Morphology and density of glandular trichomes of *Ocimum campechianum* and *Ruellia nudiflora* in contrasting light environments: A scanning electron microscopy study

Daniela A. Martínez-Natarén\textsuperscript{a,b,*}, Pedro A. Villalobos-Perera\textsuperscript{b}, Miguel A. Munguía-Rosas\textsuperscript{b}

\textsuperscript{a} CONACyT, Mexico
\textsuperscript{b} Laboratorio de Ecología Terrestre, Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional (Cinvestav), Km 6, Antigua carretera a Progreso, Mérida 97310, Mexico

**ABSTRACT**

Glandular trichome morphology and density may be of ecological importance since, in some plant species, they are strongly influenced by external factors such as temperature and light intensity. In this study, we describe the morphology and density of leaf glandular trichomes of *Ocimum campechianum* and *Ruellia nudiflora* plants growing under two different light environments (sun vs. shade) in order to determine whether there is an effect of light availability on trichome density in these plant species. The morphology and density of the glandular trichomes in both species were studied using scanning electron microscopy (SEM). Two morphologically distinct types of glandular trichomes were observed on *O. campechianum* leaf surfaces: peltate and capitate, of which the former was more abundant (ca. 3:1). In *R. nudiflora*, only one morphotype of peltate trichome was observed on both leaf surfaces. Overall, the trichome density of both species was higher on the abaxial than on the adaxial leaf surface. However, the plants exposed to full solar radiation and those in the shaded conditions presented similar glandular trichome densities (*O. campechianum*: sun = 16.7 vs. shade = 15.5 number of trichomes per mm\(^2\); *R. nudiflora*: sun = 13.1 vs. shade = 11.9 number of trichomes per mm\(^2\)). Trichome density is therefore likely to be a fixed condition in the studied species.

1. Introduction

Glandular trichomes represent an important first line of plant defense, forming a structural and chemical barrier against several environmental factors such as excessive light radiation, extreme temperatures and herbivory (Wagner, 1991; Werker, 2000). These glandular structures develop from protodermal cells and are widely distributed over the plant aerial reproductive and vegetative organs (Werker et al., 1993). Glandular trichomes are usually multicellular, consisting of differentiated basal, stalk and head cells (Turner et al., 2000); however, wide variability in their morphology has been observed among species, among the different organs of the same plant and even between different sides of the same organ. Glandular trichomes can be roughly classified into two morphological types: peltate and capitate (Werker et al., 1985). In general, peltate trichomes consist of one basal cell, one stalk cell and a large head that, depending on the species, may contain several cells (Turner et al., 2000; Werker et al., 1985). Capitate trichomes usually consist of one basal cell, more than one stalk cells and one or two head cells (Bisio et al., 1999; Werker et al., 1985). However, there are important morphological variations within each type of glandular trichome, in terms of the size and number of cells and the mode, chemical composition and function of secretions. Consequently, some authors have even suggested the occurrence of submorphotypes (Werker et al., 1993, 1985).

Previous research has examined the morphology of glandular trichomes in some plant species (Baran et al., 2010; Giuliani and Bini, 2008; Werker, 2000; Werker et al., 1985, among many others) and the morphology and density of glandular trichomes has been found to exhibit high interspecific variability even among closely related species (Dhawan et al., 2016; Tozin et al., 2015a) as well as plastic responses to biotic (Tozin et al., 2017) and abiotic (Bosabalidis and Kokkin, 1997; Martínez-Natarén et al., 2011; Pérez-Estrada et al., 2000; Tattini et al., 2000; Tozin et al., 2015b) environmental factors. Description of the morphology of glandular trichomes and their response to

---

*a* Corresponding author at: CONACyT - Laboratorio de Ecología Terrestre, Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional (Cinvestav), Km 6, Antigua carretera a Progreso, Mérida 97310, Mexico.

