The Effect of the Gall-Forming Aphid *Schlechtendalia chinensis* (Hemiptera: Aphididae) on Leaf Wing Ontogenesis in *Rhus chinensis* (Sapindales: Anacardiaceae)

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ABSTRACT The aphid *Schlechtendalia chinensis* (Bell) induces large single-chamber galls, called horned galls, on the leaf wings (an extending part of the rachis) of *Rhus chinensis* Miller. Horned galls are initiated when the fundatrix of *S. chinensis* feeds on the adaxial surface of the leaf wings. We compared the histology of intact versus galled leaf wings during various developmental stages by observing their histomorphology during their chronological development. We found that at the initiation phase, the outer epidermis and opening zone of the galls had many glandular trichomes and that pallisade tissue was replaced by parenchyma cells. The number of glandular trichomes on the outer epidermis was reduced as galls matured. The latex ducts and vascular elements became denser in the inner gall layer, and closer to the gall cavity. Stomata were found on outer epidermis in all gall developmental stages excluding the initiation phase. The effect of the gall-forming aphid on leaf wing ontogenesis is discussed.

KEY WORDS histological structure, chronological development, horned gall, phloem feeder

The relationship between a phloem-feeding insect and its host plants is a typical example of parasitism. Phloem feeders can be important pathogen vectors and may infest various plant organs, including stems, petioles, blades, flowers, and fruits (Jeffries and Lawton 1984, Vranjic and Gullan 1990, Miller 1998, Inbar et al. 2004), seriously affecting the performance and fitness of their hosts (Wang et al. 1995, Appleton et al. 1997, Withers et al. 2000, Raman and Withers 2003, La Salle 2005, Heu et al. 2006, Zvereva et al. 2010). If the parasites are aphids, they may also affect the host plant via honeydew secretion (Hussain et al. 1974, Buckley 1983, Wimp and Whitham 2001, Wäckers et al. 2008, Leroy et al. 2011).

Many insects induce galls on various plants and plant organs, and this relationship is considered to be the most sophisticated and intimate mode of herbivory. In its gall, the insect may experience better nourishment obtained from surrounding plant parts (Lewis and Walton 1958, Bianchi et al. 1989, Fay et al. 1993, Gange and Nice 1997, Wool et al. 1999, Sandström 2000, Stone et al. 2002, Stone and Schönrogge 2003, Cruz et al. 2006, Turgeon and Wolf 2009), a favorable microenvironment (Fernandes and Price 1992, Larson and Whitham 1997, Blanche 2000, Danks 2002, Miller et al. 2009), and protection against some natural enemies (Price and Pschorn-Walcher 1988, Abrahamson and Weis 1997, Crespi and Abbot 1999, Kurosu et al. 2006, Joseph et al. 2011), including fungi, parasitoids, and predators. Some gall formers may cause extensive damage and even death of their host (Wang et al. 1995, Withers et al. 2000, Raman and Withers 2003, La Salle 2005, Heu et al. 2006); indeed, some are even used as biological control agents of invasive plants (Dennill 1988, Rojo and Marcos-García 1997, Paynter et al. 2010, Impson et al. 2013).

Rhus (Anacardiaceae) galls (Chinese gallnuts) are abnormal growths of plant tissue induced by aphid of the tribe Fordini. The aphids which include 11 species in six genera form galls on *Rhus* and are common in eastern Asia, especially in southwest China. One species is found in North America (Zhang et al. 1999). The galls have historically been used for medicinal and chemical purposes, as they are rich in tannins, accounting for ≈50–80% of total gall weight, and are most often used as a source of tannic, gallic, and pyrogallic acids (Namba 1993, Zhang et al. 1999). The best known gall maker used in this manner is *Schlechtendalia chinensis* (Bell), which induces sealed horned-shape galls on the leaf wings of *Rhus chinensis* Miller. This species accounts for ≈75% of Chinese gallnut production (Tang and Cai 1957, Zhang et al. 1999).

The life cycle of *S. chinensis* includes sexual and asexual reproduction and host alternation between *R. chinensis* and certain mosses. In the early spring, a winged morph (sexupara) migrates from moss to *Rhus* and produces male and female sexuales. Each mated

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female produces a fundatrix ovoviparously, which then moves toward and feeds on new foliage, where it initiates gall formation (Zhang and Zhong 1983, Takada 1991).

