



Sunlight-induced bark formation in long-lived South American columnar cacti



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ARTICLE INFO

Article history:

Received 2 December 2014
 Received in revised form 1 May 2015
 Accepted 29 September 2015
 Edited by Shahin Zarre
 Available online 9 October 2015

Keywords:

Bark formation processes
 Columnar cacti
 Epidermis
 Hypodermis
 Sunlight exposure
 South America

ABSTRACT

Previous research has shown that sunlight-induced bark formation (epidermal browning) on vertical surfaces of tall, long-lived columnar cactus species leads to premature death of entire plants. The bark cambium that produces bark for cactus species has been shown to involve proliferation of epidermal cells only. The purpose of this research was to understand (1) the characteristics of cuticles, epidermal and hypodermal cells, (2) the process of sunlight-induced bark formation, and (3) changes in hypodermal cells during the bark formation process for many species of long-lived, columnar cacti from South America. A wide diversity of epidermal and hypodermal cells occurred among the species studied. Epidermal depths ranged from 8.7 to 49.7 μm and involved one to several epidermal cells while the thickness of hypodermal cell layers ranged from 42.7 to 661 μm among the species studied. During bark cambium formation, each epidermal cell underwent at least one anticlinal cell division prior to numerous periclinal cell divisions since lengths of initially produced bark cambium cells were half the lengths of uninjured epidermal cells. Some cactus species exhibited hypodermal cell injuries during bark formation. This study reports: (1) quantitative measurements of cuticles, epidermal and hypodermal layers, (2) the presence of anticlinal cell divisions of epidermal cells to produce the bark cambium, and (3) the destruction of hypodermal cells during bark formation for columnar cactus species of South America. Possibly these results are specific for sunlight-induced bark formation for cactus species while other types of injuries may result in bark production by other means.

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1. Introduction

There are many tall, long-lived, columnar cactus species in the Americas (Anderson, 2001; Hunt et al., 2006). Duriscoe and Graban (1992) first used the term epidermal browning (sunlight-induced stem bark) for cacti of *Carnegiea gigantea* in southern Arizona. Visually, epidermal browning can be a variety of colors from gray to light tan to dark brown (Fig. 1). Epidermal browning has occurred on vertical surfaces of 21 species of tall, long-lived cactus species throughout the Americas (Duriscoe and Graban, 1992; Evans and Fehling, 1994; Evans et al., 1994a,b,c; Evans, 2005; Evans and Macri, 2008). Epidermal browning (bark formation) is more prevalent on surfaces exposed to direct sunlight (equatorial-facing surfaces) compared with surfaces that receive less direct sunlight (polar-facing surfaces) in both North and South America (Duriscoe and Graban, 1992; Evans et al., 1992, 1994a,c, 1995; Turner and Funicelli, 2000; Evans and Macri, 2008). Epidermal browning (bark formation) caused premature morbidity and cacti with extensive

epidermal browning die prematurely (Evans et al., 2005, 2013; Evans and De Bonis, 2015). Data show that UV-B irradiation of sunlight is the causative agent that produces the initial events for bark formation (Evans et al., 2001).

Stem surfaces of many long-lived cacti have a cuticle, an epidermis, and several hypodermal cell layers (Rizzardini, 1984; Gibson and Nobel, 1986; Darling, 1989; Evans et al., 1994a,b; Terrazas and Arias, 2002). Rizzardini (1984) described the external surfaces, cuticles, epidermal and hypodermal cells and some internal cellular structures of *Echinopsis chiloensis* (Colla) H. Friedrich & G.D. Rowley. Scanning electron micrographs showed extensive epicuticular waxes on stem surfaces. Beneath the one to two-celled epidermis (Garcia et al., 2012; Soffiatti and Angyalossy, 2007), there were five to eight cell layers of hypodermal cells (Gibson and Horak, 1978; Rizzardini, 1984; Gibson and Nobel, 1986; Loza-Cornejo and Terrazas, 1996; Mauseth and Keisling, 1997; Terrazas and Arias, 2002; Mauseth, 2006). Columnar cactus species from South America have a high diversity of epidermal and hypodermal characteristics (Mauseth, 1996, 1999).

Surfaces of long-lived, columnar cactus species must remain green and must have functional stomata in order for plants to

