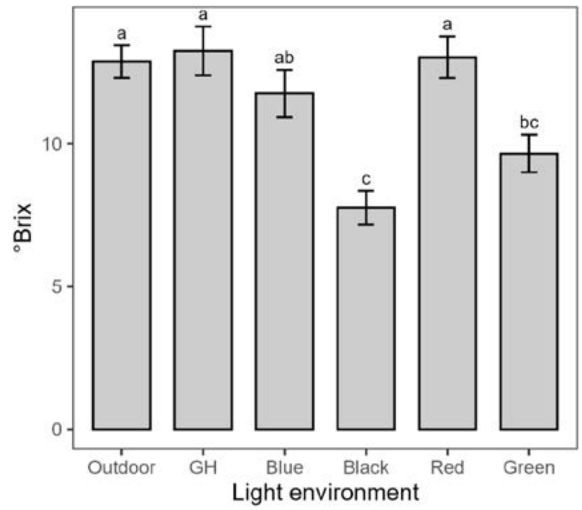

Figure 2. °Brix values measured in the pineapple of *Agave durangensis* plants grown under different light environments in a nursery. Means with a different letter indicate statistically significant differences ($p<0.05$).

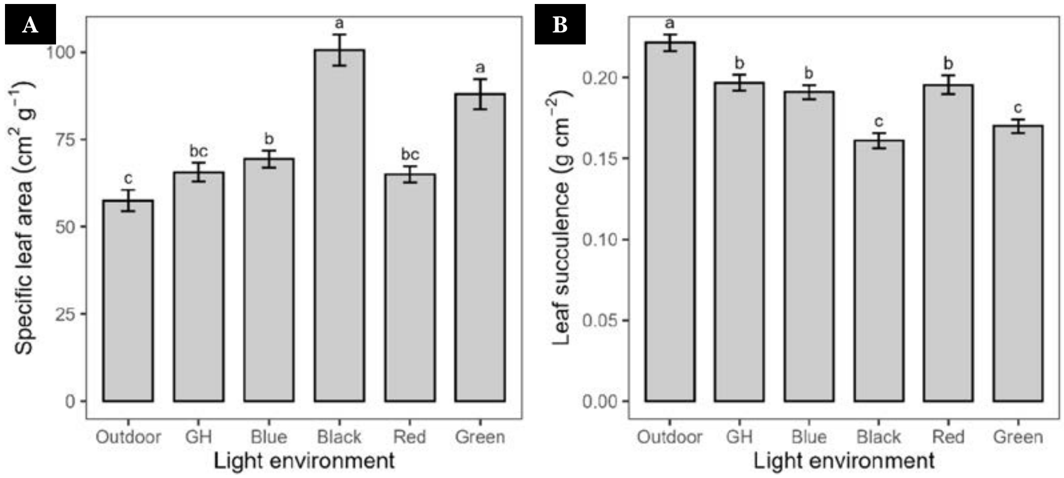

Figure 3. Specific leaf area (A) and leaf succulence (B) of *Agave durangensis* plants grown under different light environments in nursery conditions. For each variable, means with different letters indicate statistically significant differences ($p<0.05$).

exhibited the highest average LS value (Figure 3B). Comparable LS values (0.2-0.3) were reported by Cruz-García *et al.* (2019) in *Agave americana* var. *Oaxacencis* acclimated for 290 days in greenhouse conditions. LS is an indicator of a plant's capacity to store water per unit of leaf area (Mantovani, 1999). Therefore, it is suggested that plants with greater succulence have a higher water storage capacity and, consequently, greater tolerance to water stress.

Regarding stomatal characteristics, it was found that *A. durangensis* plants, like other agave species, possess tetracytic-type stomata (Figure 1). This stomatal type is typical of monocotyledons and consists of four subsidiary cells two lateral and two polar surrounding the guard cells (Rudall *et al.*, 2017; Bernardino-Nicanor *et al.*, 2012; Sosa del Castillo *et al.*, 2014). The polar and lateral subsidiary cells are taller than the epidermal cells; their basal walls are expanded towards the contact zone with the guard cells, and their upper margins form a small sunken supra-stomatal chamber (Gray *et al.*, 2020). This is a xeromorphic adaptation that enhances desert survival by preventing excessive water loss through evaporation (Davis *et al.*, 2010).

