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Grapevine bud fertility and number of berries per bunch are determined by water and nitrogen stress around flowering in the previous year

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ABSTRACT

Grapevine yield formation extends over two consecutive years (seasons 1 and 2). The inflorescence formation (around flowering in season 1) is crucial as it is involved in the formation of both the bunch number per vine and the berry number per bunch in season 2, that account for about 60% and 30% of year-to-year yield variation of grapevine, respectively. Light, temperature, water and nitrogen availability are known to affect this early stage. The aims of this work were to determine the critical periods during which inflorescence formation is sensitive to water and nitrogen stress and quantify their effects on it. To address these issues, we used a 3-year (2010–2012) field experiment (cv. Shiraz) in combination with a water balance simulation model (WaLIS) and a 6-year field experiment (cv. Aranel). In both experiments, different treatments were applied to create a gradient of water and nitrogen supply (treatments involved cover cropping, irrigation and fertilization). The grapevine yield and its components were recorded. Water and nitrogen status of grapevine were monitored throughout the season. Inflorescence formation was sensitive to water and nitrogen stress during a critical period that occurred between 400 and 700 °Cd after budburst in season 1. Bud fertility (number of bunches per shoot) and berry number per bunch in season 2 were significantly correlated with the fraction of transpirable soil water (FTSW), predawn leaf water potential and leaf nitrogen content at that time for both cultivars. Water and nitrogen stress during the critical period of season 1 determined 65–70% of grapevine yield in season 2. Our results show that the maximum yield that can be reached in season 2 is determined during the critical period of season 1 and they provide clues to estimate it. These results may help grape growers to adapt their practices (i) in season 1 to ensure a sufficient maximum yield for season 2 and (ii) to actually obtain the targeted yield in season 2 depending on the maximum yield determined in season 1.

1. Introduction

Yield formation of fruit trees usually takes place over two consecutive years. The first step of this process is floral induction, followed by flower initiation and differentiation (Wilkie et al., 2008). This early step of yield formation defines the potential number of fruits the crop will bear during the subsequent year. This is of economic importance as the number of harvestable organs is generally the major determinant of crop yield (Peltonen-Sainio et al., 2007). This has also physiological implications because the number of growing fruits has a strong impact on the ratio between the activities of assimilate sources and sinks and on the ratio between vegetative and generative growth, which have been found to be major processes of plant growth and development (Mathieu et al., 2008; Marcelis et al., 1998; Pallas et al., 2010). Moreover, variations in the number of growing fruits not only have a direct effect on yield but may have undesirable effects on the size and quality of harvested organs (Kliewer and Dokoozlian, 2005; Monselise and Goldschmidt, 1982). Numerous factors are known to affect the formation of flowers. The vegetative and reproductive growth during the current year may interact with the development of flowers for the next year depending on the timing of floral induction. The alternate-year bearing phenomenon observed on numerous fruit tree species results from endogenous factors involved in this interaction (Monselise and Goldschmidt, 1982; Wilkie et al., 2008). Other factors are directly linked with weather conditions such as temperature, light, water deficit or mineral nutrition. Little is known about the quantitative effects of these

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factors, and the understanding of year-to-year yield variations and their management remains a challenge for perennial fruit crops (Hanke et al., 2007; Meilan, 1997; Wilkie et al., 2008), especially for grapevine (*Vitis vinifera* L.) as shown by recent studies (Keller, 2010; Clingeleffer, 2010).

Grapevine yield formation extends over two consecutive years. Thereafter, they will be referred to as season 1 and season 2, season 2 being the year of production. Seasonal variations in grapevine yield usually exceed 15% and often 35% (Antcliff, 1965; Clingeleffer, 2001, 2010; Keller and Mills, 2004; May, 1961; Chloupek et al., 2004). It is now well established that the main drivers of grapevine yield are the bunch number per vine and the berry number per bunch, which account for about 60% and 30% of seasonal yield variation respectively, whereas the berry weight accounts for only about 10% of seasonal yield variation (Dry, 2000; Clingeleffer, 2001, 2010). The determination of bunch number and berry number per bunch are therefore two key processes in grapevine yield formation, and both are affected during the early stages occurring in season 1.

Grapevine is a perennial species displaying an indeterminate development pattern. Each phytomer produced by a growing shoot in season 1 bears a latent bud that will develop into a shoot in season 2. Grapevine yield formation starts with inflorescence formation in the latent buds during season 1. This process is regulated at two levels: formation of uncommitted primordia (also called anlagen) and differentiation of the uncommitted primordium into an inflorescence or a tendril (Vasconcelos et al., 2009; Carmona et al., 2008). Inflorescence primordia are formed by extensive branching of the anlage (Vasconcelos et al., 2009; Srinivasan and Mullins, 1981): bud fertility (number of bunches per shoot) and flower number per bunch are closely linked, as primary branching of inflorescences exerts a strong control over the total number of flowers per inflorescence (Dunn and Martin, 2007). This stage is reported to last from a few weeks after budburst until veraison in season 1 (about 3 months), depending on the insertion rank of the latent bud on the shoot (Vasconcelos et al., 2009). At the scale of the shoot axis, the level of differentiation follows an acropetal gradient where the distal inflorescences are less differentiated than the proximal. After veraison of season 1, the latent buds enter into dormancy. They resume their development at budburst in season 2 with resumption of inflorescence branching and differentiation of individual flowers before anthesis (Swanepoel and Archer, 1988; Watt et al., 2008; Srinivasan et al., 1972). The relative importance of branching prior to dormancy, compared with differentiation during budburst, in controlling potential inflorescence size and flower numbers is still poorly understood (Vasconcelos et al., 2009; Keller et al., 2010).

