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Effects of light intensity on the anatomical structure, secretory structures, histochemistry and essential oil composition of *Aeollanthus suaveolens* Mart. ex Spreng. (Lamiaceae)

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ABSTRACT

Aeollanthus suaveolens Mart. ex Spreng belongs to Lamiaceae family, and in the Amazon this species is cultivated by natives' people, this medicinal plant is popularly known as Catinga-de-mulata, being used by the population for general pain treatment. The present study analyzed the effects of light intensity on the anatomy, secretory structures, histochemistry and composition of essential oil of leaf and stem of *A. suaveolens*. The anatomical structure were observed in response to two light intensities, namely 50% (half shade, HS) and 100% (full sun, FS) light. Histochemical analyses were performed to detect lipids, essential oils, alkaloids, phenolic compounds, sesquiterpene lactones, mucilage, and tannins. Secretory structures were observed under a scanning electron microscope. The results obtained in the present work indicate that the light intensity can affect the histochemistry and structures of *A. suaveolens*. Cross sections of the leaves and stem revealed glandular trichomes on both leaf surfaces as well as the stem surface. Essential oil was detected by histochemical analyses in all types of secretory trichomes. These anatomical and histochemical responses suggest modifications to protect the photosynthetic apparatus from excess light, in addition we note that in the chemical composition of the essential oil the class of hydrocarbons sesquiterpene prevailed.

1. Introduction

Lamiaceae Martynov (Labiate Adanson) family comprises approximately 7200 species under 240 genera, several of which are aromatic and medicinal plants (Mesquita et al., 2019). This family is known for the synthesis of essential oils containing numerous terpenes, which accumulate in secretory structures and are distributed in both vegetative and reproductive organs. In addition, Lamiaceae species typically show antibacterial, antifungal, insecticidal, and antioxidant properties (Uritu et al., 2018).

Secretory structures are considered the sites of biosynthesis and/or accumulation of primary and/or secondary metabolites in plant secretions (Lange, 2015). The biosynthesis and accumulation of essential oils can vary according to sites, such as leaves, stem and root and usually occur in specialized structures, such as glandular trichomes (Lamiaceae, Verbenaceae and Asteraceae), differentiated parenchymal idioblasts (Poaceae, Lauraceae, and Piperaceae), lysigenous, schizolysigenous and schizogenous cavities. (Pinaceae and Rutaceae), and oil channels (Apiaceae) (Tissier, 2018). Secretory trichomes are considered the primary secretory site of essential oils in Lamiaceae species and present a great diversity in morphological types and secondary metabolite classes. Trichomes may comprise a single cell or group of glandular cells, thereby showing diverse forms and secretions (Huchelmann et al., 2017).

Histochemical tests provide information on key metabolite classes and their distribution in cells, tissues and plant organs as well as elucidate the effects of environmental factors on secretion through specialized structures (Demarco, 2017). Most secondary metabolites play

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protective functions in response to abiotic and biotic stresses, and their synthesis is associated with abiotic factors such as nutrient deficiency, water regime, temperature changes, light levels, and ultraviolet light exposure as well as biotic factors such as herbivory. These factors can also directly affect essential oil production and composition (Böttger et al., 2018; Wang et al., 2019).

Studies on the effects of specific environmental conditions on the anatomical structure of plants are fundamental to investigate the associations between plant tissue organization and metabolite production (Rambla et al., 2015). Leaf structure is a precise indicator of light availability during plant development, and various leaf structures are modified in order to adapt to the changing environments (Kong et al., 2016; Qian et al., 2019).

Genus *Aeollanthus* Mart. ex Spreng comprises 45 species of aromatic perennial or annual herbs and subshrubs. Among these, *A. suaveolens*. The species is of African origin our habitats is distributed in South Sudan, Kenya, South Africa, and Nigeria. It is Annual herb with about 20–50 cm tall, circular stem branched, petiolate leaves, coated with trichomes with aromatic essence in its pre-flowering and valve. It has metaclamideas flowers type bisexual, trimerous. Its androecium has didynamous stamens, Nutlets ovoid or oblong, smooth, with supero and unilocular carpels (Martins et al., 2016). In the Amazon, this plant is used for medicinal purposes owing to its several biological properties (dos Santos et al., 2018).

Some chemical and biological studies of *A. suaveolens* have examined the chemical composition of its secretions, which are rich in volatile compounds (de Almeida et al., 2011; Tucker et al., 2001; Zhu et al., 2014). However, there have been no morphological, anatomical, and ecological studies. In this context, the present study aimed to assess the effects of light intensity on the anatomy, secretory structures and histochemistry of *A. suaveolens*.

2. Materials and methods

2.1. Plant material

The *A. suaveolens*. was cultivated in two different groups for 60 days under two light intensities in Emilio Goeldi Museum of Pará located in geographical coordinates of the collection site were S01°27′043″and W048°26′38.3”. The first group was cultivated under 50% light (half shade, HS; the light was blocked using a Sombrite® screen), whereas the second group was cultivated under 100% light (full sun, FS). After the and grown they were collected plants they were compared with authentic samples and deposited in the Museu Paraense Emilio Goeldi Herbarium) under the registration number *MG 165.473*.

For anatomical study, leaf and stem structure, histochemical characteristics, and trichome density were examined. Leaves at the 4th nodal segment (apex-to-base direction) and internodal segments between the 3rd and 4th nodes of eight plants were used. To study the secretory structures and identify secondary metabolites, transverse and paradermic sections of the same regions were obtained.

2.2. Anatomical analysis

Transverse and paradermic sections of the stem and leaves were manually obtained using a stainless-steel blade and analyzed without staining (blank cut) to observe pigment accumulation and chloroplast movement in plants grown under FS. The obtained sections were cleared with sodium hypochlorite (2%), washed in distilled water, double stained with safranin and astra blue (Bukatsch, 1972), and mounted in 50% glycerin solution, according to the technique described by Kraus and Arduin (1997), with some modifications.

2.3. Histochemical tests

Leaf and stem cross sections were treated with the following solutions: Sudan IV for the identification of total lipids (Kirk, 1970); neutral red for total phenolic compounds (observed under a fluorescent microscope with a green UV filter) (Kirk, 1970); Wagner reagent for alkaloids (Furr and Mahlberg, 1981); vanillin–HCl for tannins (Mace and Howell, 1974); alcian blue for mucilage (Pearse, 1968); sulfuric acid for sesquiterpene lactones (Geissman and Griffin, 1971); and NADI reagent for terpenes in essential oil (David and Carde, 1964).