Stomata were observed on both leaf surfaces (*i.e.*, amphistomatic leaves), with higher density on the adaxial side (Figure 4A). The amphistomatic condition increases boundary layer conductance (Branco-Camargo & Marenco, 2012), thereby enhancing CO_2 uptake, transpiration rate, and reducing internal leaf temperature (Taiz & Zeiger, 2010). In this study, relatively low stomatal densities were found, as reported in other agave species (Bernardino-Nicanor *et al.*, 2012; Chávez-Güitrón *et al.*, 2019; Pérez-España *et al.*, 2022). In a previous study on *A. tequilana*, Monja-Mio *et al.* (2015) reported that stomatal density is highly sensitive to environmental conditions. However, in this case, no significant differences in stomatal density were found among the different light environments. Although on the adaxial surface, the effect was marginal ($p=0.099$), with plants grown under the red net showing higher density compared to those grown under black and green nets (Figure 4A).

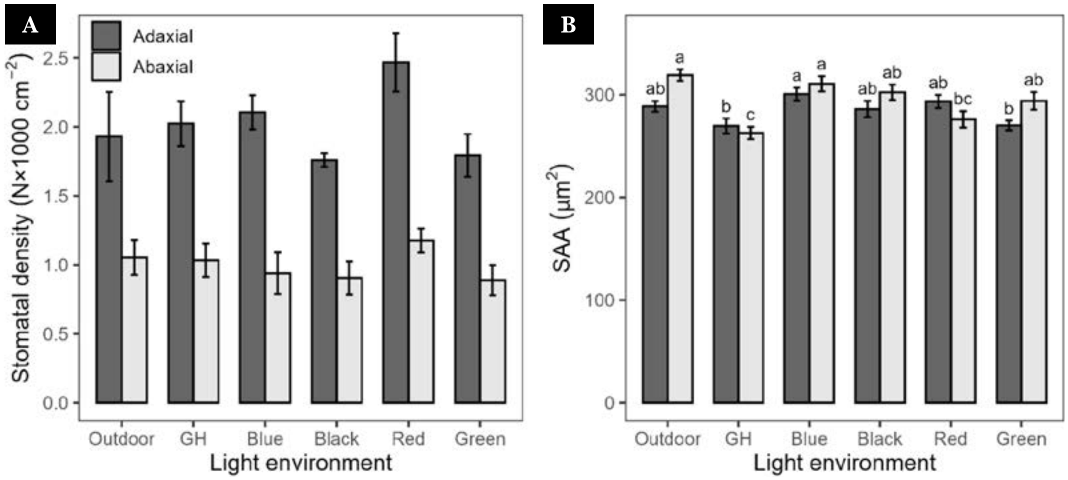

Figure 4. Stomatal density (A) and stomatal apparatus area (SAA, B) on the adaxial (dark gray) and abaxial (light gray) surfaces of *Agave durangensis* leaves grown under different light environments in nursery conditions. For the same variable and each leaf surface, means with different letters indicate statistically significant differences ($p<0.05$).

On the other hand, the stomatal apparatus area (SAA) varied significantly on both the adaxial and abaxial sides depending on the light environment. In general, plants grown under the blue net showed the highest SAA values, while those grown in the greenhouse had the lowest average SAA (Figure 4B). Under the remaining conditions, plants exhibited intermediate SAA values. Overall, the SAA values found in *A. durangensis* were lower than those reported for other species such as *A. atrovirens* (Bernardino-Nicanor *et al.*, 2012) or *A. tequilana* (Hernández *et al.*, 2003). However, such differences may be attributed to several factors, including plant age (Bernardino-Nicanor *et al.*, 2012), leaf position, climatic conditions (Monja-Mio *et al.*, 2015), and even variations in the thickness and distribution of waxes present in the cuticular membrane (García-Mendoza, 2007). It was also found that the size of the subsidiary cells varied significantly with light environment, in both diameter (SCD) and length (SCL). Plants grown under the blue net exhibited greater SCD and SCL on both leaf surfaces, while those in the greenhouse had the lowest averages (Table 4). Similarly, guard cell size was affected by light environment, but only in terms of length (GCL). These cells, responsible for stomatal opening and closing (Daszkowska-Golec & Szarejko, 2013), have been reported to be highly sensitive to environmental changes, particularly radiation (Gitz & Liu-Gitz, 2007). Accordingly, it was observed that both adaxially and abaxially, outdoor and red net conditions promoted greater GCL compared to the black net condition.

