Guttation and Growth of Bamboo Shoots

Subjects: Plant Sciences

Contributor: huifang Zheng , Jian Gao

Guttation is the process of exudating droplets from the tips, edges, and adaxial and abaxial surfaces of the undamaged leaves. Guttation is a natural and spontaneous biological phenomenon that occurs in a wide variety of plants. Despite its generally positive effect on plant growth, many aspects of this cryptic process are unknown.

anatomy bamboo shoot guttation sheath blade water transport

1. Introduction

Guttation is a very common natural phenomenon in the plant kingdom. Many plant species reportedly engage in guttation, such as rice, wheat, barley, maize, tomato, potatoes, tobacco [1][2][3][4][5]. Guttation refers to the process of liquid seeping from the tips, edges, and adaxial and abaxial surfaces of the undamaged leaves of plant species in the form of droplets [6]. This usually occurs during the early morning or late hours of the day and is a complex phenomenon affected by many internal and external factors. Some factors affecting guttation include a plant's nutritional condition, its water balance and root activity, local soil moisture, air temperature and humidity, and wind speed [7]. It is generally thought that the continual absorption of water by the root system causes water to accumulate in roots, which creates hydrostatic pressure; this pressure can move water upward to the leaves of the plant via the xylem duct network in the stem, forcing some water to exit through hydathodes located at surfaces of leaves to form the characteristic drops of guttation [7]. Guttation plays an important role in the transport of nutrients, water, proteins, enzymes, hormones, and metabolites as a plant develops and grows in size [6]. The study showed that plant guttation can provide a continuous non-destructive system for producing recombinant proteins, greatly increasing yield, eliminating extraction, and simplifying downstream processing [8]. The guttation status of plants can be used as a rapid screening technology for rice germplasm resources [9]. However, we do not yet fully understand the internal linkage between the guttation phenomenon and the growth dynamics of plants.

Moso bamboo (Phyllostachys edulis) is the most important bamboo species in China because of its paramount ecological, economic, and cultural value among all bamboo types. Within the last decade, considerable research has investigated the mechanism underpinning the rapid growth of bamboo shoots, including the morphological anatomy aspects, physiological responses, and molecular regulation [10][11][12][13]. Compared with trees, bamboo is a grass that has a unique vascular system that is likely linked to its special growth and development characteristics [13]. The shoot stage has an astounding growth rate, capable of reaching a maximum daily growth of 1 m [10]. Water dynamics figure prominently in the facilitation of the rapid growth of bamboo shoots, and guttation is a direct indicator of a plant's water status. However, the relationship between bamboo's guttation and its shoots' rapid growth is understudied, and therefore this phenomenon and its implications remain unclear.

2. The Effect of Guttation on the Growth of Bamboo Shoots

2.1. Guttation Phenomenon of Sheath Blades of Bamboo Shoots

Guttation is a common phenomenon in many plants when conditions favor absorbing water through their roots but limiting transpiration from their leaves.

The bamboo's sheath blade was the primary site of guttation and the main organ of exudation; hydathodes also were observed on its surface (**Figure 1**A). As the main transpiration organ of the bamboo shoot, many stomata are expected to be distributed on the surface of the bamboo sheath as well as the sheath blade [14]. The effect of plant structural damage as imposed here by snapping off the sheath blade or removing the culm sheath showed that following sheath removal, a large amount of liquid emerged from the wound site; this result suggests the main reason for guttation lies with the inherent physiology of the plant. This same phenomenon has been observed in Fargesia yunnanensis [14]. The damage permits the rapid leakage of much tissue fluid that disrupts the hydraulic balance in the injured plant. This may be why bamboo's growth was inhibited after stripping its sheath; this process evidently did not prevent water exudation from happening. When the hydrostatic pressure in the water guide system reaches a certain level, water can be promoted to exude from the water holes on the leaf surface to form exudate [7].