Because aphids are phloem feeders with piercing–sucking mouthparts, the structure of their galls is different in many aspects from those of other gall formers that feed with chewing mouthparts. For example, there is no special layer of nutritive cells in the chamber of aphid galls (Wool et al. 1999; Nyman and Julkunen-Tiitto 2000; Álvarez 2009, 2011). The aphids in horned galls feed on the sieve elements and latex ducts that often accompany vascular bundles in the gall wall (Lin et al. 1996, 1998; Liu et al. 2011). Zhang et al. (2001) suggested that the selectivity of feeding sites by *S. chinensis* is associated with the structure of the *R. chinensis* leaf. It seems that the fundatrix aphids choose the leaf wings as feeding sites because they are thicker than leaflets and because their palisade-to-spongy tissue thickness ratio is only one fifth that of the leaflet. While Zhang et al. (1999) and Lin et al. (1996, 1998) studied the histology of horned galls, they were focused on the structure of a certain period in the process of gall development. There are therefore few details about the ontogenesis of leaf wings and the plant's resistance to aphid feeding during the gall development. The goal of this study was to elucidate the histological changes that occur during the different stages of gall induction and development. These results may aid further research on the feeding behavior of different generations within the gall and the aphid dynamics during the transition from the slow growth phase to the rapid growth phase of gall development.

Materials and Methods

Host Plants. In 2008, saplings of *R. chinensis* were cultivated at the study site in Kunming, Yunnan province, southwest China. Conventional management was carried out to avoid infestation by diseases and insect pests. In 2010, we selected 60 trees in good condition for this experiment.

Aphids. The peak hour of sexuparae migration from the secondary hosts to *Rhus* is between 1200 and 1500 hours from late February to early March. About 2 h after flying out of their moss host, the settled sexuparae begin to produce sexuales. Therefore, during sexuparae migration period, we collected the aphids (no mouthpart and no feeding) on porcelain plates (30 by 20 cm) around 1700 hours from 26 February to 13 March 2010. Groups of 100 sexuparae were packed in a brown kraft bag and examined in the laboratory at room temperature. Sexuales were produced and mated in the bags, and consequently fundatrices were present within a month. The opened bags with the fundatrices were then hung on the branches of *R. chinensis* in April (≈140 branches in total were inoculated, with one bag per branch). The fundatrix aphids climbed out of the paper bags, onto new foliage and initiated gall formation.

Histological Examinations. Intact and galled leaf wings were collected every 20 d from April to October 2010, at least 10 of each per sampling date. Each date, trimmed samples (sections of leaf wing, ≈3 by 3 mm; and segments of gall wall, ≈5 by 5 mm) were fixed in FAA (formaldehyde 5 ml, 60% alcohol 90 ml, acetic acid 5 ml, and glycerol 5 ml) for >24 h. They were subsequently subjected to dehydrating, dealcoholizing, and washing in xylene following the procedure described by Li (2009). All reagents were purchased from the Solarbio Company (Beijing, China).

The samples were embedded in paraffin and cut transversally in serial sections with a cutting blade (Leica: RM 2126RT, Germany) set at 5 μm. Finally, sections were transferred into Safranin-Fast Green. The salivary sheaths, left behind after penetration and feeding, were dyed red with safranin. All sections were mounted on microscope slides.

Based on the changes to the feeding sites observed daily and the size of galls in the testing site, the development of horned gall was separated into six phases (Fig. 1): 1) settling phase (intact leaf wings), in which the fundatrix had just arrived at the leaf wings in mid-April; 2) early aphid-affected phase, in which the feeding sites became light yellow; 3) gall initiation phase, in which the feeding sites developed small depressions, followed by a small globular protuberance; 4) slow growth phase, in which there was little change in gall size during the three months following May; 5) rapid growth phase, in which the gall quickly developed in size and the volume of gall increased 10–15 times over that of early August; and 6) dehiscence phase (mid-October), in which the gall opened via a longitudinal split, and the alate aphids emerged. In each phase, we chose 30 slides to observe the histological features with a microscope (Nikon E800; Nikon, Tokyo, Japan) and to photograph using a camera (Nikon SM1200, Japan).