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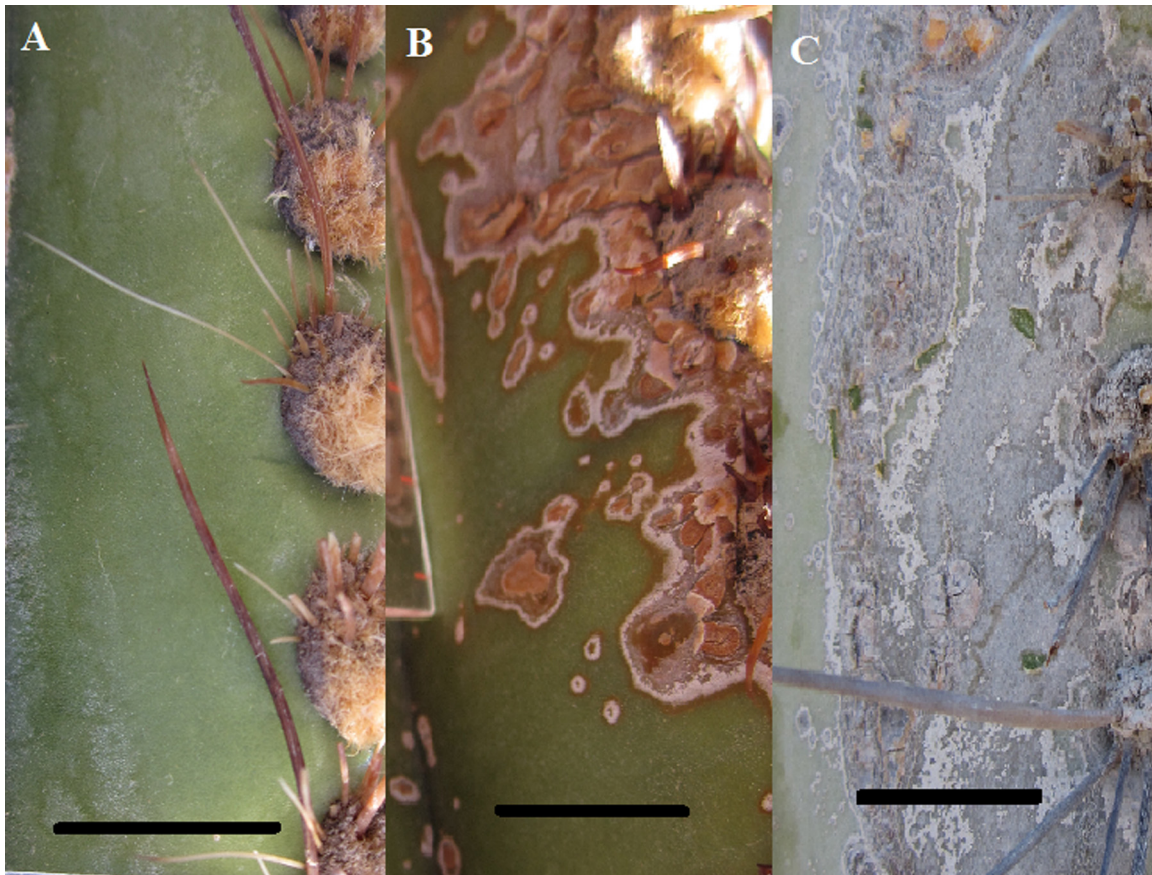


Fig. 1. Images of stem surfaces of *Echinopsis atacamensis*. (A) Image of an uninjured, green surface with areoles and spines on the right side of the image, (B) image of an injured surface. Some green areas are present but most of the surface has bark. (C) Image of a completely developed bark. Bars = 10–15 mm.

exchange gasses and remain healthy (Gibson and Nobel, 1986; Evans et al., 1994a).

Gibson and Nobel (1986) demonstrated that the phellogen (bark cambium) of some cactus species is derived from epidermal cells of stems following an injury. They provided an image of the surface of *Ferocactus robustus* Britton and Rose in which the bark cambium was present external to an intact hypodermis. This image showed that the height of bark cambium cells was similar to the height of uninjured epidermal cells. For *F. robustus*, epidermal cells became bark cambium cells and produce bark cells by periclinal cell divisions only. The scenario of the bark cambium of cactus plants producing bark cells derived solely via periclinal cell divisions has become commonly accepted. Gibson and Nobel (1986) emphasized that bark formation occurs following stem injuries.

The present study was aimed at understanding (1) the variety of characteristics of cuticles, epidermal cells and hypodermal cells of stems of various cactus species, (2) the processes involved for sunlight-induced bark formation on stems of cactus species, (3) the occurrence of the destruction of hypodermal cells during sunlight-induced bark formation for several cactus species. The overall purpose of these investigations is to understand how sunlight exposures cause bark formation on cactus surfaces.

2. Materials and methods

2.1. Species sampled

Cactus species from Argentina and Chile were observed and sampled during January 2013 while species from Peru were obtained in May and June 2013. Information from Anderson (2001);

<http://cludwigfr.dyndns.org/>), Hunt et al. (2006) and Hunt (2013) were used to locate cactus species. Eight, seven, and 24 species were studied and sampled in Argentina, Chile and Peru, respectively. For each cactus species observed, the characteristics were compared with published descriptions (Anderson, 2001; Hunt et al., 2006; Hunt, 2013). For each species, many photographs were obtained to establish the overall morphology of whole plants and characteristics of individual stems. Archived photographs (electronic images available at Manhattan College upon written request) were compared with published images and written descriptions (Anderson, 2001; Hunt et al., 2006; Hunt, 2013) to provide identification of each species. To reinforce our identification of species, we realized that most cactus species of this study had limited distributions (<http://cludwigfr.dyndns.org/>). Latitudes and longitudes were recorded from a Garmin eTrex Legend (REI.com). All species names were checked with IPNI (www.IPNI.org: Plant Name Search), Tropicos (www.tropicos.org), Hunt et al. (2006) and Hunt (2013). All species sampled are shown in Supplementary data (S1).

2.2. Stem tissues sampled

Stem tissue samples were taken to cover the range of surface injuries from several stems of each species since considerable variation in stem characteristics may occur with field samples (Nyffeler and Eggle, 1997). For these columnar cactus species, tissue samples were taken at 1.7 m above ground level on north-facing surfaces that showed bark formation. South-facing surfaces that showed few if any bark were also taken. Stem samples were taken from three plants when available. Stem tissue samples ranged from samples with no apparent injuries to samples with thick bark. Not all species

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