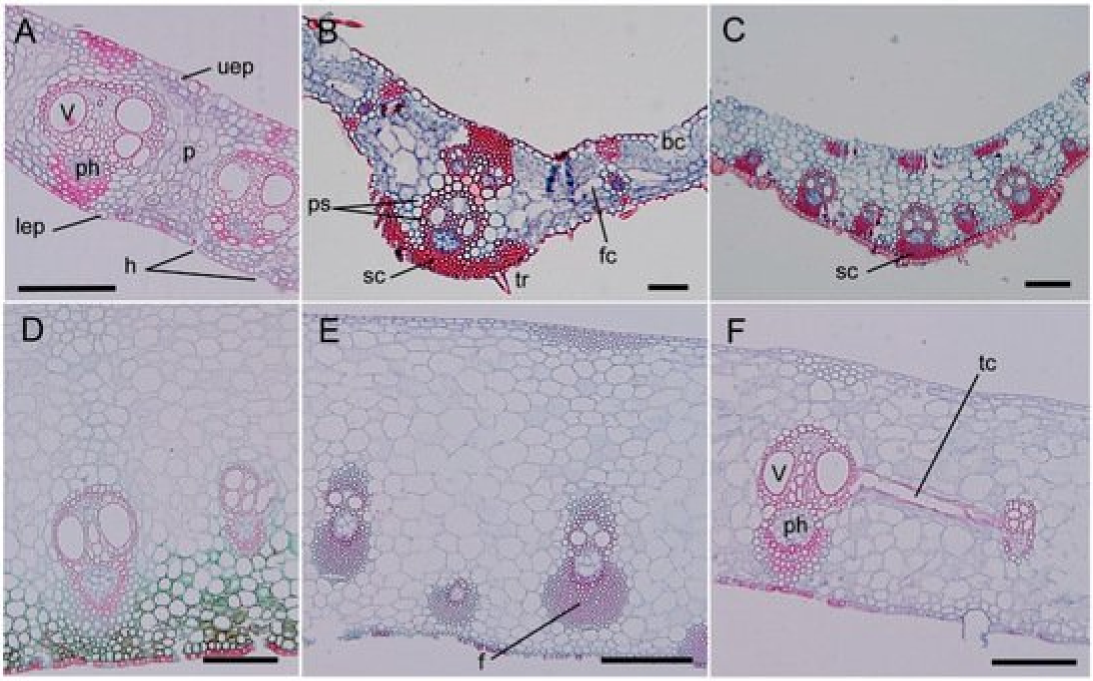

Figure 1. Transverse section of the culm sheath and bamboo leaf. (**A**) The sheath blade of moso bamboo. (**B**) The leaf of moso bamboo. (**C**) The leaf sheath of moso bamboo. (**D**,**E**) Base and upper part of culm sheath proper. (**F**) Cross-section of culm sheath proper. v, vessel element; ph, phloem; h, hydathode; p, parenchyma; bc, bulliform cells; fc, fusoid cells; sc, sclerenchyma cells; tr, trichomes; ps, parenchymatous sheath cells; uep, upper epidermis; lep, lower epidermis; f, fiber cells; tc transverse catheters. Scale bar = 100 μm.

Guttation can reflect the dynamics of water metabolism in bamboo shoots and local changes in soil moisture. Vigorous exudation is the expression of robust plant growth and normal water metabolism in the plant body, whereas non-exudation implies an imbalance or stagnation of water in the body. The intensity of exudation is a good physiological indicator of water availability to a plant, which is convenient for observation and does not damage its tissues [2].