E-mail address: daniela.martinez@cinvestav.mx (D.A. Martínez-Natarén).

https://doi.org/10.1016/j.flora.2018.08.011

Received 24 April 2018; Received in revised form 20 July 2018; Accepted 18 August 2018

Available online 22 August 2018

0367-2530/ © 2018 Elsevier GmbH. All rights reserved.
environmental factors is particularly important for medicinal plants, since these structures produce some of the active compounds (Krstic et al., 2006; Tozin et al., 2015b) and the therapeutic efficacy of these plants may therefore also be affected by environmental factors that influence the number and secretory activity of the glandular trichomes. *Ocimum campechianum* Mill. (Lamiaceae) and *Ruellia nudiflora* (Engelm. & A.Gray) Urb. (Acanthaceae) are two perennial herbs popular in the traditional medicine of the peninsular Maya people (Méndez et al., 2009; Méndez-González et al., 2012). Both plant species occur sympatrically in a wide variety of habitats ranging from heavily disturbed and highly illuminated open areas to partially shaded sites, such as secondary forest and homegardens (Méndez-González et al., 2012; Ortega-Campos et al., 2009). These plants are attributed with diverse healing properties for some gastrointestinal, respiratory and cutaneous illnesses, as well as presenting anagelse, antipyretic and anti-inflammatory properties (Ankli et al., 2002; Méndez et al., 2009; Méndez-González et al., 2012; Vera-Ku et al., 2010). Antioxidant and antimicrobial properties have also been reported in the essential oil of *O. campechianum* (Pandey et al., 2014; Sacchetti et al., 2004). The association between the medicinal properties and extractable chemical compounds of each species may also be related to the morphotype of glandular trichome on the leaves. To date, the morphology of the leaf secretory structures of *O. campechianum* and *R. nudiflora* remains unexplored.

Glandular trichomes may also be ecologically important due to their possible influence on some components of plant fitness (i.e. survival). For instance, plants that are exposed to harsh environmental conditions, such as those featuring high rates of herbivory or high solar radiation and temperatures, may present higher trichome density (Bosabalidis and Kokkini, 1997; Fernandes et al., 2016; Tattini et al., 2000; Tozin et al., 2017). It has been suggested that trichome secretion plays a protective role for the plant photosynthetic tissue. The secretion reflects excessive solar radiation and also helps to dissipate absorbed heat. Consequently, leaf temperature is maintained close to the optimal level for photosynthesis and carbon fixation (Ehleringer, 1982; Pérez-Estrada et al., 2000; Wagner, 1991). Furthermore, glandular trichome secretions protect the leaves against herbivory through their production of several anti-herbivory chemical compounds as well as organic volatiles which serve to attract natural enemies of the herbivores (Dalin et al., 2008; Tozin et al., 2017; Unsicker et al., 2009). However, trichome production may be compromised in plants growing under low solar radiation (i.e. shaded conditions). It is recognized that the production of secondary metabolites, such as trichome secretions, may not be cost-effective in poorly lit environments (Ehleringer, 1982; Lerdau et al., 1994; Liakoura et al., 1997). Plants under shaded conditions may therefore produce relatively less trichomes and be more vulnerable to extreme environmental conditions, as well as to herbivore attack.

In this study, we describe the morphology of different types (i.e. capitate and peltate) of glandular trichomes present on both surfaces (adaxial and abaxial) of the leaves of *O. campechianum* and *R. nudiflora*, using scanning electron microscopy, and evaluate the effect of light intensity on the density of glandular trichomes in both species. We predict lower trichome density under shaded conditions in both species, due to the cost associated with trichome production and its secretory activity. In addition, we expect significant differences between the trichome densities of both leaf surfaces; where higher densities would be observed on the leaf surface that is more directly exposed to solar radiation.

2. Material and methods

2.1. Studied species

*Ocimum campechianum* Mill. (Lamiaceae) is a herbaceous annual plant widely distributed from the southern United States to Central and South America and found throughout the Yucatan peninsula, frequently as a ruderal (Méndez-González et al., 2012). *Ocimum campechianum* is known locally by the Maya as *xakalaltun, kakalaltun* (wild basil) or “albahaca de monte” (Méndez-González et al., 2012). Individuals of *O. campechianum* can reach between 40 and 60 cm in height, with pseudodichotomous branching and quadrangular branches (Moreno et al., 1987). The leaves are ovate to elliptic in shape, 2–3 cm in length, slightly toothed, petiolated and highly aromatic (Moreno et al., 1987). Its white-purple flowers are small, whorled on upward spikes of 20–30 cm in length, hermaphroditic and self-compatible. It flowers and sets fruits from July to February. Seeds are ovoid, smooth and very small, at ca. 1 mm in diameter (Méndez-González et al., 2012).