Micrographs were obtained using a Canon Powershot A6 40 digital camera coupled to a Zeiss Axolab light microscope (Zen2 Blue, Ohta-ku, Tokyo, Japan), for anatomical and histochemical analysis. The trichomes were identified according to the morphology and nomenclature used by Serrato-Valenti et al. (1997) and Ascensão et al. (1999) for Lamiaceae species.

2.4. Secretory structures analysis

Previously dehydrated samples were processed in a critical-point dryer using CO_2 as the transitional medium (Guo and Liu, 2007). Mounted on stubs using a double-sided carbon adhesive tape, and coated with gold. The analysis was done on parts of the leaf and stem. The sample parts were fixed in FAA solution (formalin-acetic acid-alcohol) (Johansen, 1940) 70% for 24 h and dehydrated in an ethanol series (Berlyn et al., 1976). To obtain electron micrographs, the samples were mounted on stubs with a transparent tape and coated with a thin layer of gold for 1.5 min in a QUORU metallizer using a TESCAN system (model VEGA3 SB-EasyProbe, Libušina třída, Brno, Czech Republic). Secretory trichomes number was counted in 1 mm^2 quadrants on leaf (abaxial and adaxial sides) and stem sections, and the arithmetic mean was calculated.

2.5. Hydrodistillation

For essential oil (EO) extraction of *A. suaveolens* Mart. ex Spreng. (Lamiaceae), fresh plant material (leaves and stem; 40 g) was dried in an air circulating oven and subjected to hydrodistillation, using a Clevenger-type extractor. An equivalent volume of water to plant material was used. The extraction period was 3 h with a temperature of 100 °C. After extraction, anhydrous sodium sulfate (Na_2SO_4) was added, and the EO was centrifuged to eliminate moisture (Santana de Oliveira et al., 2020).

2.6. Volatile compound analysis

The chemical composition of essential oils was evaluated by gas chromatography–mass spectrometry (GC–MS) according to the methodologies described by (Ferreira et al., 2020; Gurgel et al., 2019) using a Shimadzu QP-2010 plus system under the following conditions: silica capillary column Rtx-5MS (30 m × 0.25 mm, 0.25 μm film thickness); program temperature of 60–240 °C at 3 °C·min^{-1}; injector temperature of 250 °C; helium as the carrier gas (linear velocity of 32 cm s^{-1}, measured at 100 °C); and splitless injection (1 μL of a 2:1000 hexane solution). Electron ionization was achieved at 70 eV, with the temperature of the ion source and other parts set at 200 °C. Volatile compounds were quantified using GC with a flame ionization detector (Shimadzu, QP, 2010 system) under the same conditions as those for GC–MS, except the use of hydrogen as the carrier gas. The retention index was calculated for all volatile compounds using a homologous series of straight-chained alkanes (C_8–C_{20}), and compounds were identified by comparing the experimentally obtained mass spectra and retention indices with the reported results (Adams, 2007; Stein et al., 2011).

2.5. Statistical analysis

Micrographs were used for anatomical descriptions and leaf thickness determination. The means obtained under the two light conditions were compared using *t*-test. Trichome density on the leaf and stem

surfaces under the two light conditions was compared using *t*-test. All analyses were performed using STATISTICA 6.0 at 95% confidence level.

3. Results and discussion

3.1. Anatomy and secretory structure

In paradermic sections of FS plants, the epidermal cells of leaves showed thin, anticlinal sinuous walls covered by a smooth cuticle and anthocyanin accumulation. Under both light conditions, amphetaminic leaves with predominantly dialytic (Fig. 1A) (rarely anisocytic) stomata were observed.

Phenolic compound accumulation was detected in the cuticle (Fig. 1B) and trichomes of FS plants (Fig. 1C). In addition, anthocyanins, another class of phenolic compounds, were detected in the epidermis of leaves (Fig. 1A) and stem of FS plants (Fig. 1I). In cross section, phenolic compounds were detected in the cuticle and epidermis of both leaf surfaces (Fig. 1D). In cross section of leaf, the epidermis showed a uniseriate layer of polygonal and a thin cuticle under both light conditions (Fig. 1E and F).

High light intensity induced anthocyanin synthesis and accumulation in the epidermal cells of *A. suaveolens* leaf and stem, perhaps as a measure of photoprotection. The association of solar radiation intensity with phenolic compound (del Valle et al., 2015; Martínez-Lüscher et al., 2019; Tattini et al., 2000; Yan et al., 2019) and anthocyanin (Fernandes de Oliveira and Nieddu, 2016; Rustioni et al., 2011; Zoratti et al., 2015) production has been reported previously.

Anthocyanins induce coloration ranging from red to blue and accumulate mainly in superficial tissues; they absorb light at wavelengths from 400 to 600 nm and act as a filter in the presence of excess radiation (Khoo et al., 2017). Synthesis of such compounds is regulated by specific enzymes in the phenylpropanoid biosynthetic pathway, and the expression of genes encoding these enzymes may be induced by light (De Oliveira et al., 2015; Kume, 2017; Tattini et al., 2017).

Cruz et al. (2012), cultivated two succulent species of *Kalanchoe* Adans. (Crassulaceae) under four light intensities and observed that plants grown under FS acquired reddish pigmentation in the epidermis of stem, petiole, and leaves. A similar response was observed in *A. suaveolens* grown under FS in this study, suggesting that anthocyanins act as solar energy dissipators, consequently protecting the photosynthetic apparatus from photooxidation.

The different light intensities affected the organization of mesophyll cells; one to two layers of palisade parenchyma and three to four layers of spongy parenchyma were observed in FS plants (Fig. 1E), whereas five to six layers of undifferentiated mesophyll cells were observed in HS plants (Fig. 1F). Numerous oleosomes in the mesophyll and collateral vascular bundles were common under both light conditions. Different light intensities affected leaf thickness in relation to stem of *A. suaveolens*, with *p*-value = 0.002). In addition to the formation of palisade parenchyma, parallel orientation of chloroplasts was observed in FS plants (Fig. 1G), whereas perpendicular orientation of chloroplasts was observed in HS plants (Fig. 1H). Fernandes et al. (2014) cultivated *Ocimum gratissimum* L. (Lamiaceae) under three light intensities (25%, 50%, and 75%) and observed mesophyll thickening in response to light as a result of cell stretching and palisade parenchyma formation, which maintained the number of constituent layers of the mesophyll. Thickening of palisade parenchyma under high light exposure may occur due to the addition of new layers of palisade parenchyma by the elongation of cells or combination of these two processes. In our study, FS plants showed greater mesophyll thickening due to the formation of one to two layers of palisade parenchyma, considering that there was no change in the number of layers of photosynthetic parenchyma.

