Morphological and Structural Characters of Trichomes on Various Organs of *Rosa roxburghii*

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Abstract. *Rosa roxburghii* Tratt (Rosaceae) of various organ surfaces are widely existing trichomes. Certain varieties have fruits that are thickly covered with macroscopic trichomes. *R. roxburghii* Tratt (RR) and *R. roxburghii* Tratt. f. *esetosa* Ku (RRE) are important commercial horticultural crops in China because of their nutritional and medicinal values. RRE is generally considered a smooth-fruit variant that arose from RR. Despite their economic importance, the morphological and anatomic features of organ trichomes have not been explored in detail for these two rose germplasms. In this research, we investigated the distribution, morphology, and structure of trichomes on leaves, stems, pedicels, fruits, and sepals in the two germplasms using scanning electron microscopy (SEM). There are many drugs, health care products, cosmetics, and functional foods that use these resources. There are many drugs, health care products, cosmetics, and functional foods that use these resources. These results suggest that the two rose germplasms are good candidates for understanding the trichome ontogeny in the genus and for further breeding of the smooth organ trait in this rose species.
and Rosas (Coyner et al., 2005; Feng et al., 2015; Finn et al., 2008; Kellogg et al., 2011). These studies did not present clear and detailed anatomic structures or the distribution of trichomes, especially in different developmental stages of trichomes. Very little is known about the structure, ontogeny, and function of trichomes in *R. roxburghii* as well as their pertinence with other trichome types. Therefore, the aims of the present study were to study trichomes of *R. roxburghii* and to analyze the differences between RR and RRE trichomes. We explain the structure, formation, and development of RR and RRE trichomes to lay the theoretical foundation for further research in the future.

**Materials and Methods**

*Plant materials.* Ten-year-old plants of RR ‘Guinong 5’ and RRE were grown on yellow soil (pH 6.3–6.5) in the fruit germplasm repository of Guizhou University, Guiyang, China (lat. 26°42′48″N, long. 106° 67′35″E), with conventional water management and fertilizer application. The stems, pedicels, fruits, sepals, and MLS were collected from the middle and upper canopy of 20 individual trees of both genotypes, respectively, in middle-late Apr. 2017. The samples of different organs were properly sized and quickly fixed in 3% glutaraldehyde solution for SEM observation after photographing with a digital camera. Samples of ripening fruits from both RR and RRE in middle-late Aug. 2017 were just used for photographing by digital camera. SEM. These samples of the appropriate size were fixed in 3% glutaraldehyde in 0.1 M phosphate buffer with a pH of 7.2 for 12 h. The fixed samples were dehydrated, subjected to a tert-butanol and ethanol mixture series (30%, 50%, 70%, 90%, and 100%), and vacuum cryodesiccation. Samples were directly placed on stubs with double-sided tape and sputter-coated with a gold thin film (Robards, 1978). The S-3400N scanning electron microscope was used to examine the types and morphology of trichomes. We have 108 clear pictures, and chose some representative pictures for the results analysis. The classification and terminology used in the description of the trichomes were based on Theobald et al. (1950), Payne (1978), and Hewson (1988).

**Results**

*Trichome distribution.* The trichomes nearly distributed on all organs observed of RR and RRE, except the MLS (Table 1). There are a large number trichomes on the surfaces of stems, pedicels, fruits, and sepals in RR and RRE (Fig. 1A–J). RRE presents an apparently glabrous phenotype with the naked eye (Fig. 1B, E, F, and H) and SEM revealed that all trichomes in this genotype were small and stunted (Figs. 2B, C, 3D–K, and 5E–Q).

*Stem.* Prickles were observed on the stem surfaces of RR and RRE, and binate prickles arose on the stem nodes in both germplasms (Fig. 1I and J).

*Pedicel.* Nonglandular trichomes were observed on the pedicel surfaces of RR. These trichomes have different shapes, including a type of papilla tuber, a species of ribbon trichome, and a acicular trichome (Fig. 2A); however, there were flagelliform trichomes only on the surfaces of early-stage RRE pedicels (Fig. 2B and C).

*Fruit.* On the pericarp surfaces of flower buds in RR, early-stage trichomes are fleshy, top passed, and have a wide base, and belong to acicular trichome (Fig. 3A and B). The middle stage of trichome development is marked by elongation, a slender apex slender, and a small base. This trichome type is referred to as ‘flagelliform,’ and they belong to the nonglandular trichome category (Fig. 3C and D). There are four different trichome types on the pericarp surfaces of RRE flower buds. Triangular trichomes (indicated with arrows) have an appearance is similar to triangle (Fig. 3E–G). Flagelliform trichomes exhibit single, unisrate, multicular, and pointed varieties (Fig. 3H, I, and P). The bases of flagelli-form trichomes have a papilla tuber (Fig. 3M, N, and Q). Capitate glandular trichomes have a short stalk as well as a round head (Fig. 3J–L). Elliptic glandular trichome (indicated by arrows) exhibit a fissure (Fig. 3O).

