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Renewal of vascular connections between grapevine buds and canes during bud break

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ABSTRACT

With the seasonal change from winter to spring, grapevine compound buds break dormancy and start a new annual developmental cycle. The rebuilding of vascular connections between buds and canes is vital to ensure normal development of the bud. We monitored the dynamic development of grapevine buds under natural field conditions, observed vascular connections using light microscopy, and investigated the uptake and transport of water in buds and canes from dormancy to bud break. During dormancy, the bud was isolated from the cane and no xylem was observed in the bud or the junction region between the bud and the cane. However, at the stage of bud swelling (stage II), xylem was observed at the cane to bud junction. The rate of water uptake through the xylem at the junction increased as bud development progressed. These results suggest that buds were hydraulically isolated from the cane during dormancy and the formation of xylem between bud and cane started with swelling of the bud. The velocity of water transport into the bud also increased with bud development. We discuss several factors that affect the formation and differentiation of xylem, including temperature, hormones and water. It is likely that the rebuilding of vascular connections between buds and canes is related to multiple factors rather than any one individual factor.

1. Introduction

For most perennial woody plants, buds are found in the leaf axils. Some buds grow during the season of formation; some remain dormant until the year following their formation, while others remain dormant for several years or permanently (Larson and Richards, 1981). A grape vine bud contains growing points, which are located in the leaf axil, just above the point of connection between the petiole and shoot. During the growing season, there are two types of buds on the shoot. One is called the lateral bud, which can grow into a lateral shoot in the season the bud is formed. The other is called a compound bud, which contains three growing points, called the primary bud, the secondary bud and the tertiary bud (Pratt, 1974; Lavee et al. 1981; Naito et al. 1986). Normally the compound bud remains dormant after it has formed until the following spring. If the primary bud has been damaged because of freezing, the secondary and tertiary buds serve as a "backup system" (Hellman et al., 2006). Some people consider viticulture as "budiculture", because the grape vine starts its annual growth from bud break, and the buds develop into shoots (Lavee and May, 1997). Before bud break, the buds have fully formed shoot primordia that include leaves, tendrils, and flower clusters. Therefore management of the bud is the focal point of winter pruning practices.

During bud growth, vascular connections are built between the bud and the parent axis, which is thought to be an important feature of structural compartmentalization in tree development (Shigo, 1985). Many studies in trees have shown how branches are attached to trunks. Some studies indicate that the xylem in the trunk above a branch connects directly with the branch, but other studies suggest that the conduction and attachment patterns at the branch-trunk junction differ among tree species (Maton and Gartner, 2005).

During winter, the grapevine is fully dormant, the xylem in the cane and trunk is emptied of water, and no water flow occurs in the plant. During this season, the buds are isolated from the cane, in that there is no vascular connection between buds and cane, and this isolation aids buds to resist freezing (Gu, 2003). During bud break, the buds build connection with the cane for water and nutrient transport. However, there is little information available on the development of these vascular connections. The purpose of this paper is to clarify how and when vascular connections between buds and canes are formed during bud development in the spring, and discuss their role in water transport and

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Table 1
The dates of beginning and ending of each stage of bud development.

Stage	Date of beginning	Date of ending	Average Duration(days)
stage II	March 12	March 28	17 ± 2.1
stage III	March 25	March 31	7 ± 1.3
stage IV	March 29	April 2	5 ± 0.8
stage V	March 31	April 4	5 ± 1.5

Values are means ± SE of N = 30.

bud break. To the best of our knowledge, this distinctive developmental process has not been reported previously.

2. Material and methods

2.1. Plant material

Mature Chardonnay grapevines on their own roots located in a vineyard on WSU tricities campus in Richland City, WA (USA, altitude 117 m, lat. 46°17′ N, long. 119°17′W) were chosen for this experiment. The vines were planted in north-south-oriented rows at 2.0 m (in rows) by 2.8 m (between rows) spacing. Vines were trained to bilateral cordon, which entailed training the vines in both directions along the cordon wire from the trunk. Vines were drip-irrigated during the growing season. On randomly selected vine trees, we selected a set of uniform healthy canes with lengths over 140 cm and basal diameter of about 1.5 cm, each selected vine was pruned to ten canes with six buds per cane in winter. Throughout the sampling period the low and high daily temperatures were recorded. The dynamic development of the bud was divided into five stages according to Andreini et al. (2009), and the date of beginning and ending of each stage was recorded (Table 1)

2.2. Measurement of bud length and width during development

One bud was sampled from each cane, and totally 30 buds from 30 canes 5 vines used in this experiment were labeled individually before bud break. We monitored elongation of each bud by recording the length and width increase from dormancy.