In addition to the formation of palisade parenchyma was observed in FS plants (Fig. 1G), whereas perpendicular orientation of chloroplasts was observed in HS plants (Fig. 1H). Chloroplast movement was evident in *A. suaveolens*. They were parallel to the direction of incident light in FS plants and perpendicular to the direction of incident light in HS plants. Chloroplast movement has been observed in algae, mosses, and vascular plants (Haupt and Scheuerlein, 1990) in response to blue light to control light absorption. These authors reported that chloroplast movement can also prevent the photodegradation of photosynthetic pigments due excess of UV radiation.

In paradermic section, the stem epidermis showed uniseriate and rectangular cells, except at the base of the secretory trichomes, where they were slightly globose, under both light conditions (Fig. 1I). In HS plants on cross-section, the stem was quadrangular and the cortex was filled with one to two layers of angular collenchyma, followed by eight to ten layers of spherical parenchyma cells. Formation of interfascicular cambium and clustering of sclerenchyma cells overlapping the phloem bundles as well as collateral bundles in fascicular regions were also observed (Fig. 1J). In FS plants, the stem showed the same tissue organization as described above; however, vascular tissues are in the form of cylinder due to the advanced cambium activity (Fig. 1K).

Fluorescent microscopy detected phenols in the cuticle of glandular and non-glandular trichomes of FS plants (Fig. 1C) but not of HS plants, indicating photoprotection even before the light reaches the epidermis containing anthocyanins in FS plants. A similar response has been observed in *Phillyrea latifolia* L. (Oleaceae) (Tattini et al., 2000), which accumulated phenolic compounds (flavonoids) in the epidermis and trichomes when exposed to high solar radiation.

In leaves, trichome density was similar on both surfaces ($p = 0.085$); however, trichome density of leaves significantly differed between the two light intensities ($p = 0.003$) high light and low light. Trichome density of the stem was not affected by light intensity ($p = 0.070$) (Fig. 2A–D). Tattini et al. (2000) examined the adaptations of *Phillyrea latifolia* cultivated in two types of environments (HS and FS) and observed that the number of leafs trichomes in FS plants was two times higher than that in HS plants and that phenolic compounds (flavonoids) were detected in the cuticle covering the trichomes.

High light intensity significantly increases the number of trichomes, which is consistent with observations in *A. suaveolens*; the number of glandular trichomes in FS plants was nearly two times higher than that in HS plants, indicating the effect of light intensity on secretory structure density.

In cross section, both surfaces of leaves and stem of *A. suaveolens* presented the following morphological types of glandular trichomes: (3 A) peltate glandular trichome with one basal epidermal cells, a short single-celled stalk, and a head with six to eight secretory cells (Fig. 3A and B); (3 B) short-stalked capitate trichome I with a basal cell, a short unicellular stalk, and a spherical bicellular head (Fig. 3C and D); (3C) short-stalked capitate trichome II with a basal cell, a short bicellular stalk, and an elliptical unicellular head (Fig. 3E); and (3D) long-stalked capitate trichome with a basal cell, a long bicellular stalk, and a spherical unicellular head (Fig. 3F). The last two glandular trichome types are rare. In addition to exogenous secretory structures (trichomes), small spherical vesicles (oleosomes) were detected in the leaf chlorophyll parenchyma under both light conditions.

3.2. Histochemistry

The classes of compounds secreted by the glandular trichomes of *A. suaveolens* showed little variation among the four morphological types and between the two light intensities (Table 1). All described morphological types of glandular trichomes contained phenolic compounds (Fig. 4A–C) and alkaloids (Fig. 4D and E) in FS plants alone and lipids (Fig. 4F–H), essential oils (Fig. 4I-L), and sesquiterpene lactones (Fig. 4M–O) in both FS and HS plants. Mucilage and tannins were not detected in trichome secretions.

The presence of phenolic compounds in trichome secretion and their accumulation in trichome cuticle of FS plants, but not of HS plants, indicate photoinduction by high light intensity. These phenols may