2.2. Various Components of the Guttation Fluid from Bamboo Sheath Blades

Some studies have shown that compared with the xylem liquid phase, the guttation fluid contains fewer amino acids [3], indicating that spouted water is not simply transported directly from the catheter to the hydathodes. Substances are reabsorbed and reused as they are transported through the xylem, and only a small amount is excreted through the hydathodes, which contain substances harmful to the plant [15][16]. However, little is known about the dynamics of substance reabsorption, transport proteins, and energy supply in the guttation of plants. As a healthy and delicious food, the composition of bamboo shoots at different developmental stages has been studied extensively [17][18][19]. Yet, surprisingly, the determination of bamboo's exudate composition has yet to be reported. Here, based on LC-MS analysis of the bamboo exudate, it found that although the liquid appeared clear, it contained a variety of organic acids, sugars, and hormones. Sugar has a central regulatory function in the coordination of plant growth. Sugars not only fuel cellular carbon and energy metabolism but also play a key role as signaling molecules. Sucrose was transported over long distances in the xylem, produced a series of sugar signaling molecules through its own metabolism, such as sucrose itself, glucose, and trehalose-6 phosphate [20]. The hormone abscisic acid (ABA), which is the most important phytohormone involved in plant growth, development, and adaptation to various stress conditions [21][22][23]. A variety of chemical components in guttation liquid indicated that guttation is a physiological performance of plants to balance water and transport substances in vivo. Recent studies have shown that the guttation droplets not only serve as a source of water for insects but also that the carbohydrates and proteins in the guttation can serve as a food source for insects [24]. As an important plant trait, guttation plays a significant role in the interaction between polytrophic insects and plants. Plant exudation, especially crop exudation, is a potential route for insect exposure to pesticides, such as nicotinamide residue in exudate from corn seeds [2][25]. The complex components in the exudate may therefore have ecological significance for the growth of the plant itself, an intriguing aspect serving further study.

2.3. Water and Substance Transport Pathways in Bamboo Shoots

Long-distance transport of water and solutes through the xylem and along vascular bundles into cells is a long-recognized concept in plant physiology [26][27]. Moso bamboo is connected by an intricate underground rhizome system. Bamboo's ability to integrate resources allows the bamboo culm to connect belowground in a small forest and redistribute water among bamboo through the rhizome system [28][29]. Bamboo shoots obtain their water from the mature bamboo, via the rhizome root and base root. Studies have shown that after severing these rhizomes, the water utilization ratio between adjacent stems is decreased by 20% [30]. One study on the diurnal variation of sap flux density in culms and subsurface flow of bamboo shoots demonstrated the stem flow of leafless bamboo shoots was dominant at night. After leaf development, the sap flux density is mainly at day, which is similar to the mature stem [28]. The freshly sprouted culms had high sap flux during the night and low sap flux during the daytime [28]. This result is consistent with the observed water exudation and the changed considerable leaf water content of bamboo mature stalks lose considerable water via transpiration during the day, but the transpiration rate at night is greatly diminished. Roots will continue to absorb water to generate high root pressure, and as bamboo mature, the need for water is greatly reduced. Compared with mature bamboo, new bamboo shoots still have higher water requirements.

The scattered distribution of vascular bundles is a common characteristic of Gramineae plants (grass). Compared with the vascular bundles of the C3 plant rice and C4 plant maize, the distribution of vascular bundles of bamboo stems more closely resembles that of maize [31][32][33]. The vascular bundle is mainly divided into phloem and xylem structural components; the former includes a sieve tube and companion cells, which are mainly responsible for the transport of assimilates, and the latter functions mainly as a conduit, responsible for moving moisture and inorganic salts. Vascular bundles also play an important role in the long-distance transportation and mechanical support of crops [34]. From our observations, the development of vascular bundles in the different internodes of bamboo shoots was variable (**Figure 2**D–F). Two large vessels in the single vascular bundle are responsible for water transport within the culm [13]. The results of the magenta staining also revealed that water could be transported up the xylem vessels, as well as from the inside to outside of the xylem vessels at the nodes. Staining was also observed in the ducts of the bamboo nodal diaphragm, suggesting that these interconnecting ducts are the basis of an efficient water transport system in bamboo. Parenchyma cells within and between the vascular bundles in the bamboo nodes featuring rapid elongation play a role in glucose metabolism and transport of substances and water [35]. Water is transferred from the node to the connected bamboo sheath along the vascular bundle and then from the bamboo sheath to the sheath blade. Under the upward push of root pressure, this liquid is exuded from the water pore on the surface of the sheath blade.