Scanning Electron Microscopy. Approximately 150 incipient gall samples were collected to examine with a scanning electron microscope in the 2 wk after aphids settled on leaf wings in April of 2011. At this point, the tissue around the feeding sites became hyperplastic and formed small depressions that soon deepened. Ten samples were collected daily during this period. All were cut into small blocks ≈3 by 3 mm, and then fixed with glutaraldehyde for >12 h and washed with phosphate-buffered saline (PBS, pH 7.2). They were then dehydrated in 75% ethanol for 30 min and laid on filter paper until complete volatilization of the ethanol, at which point they were observed with a scanning electron microscope (HITACHI: TM3000, Japan).

Results

External Morphological Characteristics. Throughout most of the developmental phases, the gall tissue differed considerably from the intact leaf tissue (Table 1). In phase 1, the leaf wings were not affected and remained similar to intact tissue (Fig. 1A). In phase 2, the feeding sites became light yellow after 3–5 d of feeding (Fig. 1B). In phase 3, the tissue of leaf wings began to grow abnormally in early May. About 2 wk

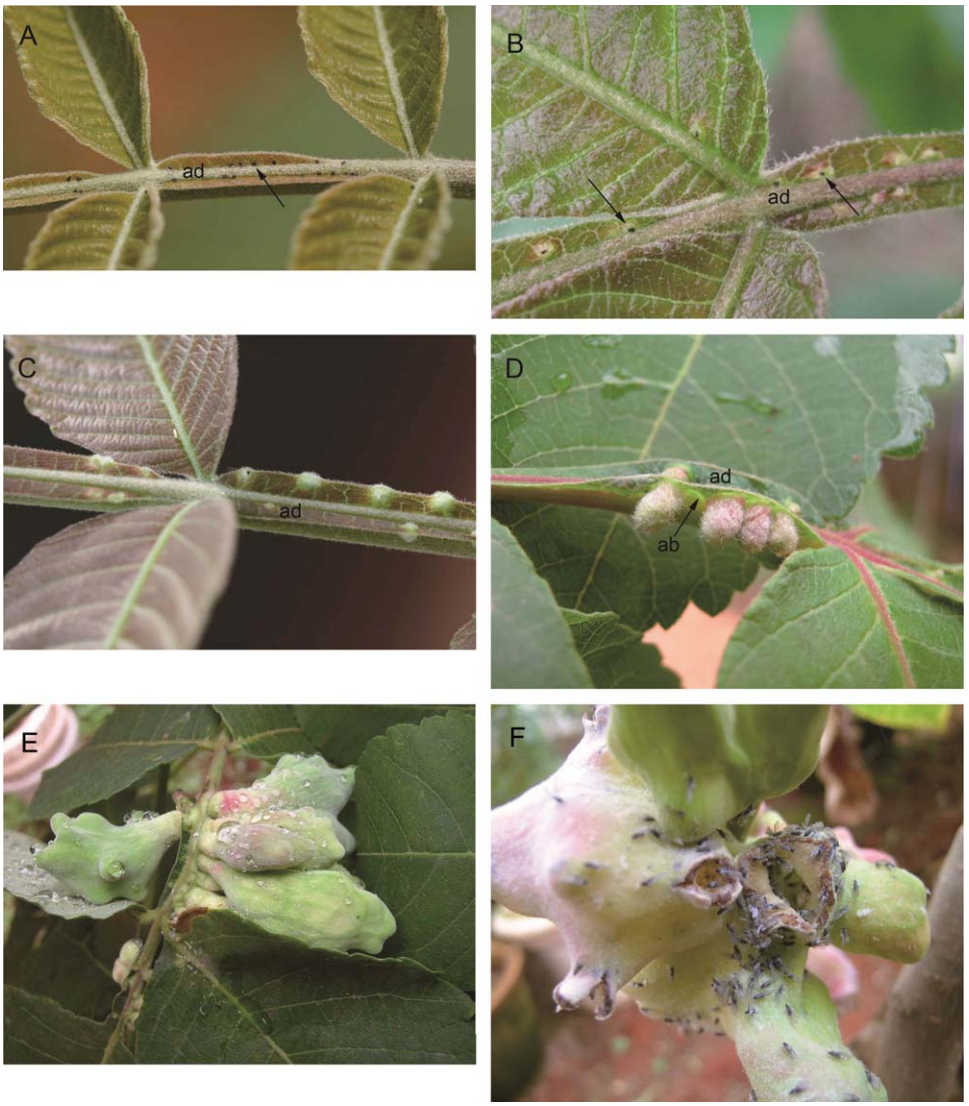

Fig. 1. Stages of development galls induced by *S. chinensis* on *R. chinensis*. (A) Settling phase (black spot at arrow indicates aphid); (B) aphid-affected phase, with tissue yellowing at feeding site (example indicated by arrow); (C) gall initiation phase, showing growth of tissue on lower side of leaf (samples indicated by arrows); (D) slow growth phase; (E) rapid growth phase; (F) dehiscence. Abbreviations: ad, adaxial surface of the leaf wings; ab, abaxial surface of the leaf wings. (Online figure in color.)