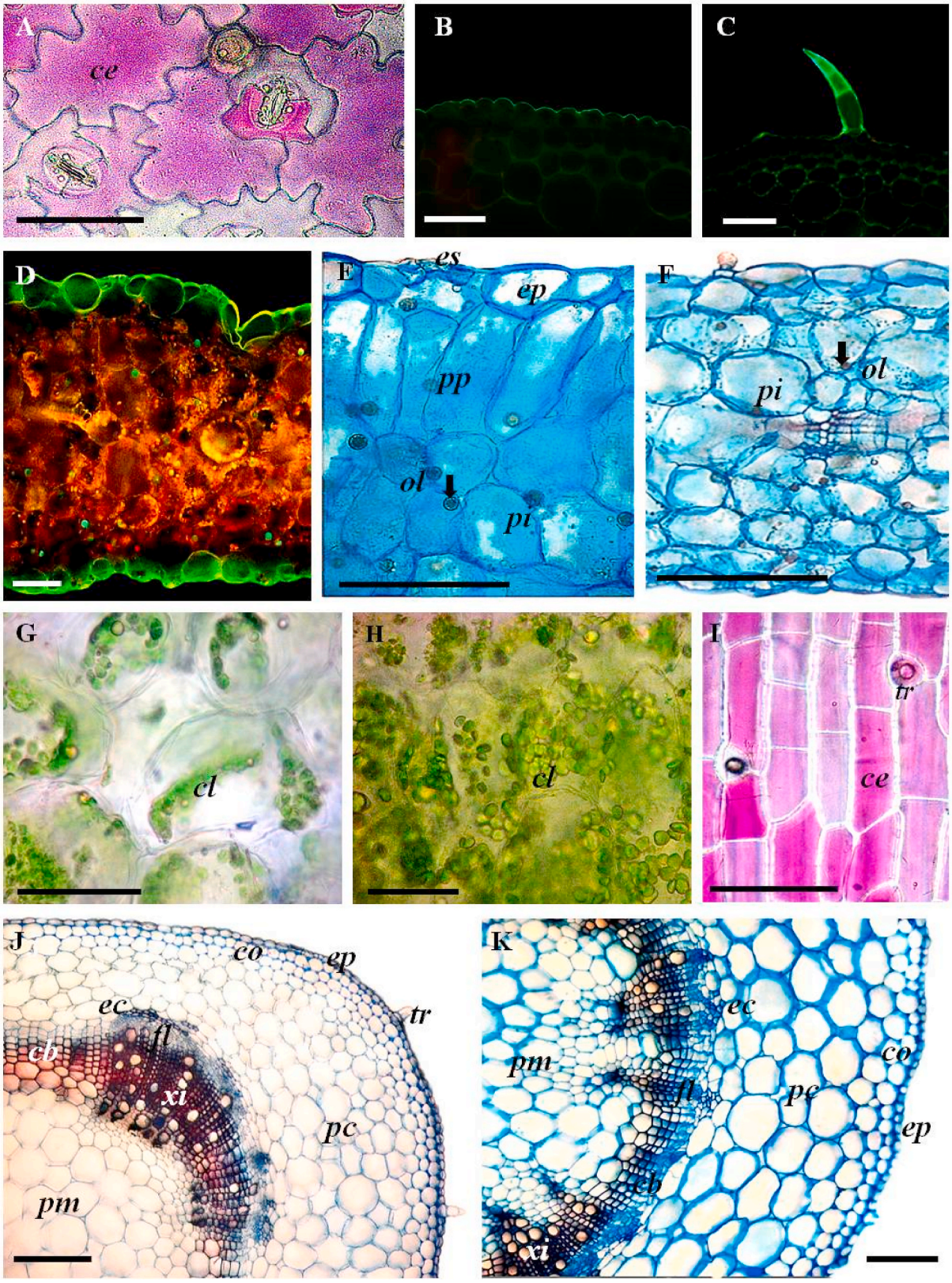

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Fig. 1. Transverse and paradermic sections of the leaf and stem of *A. suaveolens* grown in full sun and half shade. (A) *ce* in paradermic section of *A. suaveolens* showing diacitic stomata and anthocyanin accumulation in FS plants without previous staining (blank cut). (B–D) accumulation of phenolic compounds in FS plants evidenced by the histochemical test with neutral red under fluorescence microscopy: (B) cross section of the stem showing the cuticle, (C) cross section of the stem showing cuticle of non-glandular trichome, and (D) cross section of the limbus showing cuticle and epidermis of both leaf surfaces. (E–F) cross section of the limbus under double staining: (E) uniseriate layer of *pp*, *sp*, and numerous *ol* in FS plants and (F) *pi* and numerous *ol* in HS plants. (G–H) orientation of *cl* in cross-section of the limbus without previous staining (blank cut): (G) parallel to epidermis of the HS plant and (H) perpendicular to epidermis of the FS plant. (I) paradermic section of the stem showing rectangular *ce* and anthocyanin accumulation in FS plants without previous staining (blank cut). (J–K) cross section of the stem under double staining: (J) HS plant showing the formation of interfascicular *cb*, and (K) FS plant showing the formation in several regions of the *cb*. Abbreviations: *ce*, epidermal cell; *ep*, epidermis; *pp*, palisade parenchyma; *sp*, spongy parenchyma, *pi*, undifferentiated parenchyma; *ol*, oleosome; *es*, stoma; *cl*, chloroplast; *tr*, trichome; *ec*, sclerenchyma; *co*, collenchyma; *pm*, medullary parenchyma; *pc*, cortical parenchyma; *xi*, xylem; *fl*, phloem; *cb*, cambium; HS, half shade; and FS, full sun. Scales: (A) = 50 μm, (B) = 100 μm, (C–F) = 200 μm, (G–I) = 50 μm, and (J–K) = 200 μm.

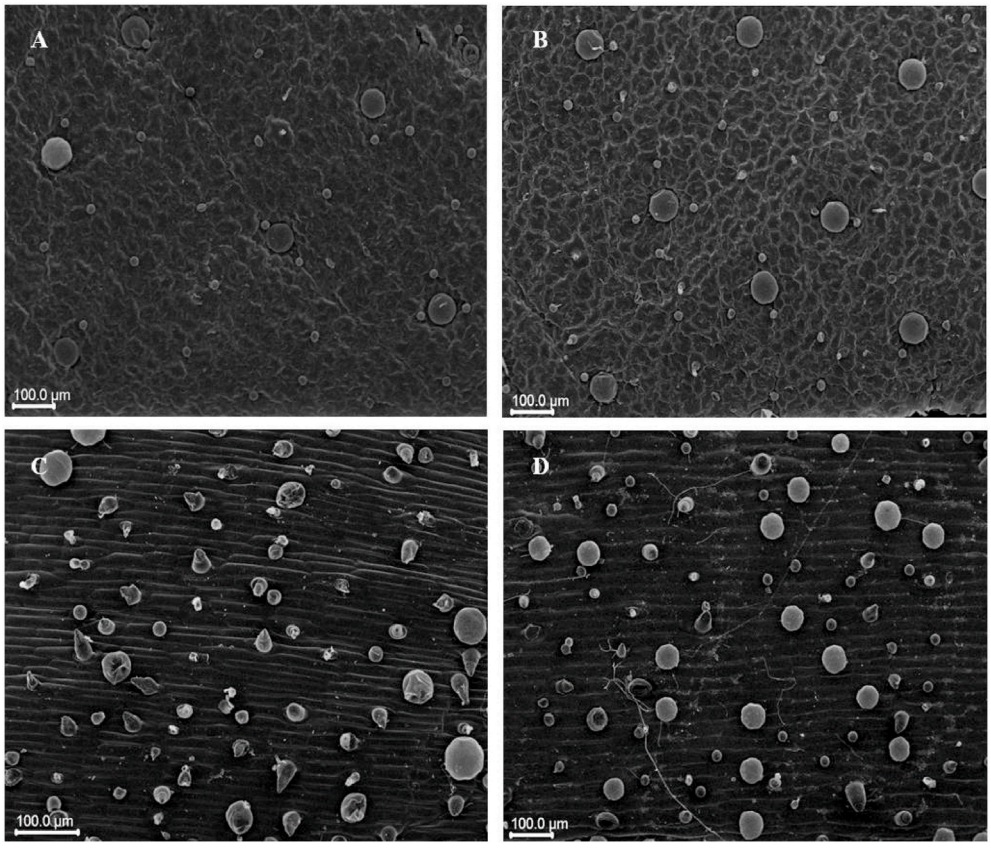

Fig. 2. Density of trichomes on the adaxial stem and leaf surfaces of *A. suaveolens* grown under half shade (HS) and full sun (FS). (A–B) adaxial epidermis of *A. suaveolens*: (A) HS and (B) FS. (C–D) epidermis of the stem of *A. suaveolens*: (C) FS and (D) HS. Scale: (A–D) = 100 μm.