*Sepal.* Two different trichomes were present on the surface of sepal in RR, including acicular trichomes and flagelliform trichomes. The basal acicular trichomes are enlarged (Fig. 4A). Flagelliform trichomes were composed of single, unisrate, multicular, and pointed types. They were also unbranched (Fig. 4B and C). However, there is another trichome architecture on the surface of sepal in RRE. These trichomes are subdivided into two subtypes: capitate glandular trichomes have a short stalk and round multicellular head (Fig. 4D, E, and H–J), and nonglandular trichomes are also unbranched, and they are similar to flagelliform trichomes in RR (Fig. 4F, G, and K).

*MLS.* No trichomes were observed on the surfaces of the MLS in the two germplasms; however, stomata were densely arranged on the MLS of RRE (Fig. 5C and D). This stomata pattern was not observed in RR (Fig. 5A and B).

*Pickle transection of stem.* Using SEM, we have defined the internal structure of prickle transections for stems of RR and RRE. The stem prickle of the epidermis in RR is composed of approximately one to three layers of cells. The cells are small, round, and tightly packed. The cell wall is thick, and the cell cavity is large. The cells of the 8 to 10 layers proximate to the inner epidermis belong to meristematic layer. The meristematic layer cells are small, round, tightly arranged, and possess a thick cell wall. This results in a small amount of intercellular space. The volumes of the inward cells are larger than the cells of the epidermis, the arrangement of the cells is loose, the cell walls appear thin, there are no secondary walls, and the intercellular space is

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**Table 1.** The trichome types and distribution in various organs of *Rosa roxburghii*.

| Specific name | Organ | R. *roxburghii* Tratt (RR) | R. *roxburghii* Tratt. f. sect. K. (RRE) |
|--------------|-------|---------------------------|---------------------------------------|
| *R. roxburghii* Tratt | Stem | Prickle | Prickle |
| Pedicel | Felid | | Felid |
| Sepal | Stem | Prickle | Prickle |
| Marginal lobule sepals | Stem | | |
large. These cells can be characterized as parenchyma cells (Fig. 6A and B). The stem prickle transection for RRE shows that the epidermis is composed of approximately one to three layers of cells. The cells are small, square, and tightly arranged. The cell wall is thick, and the cell cavity is large. The 8 to 10 layers of cells proximate to the epidermis are smaller, cell walls are thicker, and the cells exhibit a tight arrangement. These cells belong to the meristematic layer. The inward cells are parenchyma cells, and they are larger, arranged loosely, and exhibit thin cell walls without secondary walls. In addition, there is a large intercellular space (Fig. 6C and D).

Prickle transection of pericarp. We also studied the trichomes transection of pericarp and sepals in RR. The trichomes transection of the epidermis in sepals is composed of approximately one to four layers of cells. The cells are small and polygon-shaped, and they are tightly arranged. The cell wall is thick, and the cell cavity also is small. The cells of inward again five to seven layers are parenchyma cells. The cells are larger, they are loosely arranged, and their cell walls are thin. There is no secondary wall of parenchyma cells, and the intercellular space is large (Fig. 7A and B). The trichomes transection of the epidermis in pericarp is composed of approximately one to two layers of cells. The cells are small and square, and they are tightly arranged. The cell wall is thick, and the cell cavity is small. The inward cells are parenchyma cells, which gradually become larger. Their arrangement is loose, their cell walls are thin, and no secondary wall can be observed (Fig. 7C).

