



## Circadian regulation of grapevine root and shoot growth and their modulation by photoperiod and temperature

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### ABSTRACT

Some plant species demonstrate a pronounced 24 h rhythm in fine root growth but the endogenous and exogenous factors that regulate these diel cycles are unclear. Photoperiod and temperature are known to interact with diel patterns in shoot growth but it is uncertain how these environmental factors are interrelated with below-ground growth. In this particular study, the fine root system of two grapevine species was monitored over a period of ten days with a high resolution scanner, under constant soil moisture and three different photoperiod regimes. Pronounced diel rhythms in shoot and root growth rates were apparent under a fixed 14 h photoperiod. Maximal root growth rate occurred 1–2 h prior to- and until 2 h after the onset of darkness. Subsequently, during the latter part of the dark period, root growth rate decreased and reached minimal values at the onset of the light period. Relative to 22 °C, exposure to a 30 °C air and soil temperature halved root growth but stimulated shoot growth. Notably, the shoot extension rate peak shifted from late afternoon to midnight at this higher temperature zone. When plants were exposed to a delayed photoperiod or progressively shortening photoperiod, the diel changes in root growth rate followed the same pattern as in the fixed photoperiod, regardless of whether the plant was in light or dark. This suggests that light was not the predominant trigger for stimulating root elongation. Conversely, shoot growth rates were not fixed to a clock, with minimum growth consistently at the completion of the dark period regardless of the time of day. In summary, fine root growth of grapevines was found to have a pronounced diel pattern and an endogenous circadian clock appears to orchestrate this rhythm. Soil temperature modified the amplitude of this pattern, but we argue here that, as evidenced from exhausted starch reserves within root tips by early morning, carbon supply from photosynthesis is also required to maintain maximum root growth.

### 1. Introduction

Due to the rotation of the Earth, diel cycles (having the duration of 24 h) have evolved within living organisms. Plant growth is greatly rhythmic with respect to the time of day and accordingly many physiological and biochemical parameters are modulated in concert with the diel cycle (Head, 1965; Geiger and Servaites, 1994; McClung, 2001; Yazdanbakhsh et al., 2011; Simon and Dodd, 2017). The circadian clock is an endogenous, self-sustained 24 h clock that allows an organism to anticipate and adapt to the daily changing environment, such as sunrise. These circadian rhythms persist despite the absence of external cues such as light and temperature. One feature of this endogenous

clock, however, is that it can be entrained and corrected by these environmental cues (McClung, 2001; Bording et al., 2016).

The first pivotal study describing diel patterns of fine root growth in plants dates back to 1965, focusing on cherry (*Prunus avium*) (Head, 1965). Using time-lapse movies, with four hour intervals, it was observed that root extension rates peaked between late afternoon and the onset of darkness with minimum root growth between morning and noon. A subsequent field study on five perennials, including grape, apple, poplar, quince and red pine (Hilton and Khatamian, 1973) revealed that elongation rates during the day and night varied over the course of the growing season. In late spring and midsummer, roots of all five woody plants grew faster at night than during the day, but in late

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summer and autumn only quince continued in this pattern. Environmental factors such as temperature likely had a significant influence on these diel growth patterns but since they were not monitored it is difficult to ascertain their relative role compared with endogenous mechanisms.

Since those earlier studies, endogenous circadian control over diel root growth has been well established in *Arabidopsis*. Diel rhythms in root tip growth of this model plant indicates highest growth rates one hour before dawn and a minimum at dusk (Yazdanbakhsh and Fisahn, 2011). These diel patterns persisted even under constant environmental conditions, signifying self-sustained control that incorporates the regulated degradation of starch at night (Graf et al., 2010; Smith and Stitt, 2007). It was further demonstrated that in hydroponically grown mature plants the root growth clock is organ specific with communication between the clocks of the different organs (James et al., 2008). However not all species display rhythmic root growth under constant conditions. Young *Zea mays* (Walter et al., 2002), *Nicotiana tabacum* (Walter and Schurr, 2005), *Oryza sativa* and *Sorghum bicolor* (Iijima et al., 1998) seedlings failed to show circadian growth. This absence may possibly be related to the different carbohydrate partitioning and metabolism mechanisms that are characteristic of newly emerged seedlings relative to the mature *Arabidopsis* plants (Wardlaw, 1990). In the structural roots of the grapevine, starch is stored in both phloem and xylem ray parenchyma cells and these are mobilised at budburst in spring to support canopy development and root growth (Holzapfel et al., 2010; Rogiers et al., 2011). Because of the strong relationship between root growth and carbohydrate mobilisation in grapevines, it appears that photoassimilates are not critical to below-ground growth early in the season when leaves are still immature (Clarke et al., 2015).