It was found that *Agave durangensis* plants exhibited a greater length of the cuticular polar ledges (CPL) on the abaxial surface. Furthermore, this characteristic responded significantly to the light environment, with the outdoor (uncovered) condition producing plants with the greatest CPL. According to Spiegelhalder and Raissig (2021), cuticular ledges result from the formation process of the stomatal apparatus. Initially, the stomatal pore is sealed by cuticle; when this cuticle ruptures, extended ledges surrounding the stomatal pore remain known as cuticular ledges. To date, their functional role is not fully

Table 3. Averages and standard error of stomatal characteristics in expanded leaves of *Agave durangensis* grown under different light environments in a nursery.

Light Environment	SCD (μm)	SCL (μm)	GCD (μm)	GCL (μm)	PL (μm)	CPL (μm)	ECD (μm)
Adaxial surface							
Outdoor	31.2±1.1ab	44.6±1.3ab	7.0±0.5	28.4±1.3a	3.5±0.5	15.0±0.9a	43.8±3.1
Greenhouse	29.2±0.8c	41.3±1.1b	7.8±0.3	25.0±0.9ab	4.5±0.5	12.6±0.6abc	46.6±3.0
Blue net	35.2±0.8a	45.8±1.2a	7.4±0.2	25.5±0.9ab	4.0±0.3	12.5±0.4bc	45.4±2.4
Black net	33.9±1.3ab	44.4±0.6ab	6.7±0.5	22.7±0.8b	3.1±0.2	11.5±0.3c	45.3±2.7
Red net	32.6±0.7bc	43.5±1.2ab	8.1±0.3	28.0±1.4a	3.5±0.3	14.4±0.7ab	45.5±2.6
Green net	30.0±0.7abc	40.9±0.7b	7.9±0.3	25.4±0.6ab	3.9±0.5	12.8±0.3abc	42.6±1.7
Abaxial surface							
Outdoor	33.0±1.1ab	46.8±0.9a	8.9±0.5	35.9±1.6a	4.2±0.5ab	19.6±1.0a	46.5±3.0
Greenhouse	28.1±1.0c	39.8±1.1c	8.3±0.4	27.9±1.2b	5.3±0.3a	13.5±0.6c	45.4±2.0
Blue net	35.4±1.1a	46.4±1.1a	8.7±0.3	30.7±0.5ab	3.9±0.2ab	15.9±0.4abc	44.6±2.3
Black net	34.0±1.2ab	45.5±1.0ab	7.8±0.5	31.4±1.5ab	3.1±0.4b	16.9±0.8ab	50.7±1.5
Red net	29.7±1.0bc	41.9±1.2bc	8.3±0.8	30.0±2.3b	4.3±0.3ab	15.6±1.3bc	43.9±1.7
Green net	31.6±0.9abc	43.6±1.1abc	7.1±0.9	28.4±0.7b	3.6±0.5b	15.3±0.6bc	49.8±1.7

DCA: Diameter of subsidiary cells, LCA: Length of subsidiary cells, GCD: Diameter of guard cells, GCL: Length of guard cells, PL: Length of polar ledge, CPL: Length of cuticular polar ledge, ECD: Diameter of epidermal cells. For each variable and leaf surface (adaxial or abaxial), means followed by different letters indicate statistically significant differences ($p<0.05$).

understood; it is believed they help prevent water loss by improving the sealing of the pore when the stoma closes, and also prevent the entry of water upon opening (Hunt *et al.*, 2017). In agaves, cuticular ledges tend to be prominent and show considerable plasticity (Chávez-Güitrón *et al.*, 2019).

This study represents the first effort to explore the effect of manipulating light environment via photoselective coverings on morphophysiological parameters and stomatal traits of *Agave durangensis*. Beyond practical implications, the results contribute to understanding the species' acclimation capacity under heterogeneous light environments. It is imperative to continue testing different shading materials and coverings to achieve high-quality agave cenizo plant production, given that light is the primary environmental factor regulating plant growth.

CONCLUSIONS

Modifying the light environment through photoselective covers influences the morphology and stomatal characteristics of *Agave durangensis*. In general, black and green nets trigger shade-avoidance responses, resulting in increased leaf area and biomass allocation toward leaves. Plants grown under red net showed development similar to those cultivated outdoors or in greenhouse; additionally, this condition marginally favored an increase in stomatal density. Greenhouse conditions negatively affected stomatal structural dimensions, whereas the blue net had a favorable effect.

ACKNOWLEDGMENTS

We acknowledge the financial support from the projects "Technological Innovations in Commercial Mezcal Agave Plantations in the State of Durango," funded by COCyTED (Folio 974), and "Integration of Technologies for Agroecological Restoration of Marginal Lands in Semi-arid Ecosystems of North-Central Mexico," funded by INIFAP (Project No. 0265435769).

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