Discussion

Among the two germplasms investigated in this study, we encountered two trichome morphotypes on the plant organs (stem, pedicel, fruit, sepal, and MLS) (Fig. 1A–J). The trichome types in RR and RRE are documented: nonglandular and glandular. Nonglandular trichomes include the ribbon, acicular, flagelliform, and triangular trichome types (Figs. 2A–C, 3A–I, and 4A–C, F, G, K). Glandular trichomes include the capitate and elliptic glandular trichome types (Figs. 3J, K, L, O, and 4H–J). These trichomes may perform different functions in plant physiology and ecology with various morphological, mechanical, and phytochemical characteristics (Kortekamp and Zyprian, 1999; Wagner et al., 2004). Because variable morphological features of trichomes are found, it is difficult to determine the exact trichome types that are being referred to in the literature (Theobald et al., 1979). The typical trichome types of RR are ribbon trichomes, flagelliform trichomes, and acicular trichomes (Figs. 2A, 3A–D, and 4A–C). The typical trichome types in RRE are triangular trichomes, capitate glandular, flagelliform trichomes, and elliptic glandular trichomes (Figs. 3E–Q and 4D–K). It is interesting that no trichomes were observed on the surfaces of the MLS in the two germplasms. Stomata were densely arranged on the MLS of RRE, but this characteristic was not observed in RR (Fig. 5A–D). The structure of the stem prickle transection in the two germplasms is composed of epidermis, meristematic layer, and parenchyma cells (Fig. 6A–D). The trichome transections of both pericarp and sepal in RR exhibit epidermis and parenchyma cells. The epidermis cells of sepal trichomes are polygon-shaped, and fruit trichomes exhibit round epidermis cells (Fig. 7A–C).

Nonglandular trichomes. The organs of RR are covered by ribbon trichomes, acicular trichomes, and flagelliform trichomes (Figs. 2A, 3A–D, and 4A–C). There are two types of nonglandular trichomes in RRE: triangular trichomes and flagelliform trichomes (Figs. 3E–I, M, P, and 4F, G, K). Ribbon trichomes, acicular trichomes, and flagelliform trichomes are common in other plants (e.g., Chen et al., 2007; Ickert-Bond et al., 2015; Liu et al., 2013, 2016b; Ma et al., 2016; Moore, 1991; Wen et al., 2013), but reports of triangular trichomes are rare. Compared with the trichomes found on organs of fruits in RR, the triangular trichomes are a special nonglandular trichome type in RRE (Fig. 3E–G). However, there are no triangular trichomes in RR. The reason for this difference may be because of a trichome-related mutation. All types of trichomes found may do duty as a mechanical barrier against severe spring temperature, herbivores, and pathogens.
Nonglandular trichomes in mid stage of RR. (D, E, F, G) Triangular trichomes (arrows) on the pericarp of RRE. (H, I, P) Flagelliform trichomes of RRE. (J, K, L) Capitate glandular trichome (arrows) of RRE. (M, N, Q) Tuberculate processes (arrows) of RRE. (O) Elliptic glandular trichome (arrows) and have a gully of RRE. Scale bars = 200 μm (A, C, D, F, H, I, K, M, P), 20 μm (B, E, G, L, N, O, Q), and 10 μm (J).

Nonglandular trichomes in early-stage RR. (C, D) Nonglandular trichomes in mid stage of RR. (E, F, G) Triangular trichomes (arrows) on the pericarp of RRE. (H, I, P) Flagelliform trichomes of RRE. (J, K, L) Capitate glandular trichome (arrows) of RRE. (M, N, Q) Tuberculate processes (arrows) of RRE. (O) Elliptic glandular trichome (arrows) and have a gully of RRE. Scale bars = 200 μm (A, C, D, F, H, I, K, M, P), 20 μm (B, E, G, L, N, O, Q), and 10 μm (J).

Ribbons of young plant organs in RR and RRE may serve as a photo-protective mechanism against abiotic and biotic stresses. These trichomes may also assist in decreasing water loss and facilitate acclimation to xeric environments (Wagner et al., 2004). We conclude that the ribbon trichome of RR may be a morphological synapomorphy for the Rosaceae clade, and this hypothesis should be experimented with in conjunction with a fully resolved phylogeny of the Rosaceae clade in the future.

Glandular trichomes. Glandular trichomes may show uni- or multiserate stalks and uniseriate glandular heads. They can originate from the epidermis or from both the epidermis and subjacent layers. We need further study to elucidate the root of the glandular trichomes of R. roxburghii. Nonglandular trichomes have traditionally been described according to their density and overall appearance instead of their structure. For example, "villose leaves" have been used as a description for Anemopsis velutina, referring to a hairy cover of thick, straight, long, and soft trichomes (Bureau and Schumann, 1897). However, no information is helpful on the anatomy and developmental sequence of nonglandular trichomes in Rosaceae or other plant groups, such as Lamiaceae (Naidu and Shah, 1981). Nonglandular trichomes have generally been regarded as morphologically homogeneous structures. In general, the variable number of cells and variation in cell size, as well as the variable patterns of the trichome morphotype distribution on different plant parts, show the importance for more detailed morpho-evolutionary studies of trichomes.