*Ruellia nudiflora* (Engelm. & A.Gray) Urb. (Acanthaceae) is a short-lived perennial herbaceous plant (life span: 2–3 years) distributed from southern Texas to northern Honduras (Tripp, 2007). It is widely distributed in the Yucatan peninsula where it is considered an invasive species, growing in disturbed open or partially shaded areas (Munguía-Rosas et al., 2012). This species is known locally as *Kabalya’axnik, Kaamba ya’ax niik* or “maravilla de monte” (Méndez-González et al., 2012). It can reach up to 45 cm in height and possesses young erect and quadrangular stems (Méndez-González et al., 2012). The leaves are ovate and arranged in pairs (Ortega-Campos et al., 2009). *Ruellia nudiflora* has a mixed reproductive system, producing two types of flowers: (i) flowers with open corolla (chasmogamous type) that can be either self-pollinated or outcrossed, and (ii) flowers with permanently closed corolla (cleistogamous type), which require obligate self-pollination. The flowering season of the chasmogamous type occurs from May to the end of September; while the cleistogamous flower production covers a longer period of time (Ortega-Campos et al., 2009). The fruits are dehiscent capsules. They produce between seven and 12 seeds which disperse ballistically (Ortega-Campos et al., 2009). *Ruellia nudiflora* reproduces mainly by seeds and the production of fruits and seeds can occur from its first year (Munguía-Rosas et al., 2012). *Ruellia nudiflora* has been considered a sun plant, although one that is also tolerant to certain levels of shade, with saturation of the net assimilation rate recorded at very high levels (1200 mmol m$^{-2}$ s$^{-1}$) of instant photosynthetic photon flux density (PPFD) (Munguía-Rosas et al., 2012).

In the two examined species, a complete leaf lifespan is shorter than one month in duration.

2.2. Plant material and experimental design

During February 2016, *O. campechianum* plants (*n = 30*) were grown from wild seeds collected in the locality of Nohuayun, Yucatan (20°58′28.20″N, 89°58′09.33″W, 6 m a.s.l.), a site dominated by secondary vegetation with some open spaces. Plants of *R. nudiflora* (*n = 30*) were harvested from a natural population growing in a totally sunny to partially shaded environment in Molas, Yucatan (20°49′51.01″N, 89°36′44.19″W, 10 m a.s.l.). The distance between any two harvested plants was at least 3 m. Plants of both species were selected based on similarity of size (10–15 cm in height), age (juvenile or pre-reproductive stage) and leaf number (for *O. campechianum*: < eight pairs of true leaves; for *R. nudiflora*: two pairs of true leaves). Apparently healthy plants of both species were transported to an open nursery at Cinvestav-IPN, in Merida, Yucatan (21°01′17.68″N, 89°37′36.69″W, 10 m a.s.l.), which is located within the natural habitat of the species. Individual plants were transplanted into 1.5 l plastic pots containing a mixture of compost and gravel (1:1 v/v), and watered as required. After three weeks of acclimatization, 15 plants of each species underwent two light treatments over a period of two months: 1) exposure to full sunlight (i.e. sun treatment) and 2) shaded with a neutral mesh at their far-red/red photon ratio (i.e. shade treatment), reducing environmental Photosynthetically Active Radiation (PAR) by 70%. Final sample size was 30 plants for each species.
2.3. Morphology and density of glandular trichomes

To determine the morphology of glandular trichomes and evaluate the effect of light availability (sun vs. shade) on their abundance in the leaves of *O. campechianum* and *R. nudiflora*, all plants per treatment (n = 15) were analyzed. From each plant, a fully-expanded leaf (of the same mature age) was randomly collected. Due to the lifespan of leaves of the examined species, it can be assumed that the collected leaves were completely developed during the experiment. Temperature and humidity data were obtained from a weather station located 10 m from the nursery. Temperature and humidity were 26.2 °C and 69.3% on average during the study; the temperature in shaded plants was 2 °C degrees lower than in those fully exposed to the sun. Small pieces of fresh leaves (ca. 5 mm²), sampled from the central zone of the leaf blade, were mounted on metallic stubs and sputter coated with gold to 20 nm of thickness (Quorum Q150R ES). These samples were examined using a scanning electron microscope JEOL 7600 F at 500-2000 × magnification to enable description of the morphology and distribution of the different glandular trichome types (i.e. peltate and capitate), following the classification described by Werker et al. (1993). For estimation of the density of glandular trichomes, the same 15 leaves per treatment of each species previously examined with the scanning electron microscope were used. Leaf sample preparation followed the same protocol described previously for morphological description. The samples were examined at a magnification of 100 ×. The peltate and capititate trichomes were quantified in an area of 1 mm² on both adaxial and abaxial leaf surfaces.