later, as the tissue around the feeding sites became hyperplastic, the feeding sites formed small depressions that soon deepened (Figs. 1C and 2C) and enclosed the fundatrix aphids. A small globular protuberance appeared on the underside of the leaf wings. The opening of the protuberance on the upper side of the leaf wings was not completely closed, but was covered by trichomes (Fig. 2D). There were many trichomes on the outer epidermis of the protuberance simultaneously. Phase 4 began about a month after the aphid fed on leaf wings, in late May, as the gall closed completely and enlarged slowly (Fig. 1D). In phase 5, the size of gall increased quickly from August to early October. Horn-like or forked protuberances emerged as the gall devel-

Fig. 2. Transverse sections of galls at different stages of development. (A) Settling phase, the normal leaf wing; (B) aphid-affected phase of leaf wings; (C) the late phase of aphid-affected leaf wings; (D) gall initiation phase, with opening blocked by glandular trichomes; (E) the slow growth phase, with unicellular epidermis in the inner and outer wall; (F, G) the rapid growth and dehiscence phase, the gall cells hyperplasia. Abbreviations: ap, aphid; aa, aperture area of closed gall; ie, inner epidermis of gall; ld, latex duct; oe, outer epidermis of gall; vb, vascular bundle zone; ad, adaxial surface of the leaf wings; ab, abaxial surface of the leaf wings. (Online figure in color.)

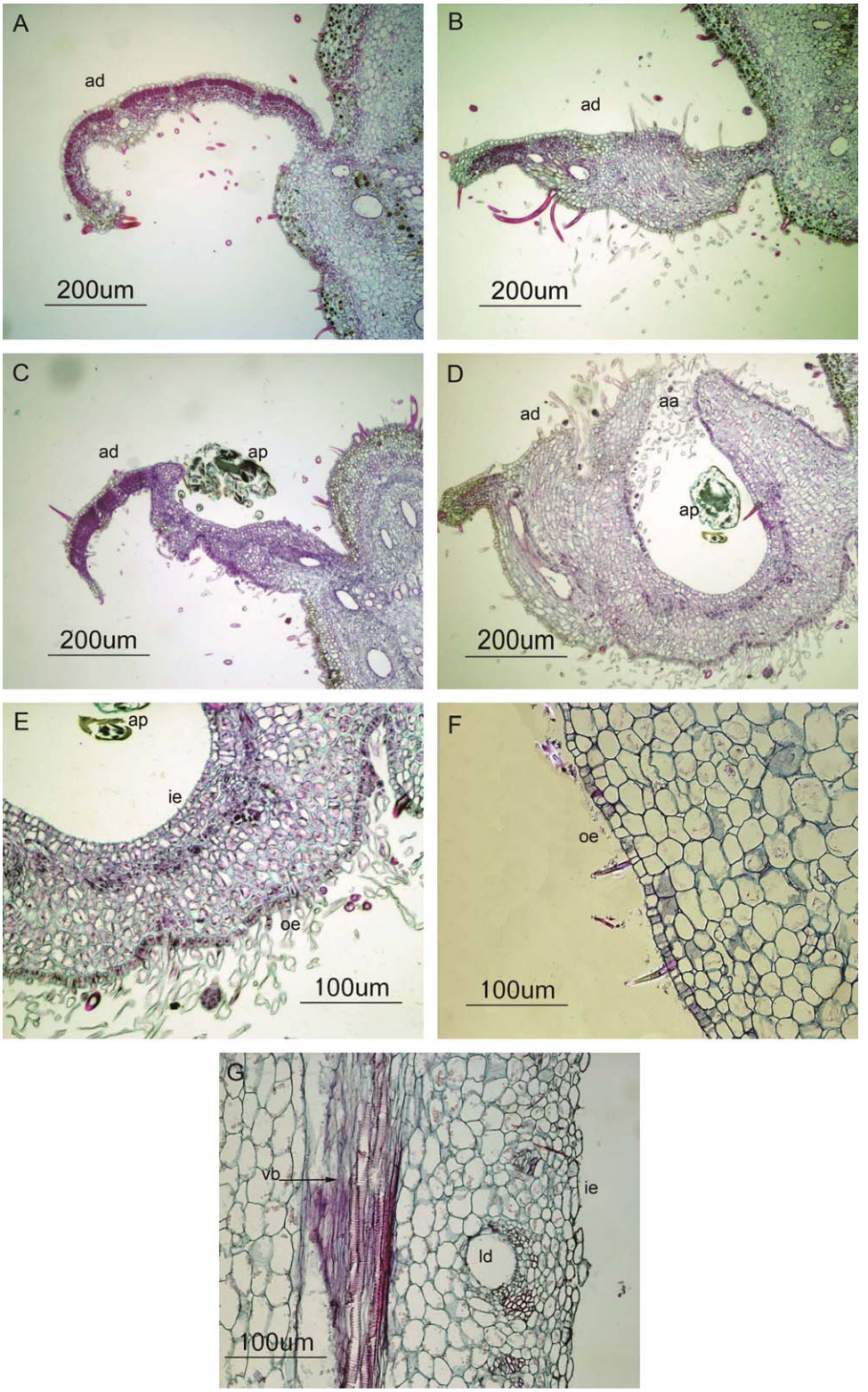
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Table 1. The histological characteristics of intact leaf wings and galled tissues at different phases