In grapevine, unlike other perennial crops, there is no evidence of competition between on the one hand initiation and differentiation of inflorescences for the following season and on the other hand the development of flowers and fruit set for the current season (Vasconcelos et al., 2009). Along with genetic potential, insertion rank on the shoot is the main factor affecting bud fertility: it increases from the base to the middle and decreases again toward the tip of the shoot (Huglin and Schneider, 1998). Light, temperature, grapevine water status and mineral nutrition are also reported to affect the formation of inflorescences during season 1 (Vasconcelos et al., 2009). Light and temperature have been the most studied factors. Quantitative relationships between temperature and bud fertility were established (Buttrose, 1970) and an optimum range of temperatures for the formation of inflorescence primordia ($20\,^{\circ}\mathrm{C} < T < 35\,^{\circ}\mathrm{C}$) was defined (Vasconcelos et al., 2009). Low irradiance on latent buds reduces inflorescence formation; this effect is likely mediated by carbon status and assimilate supply to the buds (Keller and Koblet, 1995; Dry, 2000; Lebon et al., 2008). Effects of water deficit and mineral nutrition on inflorescence formation during season 1 have been observed but never quantified according to the stress intensity. Water deficit reduces bud fertility whatever the bud position on the cane (Alleweldt and Hofacker, 1975; Buttrose, 1974; Matthews and Anderson, 1989). Buttrose (1974) observed a decrease in bud fertility of 75% (insertion rank 2) for the most stressed treatment compared to the well watered one. Nitrogen deficiency reduces inflorescence formation, and it is generally accepted that an optimum supply of nitrogen (N) is necessary for maximum formation of inflorescence primordia and differentiation of flowers (Vasconcelos et al., 2009; Keller and Koblet, 1994; Keller, 2005; Khanduja and Balasubrahmanyam, 1972; Baldwin, 1966; Srinivasan et al., 1972; Carmona et al., 2008).

The present study was based on the hypothesis that water and nitrogen stresses experienced in the field by the grapevine during season 1 are responsible for a major part of the seasonal variations in bud fertility and berry number per bunch in season 2 (assuming no adverse weather conditions at anthesis in season 2). This hypothesis is supported by the high sensitivity of vegetative organogenesis processes to water (Chapin, 1991; Wery, 2005; Muller et al., 2011; Bissuel-Belaygue et al., 2002a) and nitrogen (Lawlor, 2002; Lemaire and Millard, 1999; Gastal and Lemaire, 2002) stress for a wide range of plants and for grapevines in particular (Pellegrino et al., 2006; Lebon et al., 2006; Cramer et al., 2013).

The aims of this work were to (i) study the periods of sensitivity to water and nitrogen availability of bud fertility and berry number per bunch and (ii) quantify the effects of water deficit and nitrogen stress on these yield components during these critical periods. A 3-year field experiment on Shiraz grapevines in combination with a water balance simulation model and a 6-year experiment on Aranel grapevines were used to address these issues.

2. Materials and methods

2.1. Experiment 1

2.1.1. Experimental site and design

Experiment 1 was carried out from 2010 to 2012, during three growing seasons, on a vineyard located near Montpellier (Domaine du Chapitre) in the south of France (43°32′ N; 3°50′ E). The climate was Mediterranean with a mean annual rainfall of 700–750 mm. Soil was a deep, calcaric (mean total $CaCO_3$: 10%) fluvisol (FAO classification). It was a clay loam (30% clay, 40% silt and 30% sand) containing less than 5% of coarse elements. Mean organic matter content was about 1.5% and total nitrogen was less than $1\,\mathrm{g\,kg^{-1}}$ over the top soil layer (0–30 cm). Grapevines (*Vitis vinifera* L. cv. Shiraz) were planted in 2002, in rows oriented *NW–SE* at a density of 3333 stocks per hectare (2.5 m × 1.2 m). They were trained using a midwire bilateral cordon system to a height of 0.7 m. Vines were spur pruned to 12 nodes per vine (6 spurs and 2 nodes per spurs). About one month after bud burst, number of shoots per vine was manually adjusted to a target of 12 shoots per vine. Five treatments were designed to create a gradient of soil resources (water and nitrogen). These treatments are described below and ordered from low to high resource availability. Mechanical weed control was applied under all vine rows. A first treatment (AL) was obtained by sowing a mix of annual medics (*Medicago truncatula*, *M. rigidula*, *M. polymorpha*) in the inter-row during autumn 2009. A second treatment with bare soil (BS) was obtained by mechanical weeding in the inter-row. There was no fertilization or irrigation in these two treatments. Three other treatments were obtained by applying irrigation and fertilization on bare soil plots. One was fertilized (FERT), one was irrigated (IRR) and one was irrigated and fertilized (IRR-FERT). Irrigation and/or fertilization were applied in 2011 and 2012, not in 2010, but the vines were monitored over the 3 years. Therefore, the effects of a change in management practices could be studied. When applied, fertilization was provided by applying