2.4. Data analysis

We evaluated the effect of light treatment (sun vs. shade), leaf surface (adaxial vs. abaxial) and morphotype (peltate vs. capititate), as well as second order interaction, on the density of glandular trichomes by fitting a mixed effects linear model (a different model per species). The plant was included in the random part of the model. To improve linearity, the dependent variable (trichome density) was log transformed. An *a posteriori* examination of the residuals suggested a normal distribution. All analyses were run in R software v 2.14.0 (R Development Core Team, 2011).

3. Results

3.1. Morphology of glandular trichomes

The leaves of *O. campechianum* presented two main morphotypes of glandular trichomes, i.e. peltate and capititate, on both adaxial and abaxial surfaces (Fig. 1A). Both trichome morphotypes showed an apparently random distribution over the entire leaf surfaces and leaf veins of *O. campechianum*. In particular, the peltate trichomes of *O. campechianum* are formed by a basal cell embedded in the epidermis, a unicellular stalk and a large spherical head (ca. 60 μm in diameter) comprising four cells. A SEM micrograph of the abaxial surface of *O. campechianum* shows a partially deformed peltate trichome, partially sunken on the leaf blade of *O. campechianum*, exhibiting perpendicular creases on the cuticle of the gland caused by the underlying head cells (Fig. 1B). On the other hand, the capititate trichomes of *O. campechianum* were very small compared to the peltate trichomes, which are formed by a basal cell with a short one-celled stalk and rounded unicellular head of ca. 15 μm in diameter (Fig. 1A). The capititate trichomes of *O. campechianum* were also present on both leaf surfaces, but were more abundant on the abaxial leaf side. No submorphotypes of peltate or capititate trichomes were identified in this plant species.

In contrast, on the leaves of *R. nudiflora*, only one type of glandular trichome (i.e. the peltate morphotype) was observed on both surfaces. These trichomes were constituted by one basal cell, a short stalk cell and a broad rounded head of ca. 30 μm in diameter. The head of the peltate trichomes of *R. nudiflora* was composed of eight cells. A SEM micrograph on the abaxial surface shows a peltate trichome in an early secretory stage, over which the wrinkled folds of the cuticular cap are still visible (Fig. 1C). The peltate trichomes of *R. nudiflora* were mostly distributed on the inter-vein area of the leaves. Moreover, we observed peltate glandular trichomes with the cuticular cap completely detached, and the eight head cells and part of the secreted material released (Fig. 1D). The glandular trichomes of shade and sun leaves of both species apparently do not differ in diameter. No submorphotypes of peltate trichomes were observed in *R. nudiflora*.

3.2. Density of glandular trichomes

There was no significant effect of light treatment on the density of glandular trichomes for *O. campechianum* (*F*1, 28 = 0.33, *P* = 0.56) or *R. nudiflora* (*F*1, 28 = 0.40, *P* = 0.53). However, leaf surface (adaxial vs. abaxial) had a significant effect on the density of glandular trichomes in both *O. campechianum* (*F*1, 28 = 5.42, *P* = 0.020) and *R. nudiflora* (*F*1, 28 = 16.27, *P* < 0.001) (Table 1). On average, glandular trichome density was higher on the abaxial than on the adaxial surface. Peltate trichomes were significantly more abundant (ca. 3:1) than capititate trichomes in *O. campechianum*, regardless of leaf surface (peltate = 24.8 ± 1.3 vs. capititate = 7.5 ± 0.5 number of trichomes per mm², *F*1, 28 = 0.242, *P* < 0.001) (Table 1).

The interactions treatment × leaf surface (*F*1, 28 = 0.02, *P* = 0.87) and treatment × morphotype of glandular trichomes (*F*1, 28 = 0.95, *P* = 0.33) for *O. campechianum*, and treatment × leaf surface (*F*1, 28 = 0.01, *P* = 0.89) for *R. nudiflora*, were not significant in terms of their effect on the density of glandular trichomes (Table 1).