The substrate in which root growth takes place may also play a role in extension rates and patterns. Considering that non-destructive diel monitoring within an intact soil can be complex, even with mini-rhizotrons and sophisticated image acquisition techniques (Taylor et al., 1990; Le Bot et al., 2010), most studies have used either hydroponically grown plants or a transparent medium to facilitate the time-lapse visualisation and calculation of the small diel changes in growth rates (Wells et al., 2012). These results may, however, differ from roots grown in a more natural soil medium that confers mechanical resistance to penetration by the root tip. Advances in PET (Jahnke et al., 2009), X-ray CT (Mooney et al., 2012) and MRI (van Dusschoten et al., 2016) have allowed the 3-D visualisation of root architecture in a soil column but these techniques are not readily available and are often limited to small root systems. Accordingly, new cost-effective, accessible tools and techniques are sought to overcome the limitations of monitoring root growth in plants.

Using a modified high-resolution scanner, the results of three controlled environment studies are presented here for established grapevines in a soil medium to assess the presence or absence of rhythmic root growth and to better characterize the role of light and temperature on this growth. The first study addresses the impact of temperature by exposing plants to a fixed 14 h photoperiod and an increase in 10 °C soil temperature over 5 out of 10 days. The second study investigates the role of the day/night cue by delaying the light period by 4 h every second day but maintaining a 14 h light period and constant soil temperature. The third study examines the role of day length by shortening the light period by 4 h every second day until vines were grown in constant darkness. These vines were also maintained at a constant soil temperature.

## 2. Materials and methods

### 2.1. Culture of plants

Virus free cuttings of own-rooted *Vitis vinifera* (cv. Shiraz) and *Vitis champinii* (cv. Ramsey) were propagated in perlite at approximately 22–26 °C under glasshouse conditions. After 40 days, the plants had

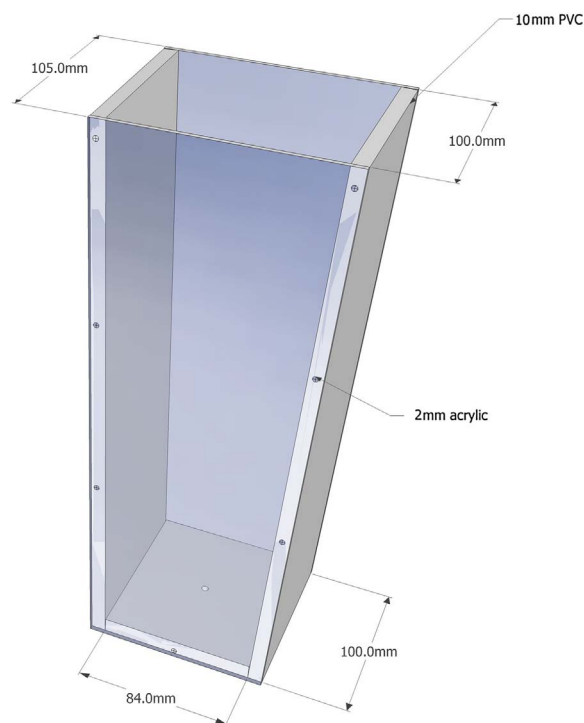


Fig. 1. A schematic diagram of the purpose-built transparent pots used to image root growth.

developed sufficient roots and were planted into 5L pots using a commercial potting mix. The vines were watered daily to field capacity using an automatic irrigation system and fertilized fortnightly with 50 mL per vine of 10:1 diluted complete liquid fertilizer (MEGAMIX PLUS®). To prevent powdery mildew and blister-mite infections, the vines were sprayed with sulphur (5 g/L) every 14–28 days during the growing season.

Following one year of establishment, 10 similar sized vines of each species were selected. During dormancy, the vines were pruned to two buds and replanted into transparent pots. The plants were removed from the pot and the soil was carefully washed from the roots. The roots were trimmed to half the original length and the plants were weighed prior to re-planting in the transparent pots filled with a premium garden mix.

### 2.2. Transparent pot assembly

Purpose-built pots were designed to allow visual observation and measurement of growing roots. The pots had a rectangular cross section with top dimensions of 130 × 100 mm, height of 310 mm, and tapering to a square base of 100 × 100 mm (Fig. 1A). Two transparent sides were composed of a 2 mm thick clear acrylic plastic sheet screwed to the body frame (Fig. 1B). For the two non-visible sides and base section, 10 mm thick grey polyvinyl chloride was used. After the plants were potted in these transparent pots, they were placed into larger 50 L black plastic pots in sets of four (Fig. 1C) on a 5 cm layer of gravel to provide free drainage. The remaining space between the four pots was filled with fine sand in order to keep the pots in position and to protect the acrylic plastic and emerging roots from direct sunlight. Aside from *V. vinifera* and *V. champinii*, two other species were inserted into each black container so that each container had a total of four species, however only the first two were monitored for root growth due to time constraints. Two shoots on each plant were trained vertically on bamboo stakes and lateral growth was removed.

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