provide protection against excess radiation. Tattini et al. (2000) detected phenolic compounds in trichomes of *Phillyrea latifolia* cultivated under FS, which is consistent with our observations in *A. suaveolens*. Together, these results confirm the role of light in the synthesis of phenolic metabolites.

Phenolic compounds are responsible for the absorption of UV-B radiation and are accumulated in superficial tissues, such as epidermal cell vacuoles and trichomes, absorbing and/or dissipating UV-B rays without altering photosynthetically active radiation (Agati and Tattini, 2010; Morales et al., 2010; Nunes et al., 2018). Phenolic compounds show diverse structures and derivatives and can act as reducing agents, free-radical scavengers, or singlet oxygen deactivators (Mathew et al., 2015; Villaño et al., 2007); therefore, *A. suaveolens* likely accumulated phenols in response to high light intensity.

Light intensity affected alkaloid synthesis in plants cultivated under FS, possibly indicating a photoprotection strategy against UV-B rays. Histochemical characterization of *Isodon rubescens* Hemsl. (H.) Hara (Lamiaceae) by Meng-qi Liu and Liu (2012), *Salvia officinalis* L. (Lamiaceae) by Corsi and Bottega (1999), and *Ocimum obovatum* Benth. (Lamiaceae) by Naidoo et al. (2013) confirmed the presence of phenolic compounds and alkaloids in the secretions of peltate and capitate trichomes, which is similar to the composition observed in the trichome secretion of *A. suaveolens* grown under FS in this study. The scarcity of studies on the effects of environmental factors on trichome secretion in Lamiaceae and the great variations in secreted metabolites among various morphological trichome types make it difficult to understand such processes.

Conjugated alkaloids show biological activities related to protection against herbivory- and UV-B radiation-induced damage (Takshak and Agrawal, 2019). Matsuura and Fett-Neto (2013) subjected specie of *Psychotria leiocarpa* Cham & Schltdl, (only one of them accumulates a monoterpene indole alkaloid in the leaves) to UV-B exposure for 96 h and found that the species lacking the monoterpene indole alkaloid accumulation showed photodegradation, while the species accumulating the alkaloid did not show photodegradation. In addition, hydrogen peroxide was note formed in the species accumulating the monoterpene indole alkaloid after the exposure period, indicating that the alkaloid may have antioxidant activity. *A. suaveolens* may have