Development phase	Date	Trichomes		Palisade tissue	Epidermic cell layer		Stomata
		Inner	Outer		Inner	Outer	
Settling phase	Early April	●	●	●	—	—	●
Early aphid-affected phase	Middle April	●	●	○	Mo	Mo	○
Gall initiation phase	Late April	◐	●	○	Mo	Mo	○
Slow growth phase	May to July	○	◐	○	Mu	Mo	●
Rapid growth phase	Aug. to early Oct.	○	◐	○	Mu	Mo	●
Dehiscence phase	Middle or late Oct.	○	◐	○	Mu	Mo	●

●, many; ◐, little; ○, nothing; —, inexistence; Mo, monolayer cells; Mu, multilayer cells.

oped (Fig. 1E). By then the gall entered its last dehiscent phase around mid- or late-October. The gall split open longitudinally, releasing the alate aphids (Fig. 1 F).

Histological Characteristics. The structure of intact leaf wings of *R. chinenses* had a typical arrangement of adaxial epidermis, palisade tissue, parenchyma cells, and abaxial epidermis in a top–down manner (Fig. 2A). After feeding by the aphid, the tissues underwent significant changes. The main modifications of sections featured in the initial and latter periods are described in the following sections.

Changes to the Epidermic Layer. In the initial phase, the epidermic layers of the inner and outer gall tissues were monolayer (Fig. 2E), while in the rapid growth and dehiscent phases, the inner epidermis had two to three layers, while the outer epidermis remained a unicellular layer (Fig. 2F and G).

The Number of Trichomes. In initiation phase, the surface and the opening zone of the gall were covered by dense unicellular and multicellular glandular trichomes (Figs. 2D and 3A). As the gall developed, it became tightly sealed by cell hyperplasia (Fig. 3B) and grew continually, at which point the trichomes on the outer epidermis became sparse (Fig. 3C).