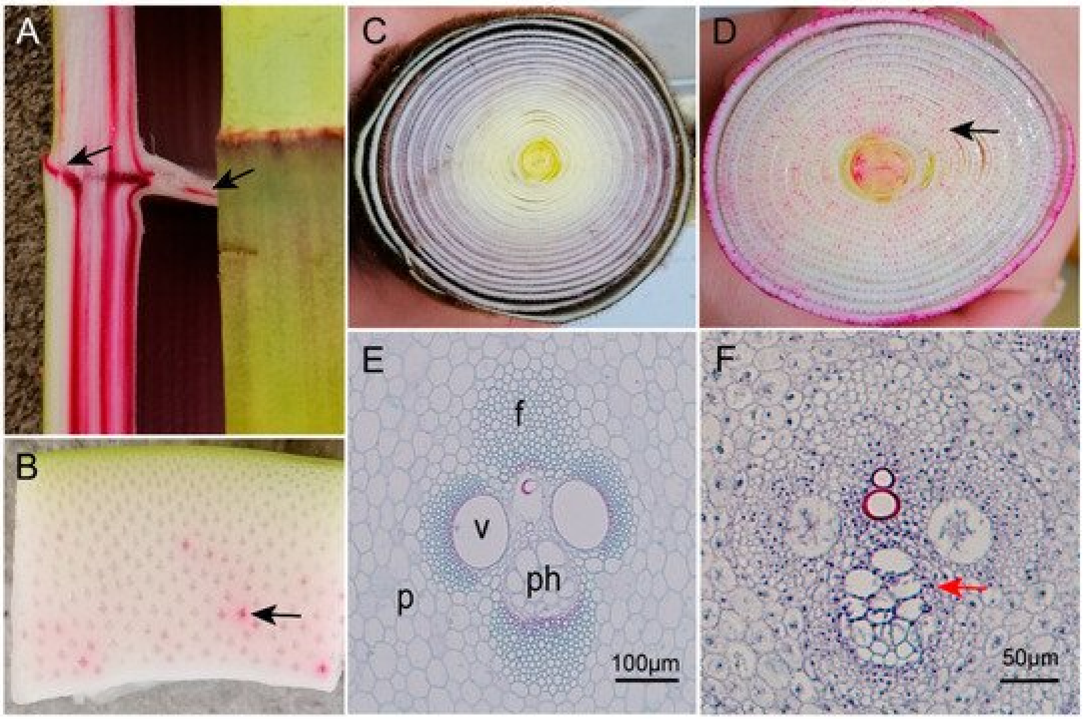

Figure 2. (**A**) Bamboo shoot stained with magenta; (**B**) Cross-cut section view of the culm in panel A. (**C**) Unstained bamboo sheaths. (**D**) Bamboo sheaths stained with magenta. (**E**) The vascular bundles at the base of a bamboo shoot; (**F**) The vascular bundles at the upper of a bamboo shoot; the black arrow indicates vascular bundles stained with magenta; the red arrow indicates nucleus. v, vessel element; ph, phloem; P, parenchyma; f, fiber cells.

Aquaporins (AQPs) are known as water-channel proteins, and they are associated with energy-dependent cells and intercellular and long-distance water transport (and of other small solutes) [36]. Accordingly, AQPs are crucial for the maintenance of plant water physiological functions, which include many aspects of plant development. Plant leaves can rapidly change their hydraulic conductivity by the regulation of plasma membrane AQPs [37]. Furthermore, light intensity can affect the activity of an aquaporin [38], and the expression patterns of several AQP genes in stomatal complexes have been well documented [39]. Further, there is evidence of their involvement in conferring immunity to pathogen infections [40]. Therefore, given our results, we think the in-depth study of the distribution and physiological activity of aquaporin at each cell layer along the vascular bundle is necessary. During the growth process of bamboo, especially bamboo shoots, many phenomena related to water dynamics at the physiological level have yet to be fully understood. Since the underlying mechanism of water transport from the mature stem to the bamboo shoots as well as its relationship with carbohydrate transport remains unclear, further investigation is warranted. Future research should pay more attention to the molecular mechanisms of guttation, water transport, and aquaporin regulation.