4. Discussion

In general, the glandular trichomes found on the leaf surfaces of *O. campechianum* and *R. nudiflora* varied in structure, size and proportion. According to our findings, the peltate glandular trichomes observed on the leaves of *O. campechianum*, composed of a four-celled head, morphologically resembled those found on the leaves of other Lamiales species (Bisio et al., 1999; Krtic et al., 2006), including the related species *O. gratissimum* L. and *O. basilicum* L. (Tozin et al., 2017; Werker et al., 1993). Overall, the head of the peltate trichomes of *O. campechianum* exhibited a common spherical shape due to cuticle expansion during the accumulation of secretory products in the subcuticular space (Gang et al., 2001; Werker et al., 1993). The capititate trichomes present on *O. campechianum* leaves belonged to only one morphotype, with a rounded single cell head. However, two submorphotypes of capititate trichomes have been distinguished in *O. gratissimum* and *O. basilicum*, with an elongated and oval unicellular or a bicellular head (Tozin et al., 2017; Werker et al., 1993). The limited number of capititate trichome submorphotypes found in the *Ocimum* species contrasts with the large number of submorphotypes reported for other species such as *Salvia argentea* L. and *Lavandula pedunculata* (Mill.) Cav. (Baran et al., 2010; Zuzarte et al., 2010). The morphology and type of glandular trichomes is often related to the type of product they secrete. In this regard, some studies have demonstrated that the secretions of capititate trichomes of some plants contain predominantly polysaccharides, which have been suggested to act as a lubricant to facilitate leaf expansion (Ascensão and Pais, 1998). Werker et al. (1985) reported that the different morphological structures of some capititate trichomes could even be related to the production of different chemical substances, which may be involved in distinct functional roles. For *O. campechianum*, in particular, the greater abundance and size of the peltate compared to the capititate trichomes on both leaf surfaces may reflect the major role played by the peltate trichomes in the biosynthesis of the essential oil of this aromatic species. Some reports have even shown a positive correlation between...
the density of peltate glandular trichomes and the yield of essential oil in various aromatic plants (Bosabalidis and Kokkini, 1997; Kofidis et al., 2003).

To our knowledge, this study is the first report of glandular trichomes in R. nudiflora, while some taxonomic studies on the Acanthaceae refer to the presence of glandular trichomes on the leaves (Daniel, 2004; McDade and Tripp, 2007); few studies have investigated the morphology of these structures in detail. Some studies even report the occurrence of these glandular trichomes as rare in this family (Bhatt et al., 2010). The peltate trichomes observed in R. nudiflora show morphological similarities to those found in Hypoestes aristata (Vahl) Roem. & Schult. (Acanthaceae), with both consisting of a short basal cell, a short stalk cell and a large multicellular central head (Bhatt et al., 2010). Unlike the glandular trichomes of the Lamiaceae, those of the Acanthaceae have still not been associated with any particular function. However, the Acanthaceae family is not known for being aromatic. Further research on the histochemical and ultrastructural characterization of the different morphotypes of glandular trichomes found in O. campechianum and R. nudiflora will contribute to our understanding of the potential role of such structures in these plant species.

Contrary to our prediction, the results of this study indicated that light environment did not affect the density of glandular trichomes in the leaves of the examined species. Plants exposed to full solar radiation presented similar trichome densities to those established under shaded conditions. These results contrast with previous studies that have reported the dependency of trichome density on light availability (Bosabalidis and Kokkini, 1997; Liakoura et al., 1997; Pérez-Estrada et al., 2000; Tattini et al., 2000). This result is unexpected since we know, based on previous studies conducted by our research group, that the level of light reduction employed in our experiment reduces biomass allocation to both vegetative and reproductive tissue in the study species. The difference between shade and sun plants, in terms of total dry mass, was -25.5% for O. campechianum and -36.4% for R. nudiflora. In terms of the number of seeds, this difference was -39.5% for O. campechianum, and -35.2% for R. nudiflora, and for fruit production, the difference between shade and sun plants was -53.4% for R. nudiflora. Thus, while shade reduces valuable resources for vegetative and reproductive functions, trichome density appears to remain unaffected and is therefore likely to be a fixed condition in the study species. Indeed, trichome density is a phylogenetically conservative trait in some families (Adedeji et al., 2007; Krstic et al., 2006). It seems that a plastic response of trichome density to environmental factors has evolved only

Table 1

Density (number of trichomes per mm−2) of the different morphotypes of glandular trichomes on both leaf surfaces of O. campechianum and R. nudiflora, growing under two light conditions (sun and shade [30% of natural sun light]). N = 15 in each treatment combination.