Palisade Tissue Reorganization. The stylets of fundatrix punctured the epidermal tissue and reached the palisade tissue (Fig. 4C). The palisade tissue of galled leaf wings were reorganized and replaced by parenchyma cells (Fig. 4A,B). Galled and nongalled zones were connected by a vascular bundle during the gall

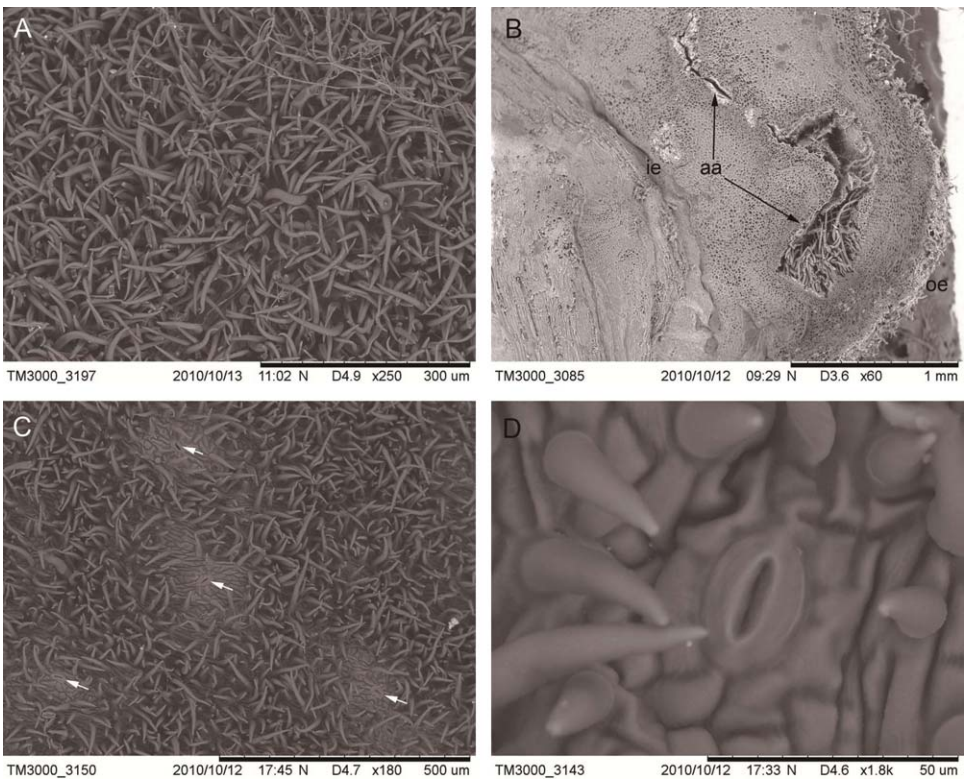

Fig. 3. The pictures of scanning electron microscopy. (A) The surface of initial gall was covered by dense unicellular trichomes; (B) the traces of original opening in the closed gall; (C) the late phase (rapid and dehiscence phase), the trichomes and stomata on outer epidermis, the white arrow was headed out toward stomata; (D) the stomata. Abbreviations: aa, aperture area of closed gall; oe, outer epidermis of gall.