2.4. Bamboo Sheath Affects Internode Growth

Studies have shown that culm sheath plays an important role in controlling water and assimilative transport [41]. It also observed in the bamboo forest that after culm sheaths were removed, the internodes of bamboo shoots could not develop normally, internodes became short and brown, and the younger the internodes were affected more (**Figure 3**). In addition to the apical meristem [42], there was an intermediate meristem in each segment of bamboo. The division and elongation of a large number of cells in a short period is the main reason for the rapid growth of bamboo [10]. The anatomic study showed that the developing internodes were divided into meristem, elongate, and mature regions. The meristem and elongate regions were near the base of internodes [43]. The rapid expansion of basal internode meristem cells in bamboo shoots requires intracellular turgor pressure to maintain growth [44]. Culm sheath growing at the base of internodes provides strongly mechanical support for tender internodes. Bamboo shoots have vigorous cell division, strong metabolic activity, and generate a lot of heat [10]. Sheaths wrapped in layers can reduce heat loss and maintain a high temperature, especially at night with low temperature, which may be the reason why bamboo shoots can maintain a fast growth rate at night.

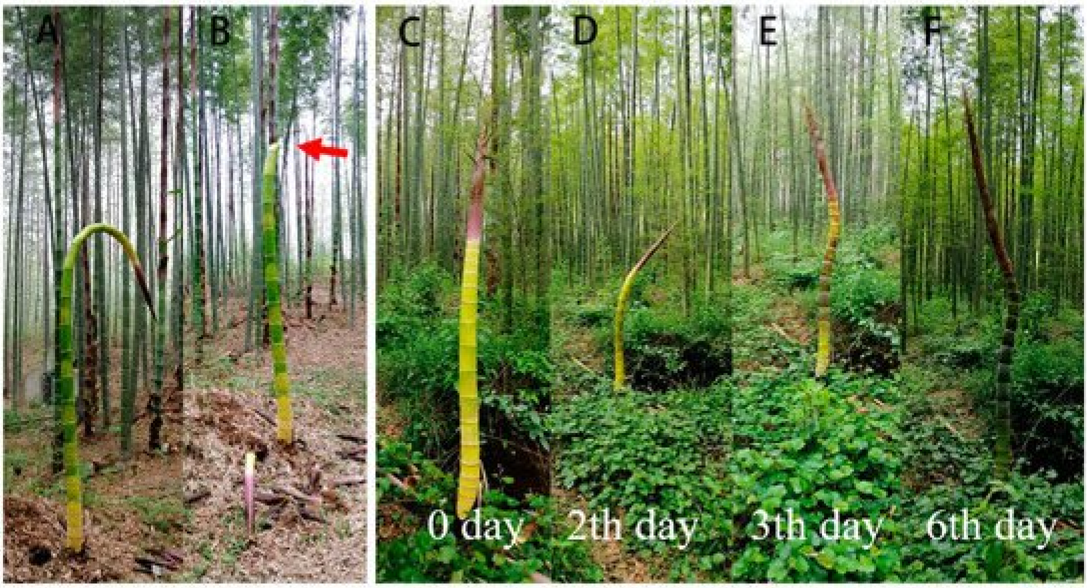

Figure 3. Stripped culm sheaths of bamboo shoots. (**A**,**B**) The upper part of the bamboo shoot after stripping was bent and broken. (**C**–**F**) Ensuing structural changes of a bamboo shoot over a 1-week period after stripping the sheath. The red arrow shows where the bamboo shoot has broken off.

3. Conclusions

The sheath blade was the main organ of guttation in bamboo shoots, whose guttation droplets contain organic acids, sugars, hormones, and other compounds. The abundant conduit in the culm sheath was connected with that for the node of the bamboo shoot, which channels water and carries other substances to the culm sheath. The guttation process was jointly influenced by the local environment and physiological conditions of the bamboo plants. Removing their culm sheath damaged the internal homeostasis of water and material transport, thereby impairing the normal growth of bamboo shoots.