Acicular trichomes and flagelliform trichomes are commonly called simple trichomes. Simple trichomes differ in size, density, cell number, length, color, and distribution. Obviously, simple trichomes of RRE were longer and denser than RR (Figs. 2A–C and 4A–C, F, G). Simple trichomes on the two germplasms of R. roxburghii may protect plant organs against damage. This is the case in other germplasms of R. roxburghii. In many germplasms, a dense indumentum composed of simple trichomes serves as a filter protecting plant tissues against hurt from ultraviolet-B radiation and as a deterrent to insect activity and so on (Karabourniotis et al., 1995; Levin, 1973; Liakoura et al., 1997; Manetas, 2003; Yan et al., 2012). Short simple trichomes have no effect on the oviposition of leafhoppers, but they did reduce the Anagrus spp. parasitism rate. In contrast, long simple trichomes could make a difference of the leafhopper oviposition on different herbaceous plants (Pavan and Picotti, 2009).

The nonglandular trichomes of representatives of Rosaceae have hardly been described in detail (e.g., Kellogg et al., 2011), and there has been no research on nonglandular trichomes of germplasms in R. roxburghii. Nonglandular trichomes have traditionally been described according to their density and overall appearance instead of their structure. For example, "villose leaves" have been used as a description for Anemopsis velutina, referring to a hairy cover of thick, straight, long, and soft trichomes (Bureau and Schumann, 1897). However, no information is helpful on the anatomy and developmental sequence of nonglandular trichomes in Rosaceae or other plant groups, such as Lamiaceae (Naidu and Shah, 1981). Nonglandular trichomes have generally been regarded as morphologically homogeneous structures. In general, the variable number of cells and variation in cell size, as well as the variable patterns of the trichome morphotype distribution on different plant parts, show the importance for more detailed morpho-evolutionary studies of trichomes.

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Terpenes, phenolics, alkaloids, and lipophilic compounds can be secreted by glandular trichomes, or other substances that deter or poison herbivores and pathogens (Levin 1973; Tissier 2012; Werker 2000). These glandular trichomes can also secrete resin to provide a protective layer of the developing tissues against cold temperatures (Lapinjoki et al., 1991). Secreted mucilage from Drosera serve as an adhesive trap for insects (Outenreath and Dauwaldert, 1986). This trichome type may serve as a defense mechanism against insects. The composition of mucilage and secondary metabolites of RRE will be explored in the future. It has been reported that the extraplasmic and intercellular spaces of leaves, stems, and other organs. The structure of stem prickles in two germplasms of R. roxburghii is composed of epidermis, a meristematic layer, and parenchyma cells, but there is a major distinction between epidermis cells and meristematic cells in the two varieties (Fig. 6A–D). The determination of the specific functions of the previously mentioned structures still requires further study. The anatomic results show that the R. roxburghii epidermis does not exhibit obvious vascular tissue. This is similar to the reports of the predecessors of the Rose cultivars ‘Laura’ and ‘Shortcake’ (Asano et al., 2008; Kellogg et al., 2011).

**Trichome initiation in RR and RRE.** The results show that there are flagelliform trichomes on the fruits of RR (Fig. 3C and D). The flagelliform trichomes of RR are similar to the multicellular trichomes in fruits of wild-type cucumber. These flagelliform trichomes belong to the simple trichome type (Liu et al., 2016a). Four trichome types were found in RRE: triangular trichomes, capitulate glandular trichomes, elliptic glandular trichomes, and flagelliform trichomes (Figs. 2C, D, 3E–Q, and 4D–K). Capitate glandular trichomes in RRE were similar to type I trichomes found in three trichome-related mutants of cucumber, reported as MICT, TBH, and CsGL1 (Chen et al., 2014; Li et al., 2015; Zhao et al., 2015). These trichomes have a small papillar-shaped head. Furthermore, the trichome initiation and development in RR was controlled by two allelic genes, in which two dominant genes made the fruit prickles stiff, and two pairs of recessive genes made fruits similar to those found in RRE (Gao and Luo, 1994). In cucumber, there were also two allelic genes. The main difference is that recessive genes override the effect of dominant genes (Yan et al., 2015). The two genes (Csa3M748220 and Csa6M514870) that referred to multicellular trichome development in cucumber were not found in the transcriptional data in RR (Yan et al., 2015). The trichome development positive regulator pathway model in RR may be different from that used in cucumber. The genetic determinants of these traits require further study. Our current knowledge of the trichomes relevant gene regulatory networks is primarily restricted to the unicellular trichomes of the model plant Arabidopsis. Not much is known about control the development of multicellular trichomes in RR. Future studies should focus on the analysis of diverse expression data generated by RNA-sequencing that may show new information for identifying assumed key transcription factors of multicellular trichome development in RR.
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