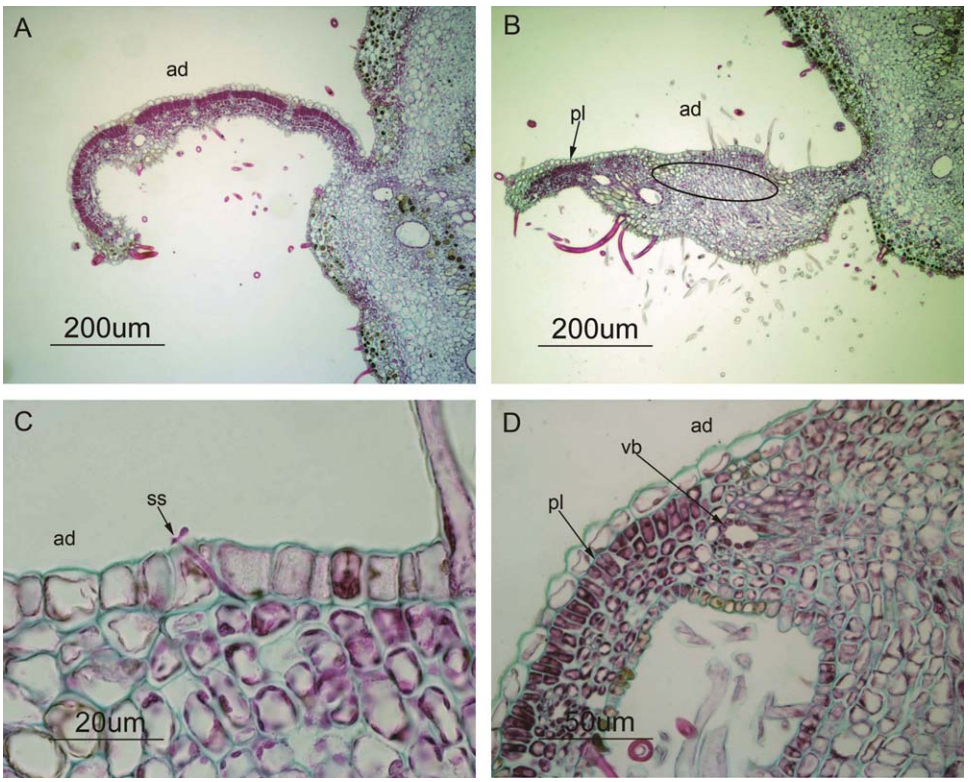

Fig. 4. Degradation of palisade cells. (A) The structure of the normal leaf wings; (B) the palisade tissue was reduced and replaced by parenchyma cells in the ring area; (C) the stylets reached the upper side of palisade tissue; (D) The galled and nongalled zones were linked by a vascular bundle. Abbreviations: pl, palisade layer; ss, saliva sheath; vb, vascular bundle; ad, adaxial surface of the leaf wings. (Online figure in color.)

initiation phase (Fig. 4D: *vb;* 37 galls and 574 slides of histological specimens). Intact leaf wings had a typical palisade layer, which was absent in the galled tissue.

The Position of Vascular Bundle. In the initiation phase, the edges of the gall aperture was free of schizogenic ducts and vascular bundles (Fig. 2D). During the growth process, gall tissue cells proliferated irregularly and most schizogenic ducts and vascular elements became closer to the gall cavity, with the exception of one or two ducts (Fig. 5A and B).

Excluding the initial gall phase, the stomata could only be observed on the outer epidermis of horned galls (Fig. 3C and D). Dyeing the saliva sheath with safranin allowed us to determine that the stylets of aphids passed straight through the leaf wing tissue during penetration (Fig. 6A and B).

Discussion

There are ≈4,401 species aphids in the world, of which ≈10% are gall makers (Wool 2004). Like other gall-inducing insect taxa, the most striking characteristic of aphid galls is the variability in gall position, morphology, and structural diversity (Shorthouse and Rohfritsch 1992, Inbar et al. 2004, Miller 2005). Although horned galls are found on both leaf wings and leaflets of *R. chinensis,* galls formed on leaflets are small and will be abscised before maturity. Their histological structure was, therefore, not examined in this study.

We found gall development was characterized by several changes and modifications of the epidermis, parenchyma, and phloem tissues. Several types of unicellular, multicellular, or both, trichomes are found on plant leaf surfaces, and these may protect the plant from herbivorous insects, disease, or damage from abiotic factors such as rainfall (Banks 1957, Neal et al. 1990, Goundoudaki et al. 2003, Buchman 2008). Trichomes on our study plant were denser on galled leaf wings than on intact leaf wings and were particularly numerous at the "entrance" of the horned galls. The presence of thick trichomes in the entrance of the initial galls could provide mechanical protection against pests and rainfall, which would be in agreement with events in other gall-forming systems (Simmons et al. 2003, Arduin et al. 2005, Álvarez et al. 2009). The disappearance of trichomes in the advanced developmental phases may suggest that sealed galls have no further need for such defense mechanisms.

We found that the palisade tissue in intact leaf wings was reorganized and replaced by many parenchyma cells during the initial stage of gall formation because of fundatrix feeding (Fig. 4C). Likely, *S. chinensis* chose the leaf wings as feed sites because these have