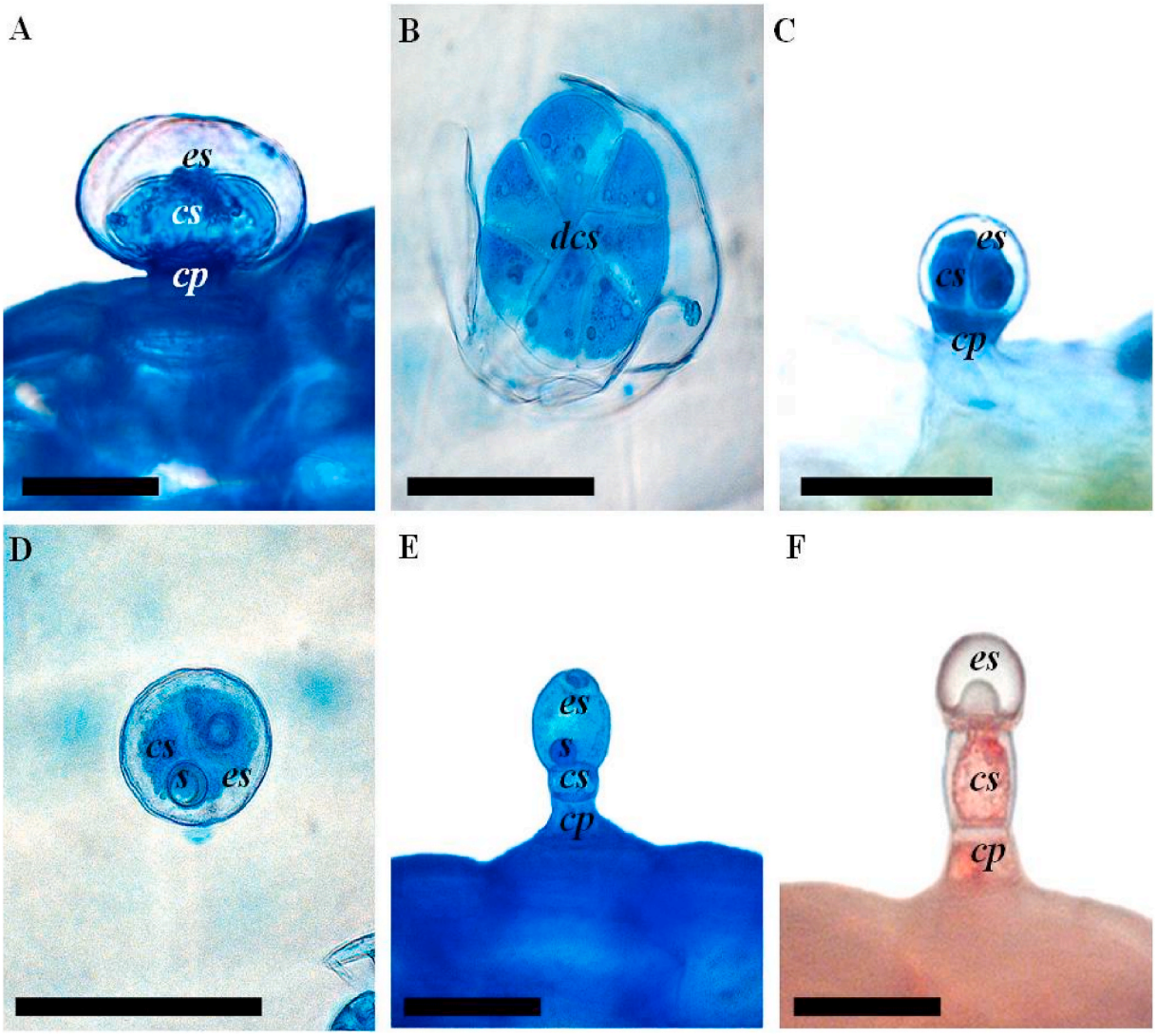

Fig. 3. Morphology of glandular trichomes of the in leaf of *A. suaveolens* in cross-section and longitudinal section. (A) cross sectional view of PGT showing a bicellular *cp*, a *cs* and large discoid *es*; (B) frontal view of PGT showing a *dcs* with seven cells and a broken cuticle; (C) cross sectional view of SSCT I showing bicellular *cp*, two apical *cs*, and small spherical *es*; (D) frontal view of SSCT I with two apical *cs* and *s* formation; (E) cross sectional view of SSCT II showing a bicellular *cp*, a *cs* with a large ovoid *es* and (F) cross sectional view of LSCT showing an elongated bicellular *cp*, an unicellular *cs*,. Abbreviations: *dcs*, secretory cell disc; *es*, subcuticular space; *cs*, secretory cell; *cp*, stalk cell; *s*, secretion; SSCT I, short-stalked capitate trichome I; SSCT II, short-stalked capitate trichome II; LSCT, long-stalked capitate trichome; and PGT, peltate glandular trichome. Scale (A–F) = 50 μm.

Table 1
Class of metabolites present in the secreted material of glandular trichomes and in the mesophyll of *A. suaveolens* grown under full sun (FS: 100% light) and half shade (HS: 50% light).

Histochemistry/Coloring	Class of metabolites	In mesophyll FS HS	PGT FS HS	SSCT I FS HS	SSCT II FS HS	LSCT FS HS
Sudan IV (Orange)	Lipids	+ +	+ +	+ +	+ +	+ +
Wagner Reagent (Red)	Alkaloids	- -	+ -	+ -	+ -	+ -
Vanillin–HCl (Brown)	Tannins	- -	- -	- -	- -	- -
Neutral red (Green)	Phenolic compounds	- -	+ -	+ -	+ -	+ -
NADI Reagent (Purple)	Essential oil	- -	+ +	+ +	+ +	+ +
Sulfuric Acid (Yellow)	Sesquiterpene lactone	- -	+ +	+ +	+ +	+ +
Alcian Blue (Blue)	Mucilage	- -	- -	- -	- -	- -

developed a similar response, since its synthesized alkaloids and phenolic compounds only when grown under FS for protecting secretory cells from damage caused by exposure to UV-B radiation.

The light intensities used in this study did not affect the synthesis of terpenes and sesquiterpene lactones in the secretion of all described morphological types of trichomes, indicating low specificity. Sesquiterpene lactones are common to Asteraceae (Salapovic et al., 2013), and there are little data on these compounds in Lamiaceae. In biological studies, extracts and essential oils of *Artemisia campestris* L. (Asteraceae) demonstrated anti-inflammatory, analgesic, antioxidant, anti-diabetic,