<table>
<thead>
<tr>
<th>Species</th>
<th>Surface</th>
<th>Morphotype</th>
<th>Treatment</th>
<th>Sun</th>
<th>Shade</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>O. campechianum</td>
<td>Adaxial</td>
<td>Peltate</td>
<td>23.8 ± 2.7</td>
<td>20.9 ± 2.1</td>
<td>14.6 ± 1.3</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Capitate</td>
<td>6.6 ± 0.9</td>
<td>7.3 ± 0.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>15.2 ± 2.1</td>
<td>14.1 ± 1.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Subtotal</td>
<td></td>
<td></td>
<td>26.3 ± 2.7</td>
<td>17.6 ± 1.6</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Abaxial</td>
<td>Peltate</td>
<td>28.0 ± 2.7</td>
<td>7.6 ± 1.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Capitate</td>
<td>8.3 ± 1.0</td>
<td>7.6 ± 1.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Subtotal</td>
<td></td>
<td></td>
<td>17.0 ± 2.2</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td></td>
<td>16.7 ± 1.6</td>
<td>15.5 ± 1.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>R. nudiflora</td>
<td>Adaxial</td>
<td>Peltate</td>
<td>9.9 ± 1.1</td>
<td>8.6 ± 0.8</td>
<td>9.2 ± 0.7</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Abaxial</td>
<td>Peltate</td>
<td>16.4 ± 1.9</td>
<td>15.0 ± 1.7</td>
<td>15.8 ± 1.3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td></td>
<td>13.1 ± 1.3</td>
<td>11.9 ± 1.1</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Significant differences at P < 0.05.
** Significant differences at P < 0.01.
in certain groups of plants. It is likely that plasticity in trichome production was not selected in the study species since they are well adapted to intense solar radiation, and its occurrence in a heavily shaded microhabitat is unlikely (Munguía-Rosas et al., 2012). Although trichome density was not affected by light intensity in the study species, these structures may be important in other ecological aspects such as a defence against herbivory (Pérez-Estrada et al., 2000). It is well known that trichome density deter herbivore attack (Aide, 1988) and therefore, high density of trichomes can be selected even in shaded habitats if herbivory is particularly high (e.g. Cronin and Lodge, 2003). In support of this notion, it is known that herbivory is strong and unaffected by light intensity in R. nudiflora (Munguía-Rosas et al., 2013, 2015).

While trichome density is not plastic, it seems that, as predicted, more trichomes are located on the surface with more exposure to light in O. campechianum and R. nudiflora. Previous research has reported some plant species, in which the abaxial leaf surfaces were more directly exposed to solar radiation from the early stages of leaf development or were exposed to sunlight reflected from the soil surface (e.g. in sandy or stony soils). Therefore, such conditions have been suggested to increase the production of glandular trichomes (Maffeï et al., 1989; Tattini et al., 2000). Higher densities of glandular trichomes occurring on the abaxial than on the adaxial surface have also been reported to occur in the matures leaves of other species, including Mentha × piperita L., Ocimum basilicum and Lippia graveolens Kunth (Dhawan et al., 2016; Maffeï et al., 1989; Martínez-Natário et al., 2011). Determination of the morphological and structural differences between the two surfaces of the leaf, such as the angle of the leaf, the thickness of cuticle and epidermis of both surfaces, might also help to elucidate the mechanism of acclimation of plants to different light conditions (i.e. to shade or full solar radiation). We did not explore the lateral trichomes, which have been reported in other species (Giuliano and Bini, 2008; Zuzzare et al., 2010). Consequently, we cannot rule out the possibility that trichomes exist on this part of the leaves in response to environmental variation and further research is required in this regard.

In conclusion, the morphology of glandular trichomes reveals that the leaves of O. campechianum possess peltate and capitate glandular trichomes on both (adaxial and abaxial) surfaces, of which the peltate morphotype was three times more abundant. In contrast, only one type of peltate trichome was observed in R. nudiflora. The trichome density of both species was higher on the abaxial relative to the adaxial leaf surface. Glandular trichome density is unaffected by light intensity. Since trichome density is usually related to its secretory activity, we suggest that the metabolites associated with these structures may also be unaltered by the light environment.

Acknowledgements

We thank a. Cristóbal from LANBIO, Cinvestav-IPN (FOMIX-Yucatan 2008-108160 and CONACYT LAB-2009-01 no. 123913) for technical assistance in obtaining the SEM micrographs. We thank L.M. Calvo and G. Dzib of CICY A.C. for providing part of the plant material. We thank A. Cristóbal from LANBIO, Cinvestav-IPN (FOMIX-Yucatan 2008-108160 and CONACYT LAB-2009-01 no. 123913) for technical assistance in obtaining the SEM micrographs. We thank L.M. Calvo and G. Dzib of CICY A.C. for providing part of the plant material. We thank L.M. Calvo and G. Dzib of CICY A.C. for providing part of the plant material.