2.3. Measurement of bud weight at differential stages

At each bud developmental stage, 50 buds in the same developmental stage were collected from 25 canes of 5 vines (2 buds per cane and 5 canes per vine) for bud weight (fresh and dry) measurement. Fresh weight (FW) of buds were weighed after the buds were taken back to the lab, then dried in a forced air oven at 110 ℃ for 12 h and weighed again for dry weight (DW) determination

2.4. Measurement of bud water content at different stages

At each stage of bud development, at least 50 buds in the same developmental stage were collected from 25 canes of 10 vines for measuring water content. The total water content was calculated from the following equation: total water content (WT) = (FW − DW)/FW. The free water content in buds was measured using refractive index according to Klymchuk et al. (2008). The difference between total water content and free water content was a measure of bound water content (Klymchuk et al., 2008).

2.5. Dynamic change of water content in buds and canes

The dynamic change of water content in buds and canes was measured every week from February 1 to April 6. On designated dates, 10 canes with similar thickness from 5 vines were sampled and taken back to the lab within half an hour. All buds were cut from the canes, the fresh weight of buds and canes were weighed separately, then dried in a forced air oven at 110 ℃ for 12 h and weighed again for dry weight (DW) determination.

2.6. Dye uptake and transport

The rate of dye uptake and transport was determined based on the method of Essiamah and Eschrich (1986). At each stage of bud development, 18 canes (3 canes from each of 6 vines) were collected from the field, and immediately taken into the laboratory. Each cane was cut under water into 15 cm lengths with 2 buds. The canes were placed with their base in a reservoir of apoplastic dye solution consisting of 15 mL 0.5% solution of acid fuchsin dye. Dye uptake into the cane and the top bud after 1, 3, 5, 10 and 15 h was recorded.

2.7. Anatomy and histology of buds and canes

The anatomical structure of buds and canes was studied using fresh free-hand sections and paraffin sections as described by Bondada and Keller (2012) and Ruzin (1999). For fresh free-hand sections, transverse and longitudinal sections were cut using a new double-sided razor blade and transferred to a 5% NaOH solution at room temperature and held for 7 days to make the sections clear. For the paraffin sections, the experimental material was fixed using FAA, and then cut into 10 µm thick sections. The sections were then observed under a fluorescence microscope (Carl Zeiss, Thornwood, NY) equipped with a digital camera (DXM 1200 C; Nikon Instruments, Melville, NY), which was used to capture digital images.

2.8. Statistical analysis

A one-way ANOVA (SPSS 19.0) was used for comparisons of changes among different developmental stages. All the acquired data were expressed as the mean (M) ± tandard error (SE).

3. Results

3.1. Major stages of dormant bud break

As temperature increased in the spring, buds broke dormancy and started to grow. We observed the entire process of bud break in grape, and identified five major stages based on distinct changes in bud morphology (Fig. 1). Stage I: dormant bud, before bud breaks in spring, the buds were hard, compact, and contained pubescence (tomentum), which protected the tender primordia (Fig. 1A and a). Stage II: start of swelling, the apex of bud scales was broken, and the white wool-like tomentum was seen from the split. During this stage, the compressed shoot in the bud started to grow, the bracts at the base of the bud started to swell, and the tomentum in the bud appeared less compact than stage I (Fig. 1B and b). Stage III: bud scales started to open, with sustained swelling of the bud and gradually lost their protective function (Fig. 1C and c). Stage IV: woolly bud, the bud scales disappeared from the bud or only covered the base of the bud, and the bud was still covered by woolly tomentum. Compared to stage III, there was greater growth in bud width and length (Fig. 1D and d). Stage V: rosette of leaf tips visible, the green leaf tip was seen through the wool and the compact shoot showed an accelerated elongation (Fig. 1E and e).

3.2. Changes in bud growth and water content during bud development

Bud length was measured to evaluate the size of bud swelling. Bud elongation started in stage II, but the rate of growth was slow during stage II and III, then accelerated in stage IV and V (Fig. 2). Associated with bud swelling was an increase in water content and fresh weight, but the increase of bud dry mass was slower (Fig. 2). During the breaking of bud dormancy, water content of the bud changed