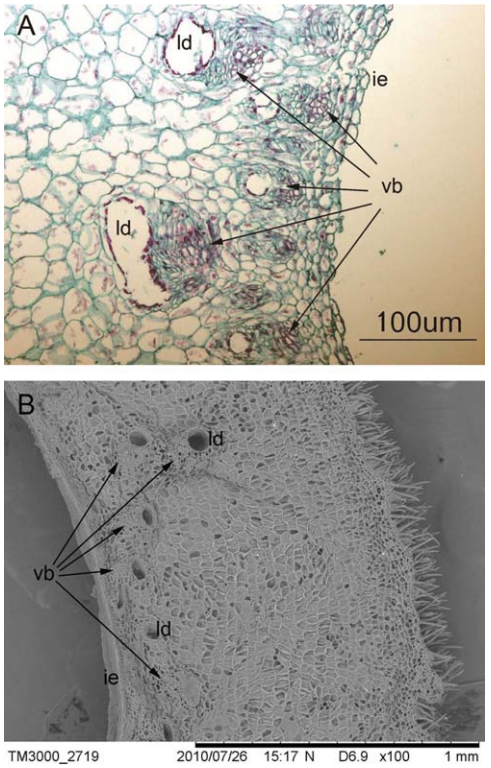

Fig. 5. (A, B) Detail structures near the inner gall chamber. The latex ducts and vascular tissue concentrated near inner chamber of gall. Abbreviations: ie, inner epidermis of gall; vb, vascular bundle; ld, latex duct. (Online figure in color.)

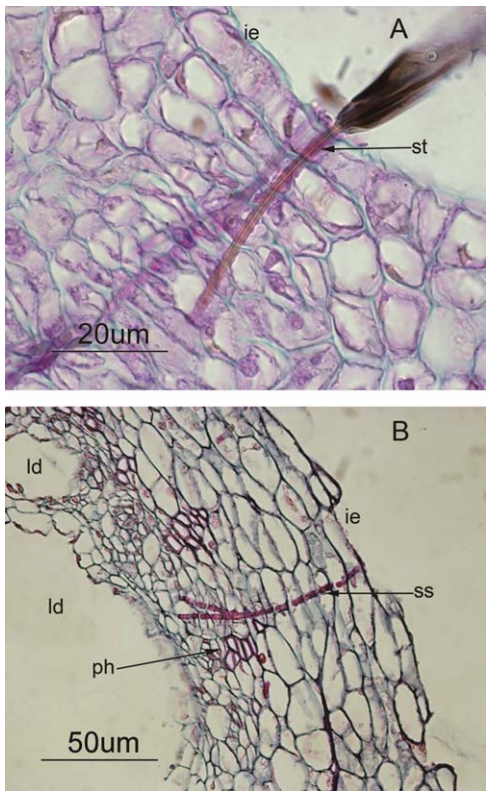

Fig. 6. Feeding traces in gall wall in (A) immature phase and (B) mature. (A) Detail showing tip of aphid rostrum with stylets inserted into tissue and traces of previous probing; (B) saliva sheath penetrating to region of phloem tissue, showing branching trace owing to multiple probing. Abbreviations: ld, latex duct; ph, phloem; ss, saliva sheath; st, stylets; ie, inner epidermis of gall. (Online figure in color.)

a thinner palisade tissue than leaflets (Zhang et al. 2001). It seems likely, therefore, that the subsequent absence of palisade tissue is associated with aphid feeding and that one or more constituents of aphid saliva may play a role in palisade reorganization. Another change manipulated by aphids was that the schizogenic ducts and vascular elements became closer and denser around the gall cavity, providing the aphids with easy access to the vascular system for nourishment (Wool et al. 1999).

In the aphid tribe Fordini, there are two vascular bundle types: one distant from the chamber and the other separated from chamber by only few cells (Álvarez 2012). In this study, both types of vascular bundles existed in the gall wall, but most of the vascular bundles were the latter type. The shorter distances between the vascular bundles and the gall chamber made feeding much easier, as aphids inside the gall chamber were able to pass through the cell walls to feed directly on the phloem sieve element (≈78% in all sections showed aphid penetration pathways; Fig. 5).

The sections also showed numerous saliva sheaths in gall tissues. Dyeing the saliva sheaths allowed us to trace the aphid's feeding, from that we can see that the aphid stylets passed straight through the leaf wing tissue and reached the sieve elements during penetration. Thus, by avoiding the high concentration of phenols that accumulate in the wall tissue, aphids may change their route of feeding and overcome the plant's defenses (Wang et al. 1995, Lu et al. 2010).

In this study, we characterized the histological changes during the chronological development of the horned gall and discussed various alterations and modifications. Further investigation of aphid-induced alterations of the structure of leaf wings, of the nutritional composition of phloem sap of *R. chinense*, and of the effective components of saliva in aphid antidotal mechanisms, are required to better understand the feeding behavior of generations within the gall and to associate aphid dynamics with the transition from the slow growth phase to the rapid growth phase of gall development.

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