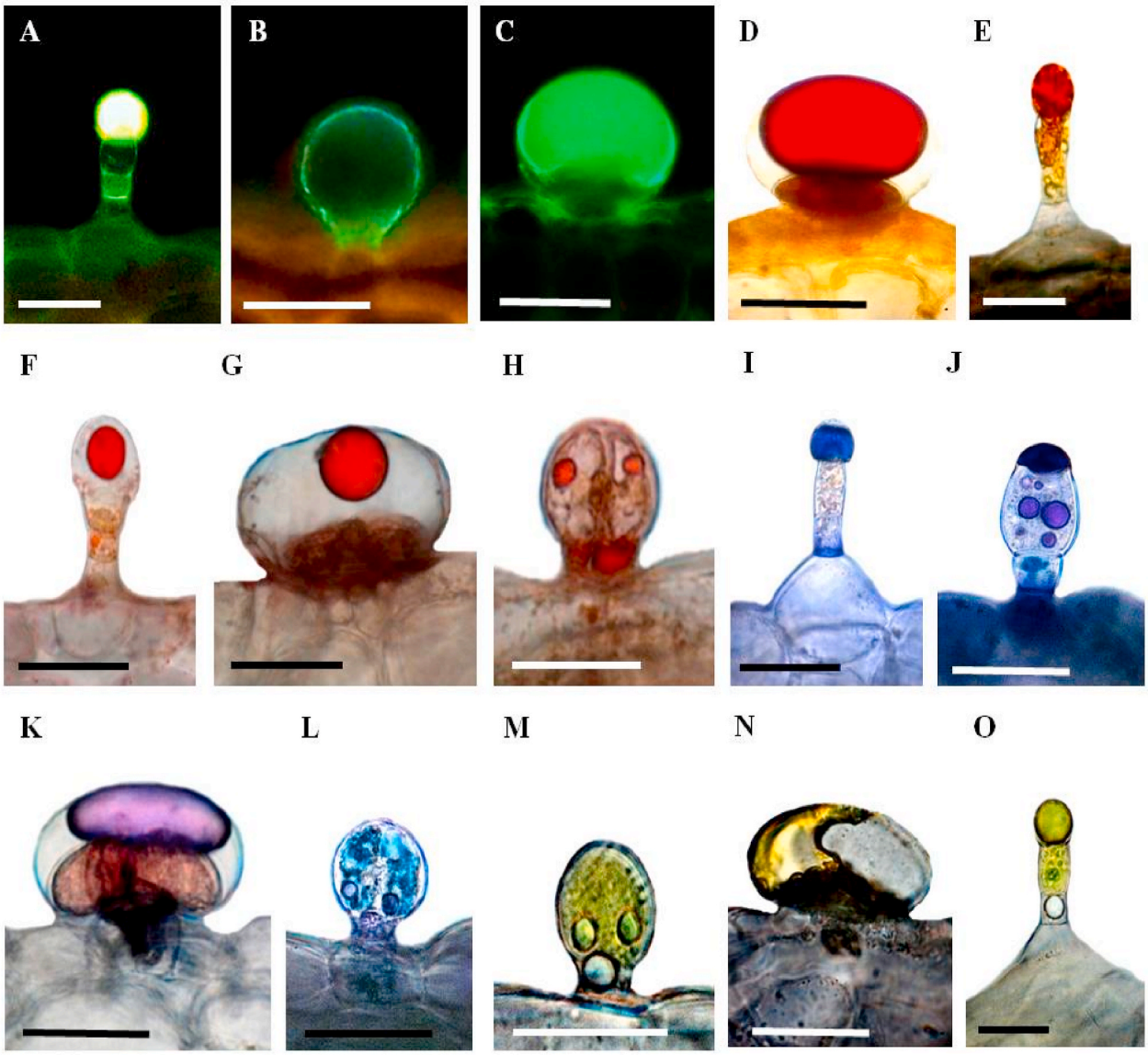

Fig. 4. Histochemical characterization of glandular trichomes secretion and oleosomes of *A. suaveolens*. (A–C) LSCT, SSCT I, and PGT, respectively showing phenolic compounds in the cuticle and secretion of FS plants. (D–E) PGT and LSCT reacted positively with alkaloids. (F–H) reacted positively with lipids respectively. (I–L) PGT, SSCT I, SSCT II, and LSCT reacted positively with essential oil. (M–O) PGT, SSCT I, and LSCT reacted positively with lactones. (P–Q) oleosomes in the mesophyll on cross-section of the leaf: (P) showing positive reaction with lipids and (Q) showing positive reaction essential oil. Abbreviations: PGT, peltate glandular trichome; SSCT I, short-stalked capitate trichome I; SSCT II, short-stalked capitate trichome II; LSCT, long-stalked capitate glandular trichome. Scale (A–F) = 50 μm.

anti-hypertensive, anti-leishmaniasis, anti-nociceptive, and wound-healing properties (Dib and El Alaoui-Faris, 2019). Sesquiterpene lactones were detected in the peltate and capitate trichomes of *Salvia officinalis* L, (Corsi and Bottega 1999).

Unlike lactones, phenolic compounds and alkaloids, which were detected in FS plants, act as protective metabolites against photooxidation, as the response to this type of stress may be slow and/or delayed (Isah, 2019).

3.3. Chemical composition of essential oil

The mass yields of oils, the leaves showed a yield of 0.2 g when the stem samples were only essential oil pulls enough to perform the chemical composition analysis. The chemical composition of essential oil of the *A. suaveolens* in leves is summarized in Table 2. In general, seven classes of predominant compounds were identified in the leaves of HS and FS plants and stems of FS plants, respectively: hydrocarbons monoterpene (4.35 and 6.89%), oxygenated monoterpenes (27.7 and 31.79%), hydrocarbons sesquiterpene (45.2 and 37.76%), oxygenated sesquiterpenes (0.63 and 0.9%), lactones (17.28, and 18.74%), phenylpropanoids (2.07 and 2.14) and diterpenoids (0.25 and 0.03%), These values were similar to those obtained by Lupe et al. (2007).

Among compounds in essential oil from the leaves of HS and FS plants and stems of FS plants, the hydrocarbons sesquiterpene (*E*)-β-farnesene was present at the highest concentrations, followed by the monoterpenes oxygenated linalool and massoia lactone. Other compounds including α-terpineol; linalyl acetate, geranyl acetate, *cis*-α-bergamotene, α-santalene, *trans*-α-bergamotene were also identified at lower concentrations with: α-santalene and trans-α-bergamotene were identified at lower concentrations.

These results indicate that light intensity affects the chemical composition of leaf essential oils, which is also related to plant phenotypes and genetic factors (Pacheco et al., 2016). Tucker et al. (2001) demonstrated the predominance of compounds such as linalool (41.8%), linalyl acetate (15.83%), and (*E*)-β-farnesene (14.02%), while Lupe et al. (2007) demonstrated the predominance of compounds such as

Table 2
Chemical composition of different fractions of *A. suaveolens* essential oil under different light intensities.RI (L): Literature Retention Index. RI (C): Calculated Retention Index. (Adams (2007)); * Nist (Stein et al., 2011). Leaves dried under half shade (50% Light); Leaves dried under full sun (100% Light); Branches dried under full sun (100% Light)

RI_L	RI_C	Constituents	Leaf	
			FS50% light	FS100% light
926	923	Tricyclene		0.04
939	935	α-Pinene		0.31
946	949	Camphene	0.12	0.47
969	971	Sabinene		0.03
974	977	β-Pinene	0.08	0.18
988	989	Myrcene	1.20	1.77
1020	1024	para-Cymene		
1024	1026	Limonene	0.14	0.23
1032	1034	(*Z*)-β-Ocimene	0.85	1.21
1044	1045	(*E*)-β-Ocimene	1.43	1.90
1086	1085	Terpinolene	0.31	0.43
1095	1110	Linalool	15.56	18.07
1128	1130	Alloocimene	0.22	0.32
1165	1170	Borneol	0.14	0.15
1174	1177	Terpinen-4-ol	0.09	0.10
1186	1190	α-Terpineol	4.23	4.49
1214	1212	Linalyl formate	0.35	0.70
1218	1215	endo-Fenchyl acetate		
1227	1226	Nerol	0.16	0.16
1232	1228	Thymol methyl ether		
1235	1230	Isobornyl formate		0.03
1254	1252	Linalyl acetate	6.15	6.91
1264	1259	Geraniol	0.03	0.03
1280	1276	Neryl formate	0.30	0.33
1287	1284	Bornyl acetate	0.75	0.80
1298	1298	*trans*-Pinocarvyl acetate		
1298	1299	Geranyl formate	0.28	0.68
1300	1302	α-Terpinyl formate	0.01	0.04
1324	1322	Myrtenyl acetate	0.03	
1349*	1346	α-Terpinyl acetate	0.07	0.07
1356	1350	Eugenol	0.45	0.55
1359	1359	Neryl acetate	1.52	1.52
1379	1380	Geranyl acetate	2.55	2.49
1387	1381	β-Bourbonene	0.03	0.04
1389	1389	β-Elemene	0.22	0.17
1403	1398	Methyleugenol		
1390	1402	7-epi Sesquithujene	0.46	0.37
1411	1413	*cis*-α-Bergamotene	2.30	1.86
1416	1422	α-Santalene	5.02	4.28
1423*	1429	β-Cedrene	0.27	0.27
1432	1434	*trans*-α-Bergamotene	3.73	3.26
1440	1440	(*Z*)-β-Farnesene	0.21	0.16
1439	1444	Aromadendrene	0.30	0.11
1445	1446	epi-β-Santalene	0.53	0.38
1454	1460	(*E*)-β-Farnesene	27.22	22.98
1471	1474	Massoia lactone	14.31	15.44
1483*	1483	*trans*-β-Bergamotene	1.60	0.63
1484	1484	Germacreno D		
1469	1486	β-Ecoradiene		
1489	1488	β-Selinene		
1493	1492	δ- Decalactone	0.58	0.96
1493	1495	α-Zingiberene	0.27	0.11
1500	1498	α-Muurolene	0.22	0.17
1505	1504	(*E,E*)-α-Farnesene	0.17	0.13
1505	1507	β-Bisabolene	0.46	0.34
1514	1511	(*Z*)-γ-Bisabolene		0.09
1514	1512	β-Curcumene	0.28	0.11
1512	1513	γ-Cadinene	0.25	0.18
1521	1518	β-Sesquiphellandrene	0.35	0.29
1522	1519	δ-Cadinene	0.38	0.55
1529	1525	(*E*)-γ-Bisabolene	0.13	0.07
1528	1528	(*E*)-iso-γ-Bisabolene	0.03	0.03
1532	1530	γ-Cuprenene	0.04	0.11
1537	1535	α-Cadinene	0.07	0.06
1540*	1538	(*E*)-α-Bisabolene	0.08	0.05
1542	1541	cis-Sesquisabinene hydrate		0.04
1561	1566	(*E*)-Nerolidol	0.48	0.74
1607	1604	β-Oplopenone	0.05	0.08
1607	1612	(*Z*)-Sesquilavandulol	0.08	0.04
1638	1635	epi-α-Cadinol		
1652	1650	α-Cadinol	0.02	
1685	1684	Massoia dodecalactone	0.07	0.11
1685	1685	α-Bisabolol		
1734	1733	Eremophilone		
1736	1735	Phytone	0.25	
1860	1855	(Z,Z)-Farnesyl acetone		0.01
Hydrocarbon monoterpenes			4.35	6.89
Oxygenated Monoterpenes			27.7	31.79
Hydrocarbon sesquiterpenes			45.2	37.76
Oxygenated Sesquiterpenes			0.63	0.9
Lactones			17.28	18.74
Phenylpropanoids			2.07	2.14
Diterpenoids			0.25	0.03
Total			97.48	98.25

β-bisabolene (29.5%), linalool (23.6%), and massoia lactone (13%). Overall, the results obtained in the present study were similar to those obtained in previous studies (Maia et al., 2003; Martins et al., 2016).

In addition, the substances identified in the present work have also been identified in other studies, wherein their biological activities were demonstrated (Table 3). Among the substances identified at higher concentrations, only neryl acetate, cis-α-bergamotene, and trans-α-bergamotene lack studies on the biological activities of their isolated molecules. The biological activities of these molecules demonstrate that the essential oil of *A. suaveolens* can have several therapeutic applications, being a potential plant for medicinal use.

4. Conclusion

Under FS conditions, light significantly increased trichome density on the leaf of *A. suaveolens*. The number of glandular trichomes in FS plants was nearly double the number in HS plants, indicating the effect of light intensity on the density of secretory structures. The presence of lactones in secretions suggests that the plants develop chemical mechanisms against a possible herbivory attack, since chemical defense in an induced mechanism and there may thus be a considerable lag between the attack and the immune response, which could compromise plant development and reproduction. There results indicate the possible functions of lactones as chemical protectors. Phenolic compounds and alkaloids induced in FS can act as protectors against photooxidation, as response to this type of stress may be slow and/or delayed. In addition, our results showed that light intensity affects the chemical composition of *A. suaveolens* leaf essential oil. The predominant classes of metabolites were sesquiterpene hydrocarbons, oxygenated monoterpenes, lactones.

Authorship statement

All persons who meet authorship criteria are listed as authors, and all authors certify that they have participated sufficiently in the work to take public responsibility for the content, including participation in the concept, design, analysis, writing, or revision of the manuscript. Furthermore, each author certifies that this material or similar material has not been and will not be submitted to or published in any other publication before its appearance in the ***Biochemical Systematics and Ecology***.

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Table 3
Main chemical compounds identified in *A. suaveolens* and their biological activities.

Constituents	Biological Activities	References
Linalool	Sedative, anxiolytic, analgesic, anticonvulsant, anti-inflammatory, local anesthetic, antifeedant, molluscicidal and larvicidal, acetylcholinesterase, and GABAergic properties.	(Aprotosoaie et al., 2014; Bianchini et al., 2017; Usha Rani et al., 2014; Yang et al., 2014)
α-Terpineol	Antifungal, antibacterial, antioxidant, anticancer, anticonvulsant, antiulcer, antihypertensive, and antinociceptive activities.	(Khaleel et al., 2018; Li et al., 2014; Oliveira et al., 2016; Zhou et al., 2014)
Linalyl acetate	Anti-inflammatory and antimicrobial activities; melanogenesis alteration effects; cytotoxicity in human neuroblastoma cells.	(Blaskó et al., 2017; Khayyat, 2020; Peana et al., 2002; Peng et al., 2014; Russo et al., 2013)
Geranyl acetate	Antifungal, anti-inflammatory, antimalarial, antioxidant antinociceptive, anesthetic properties, and redox potential;	(Gonçalves et al., 2012; Ohtsubo et al., 2015; Quintans-Júnior et al., 2013; van Zyl et al., 2006)
α-Santalene	Hormonal and aphicidal activities.	Baadhe et al. (2015)
(*E*)-β-Farnesene	Aphicidal	(Cui et al., 2012; Qin et al., 2016; Zhang et al., 2017)
Massoia lactone	Potential anticancer and anti-inflammatory effects. Insect venoms.	(Barros et al., 2014; Cavill et al., 1968)

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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