



Fruit load in almond spurs define starch and total soluble carbohydrate concentration and therefore their survival and bloom probabilities in the next season



Eduardo Fernandez^a, Graeme Baird^b, Daniela Farías^a, Eduardo Oyanedel^a, José A. Olaeta^a, Patrick Brown^c, Maciej Zwieniecki^c, Aude Tixier^c, Sebastian Saa^{a,*}

^a Escuela de Agronomía, Pontificia Universidad Católica de Valparaíso, Casilla 4-D, Quillota, Chile

^b Department of Environmental Studies, University of California, Santa Cruz, CA, USA

^c Department of Plant Sciences, University of California, Davis, CA, USA

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ABSTRACT

Nonpareil almonds trees have compact shoots, known as spurs. Spurs are the main bearing structure of many fruit trees. However, in almonds, spurs show alternate bearing and low winter survival if fruit load is high or if leaf area is low at the spur level. To better understand the source sink relationships that govern the effects of fruit load on spur survival and return bloom, a total of 1920 spurs with varying fruit load (non-fruiting spurs, one fruiting spurs, two fruiting spurs, and one fruiting spurs de-fruited at 40 and 70 days after full bloom) were labeled and tracked for two seasons in fully mature trees. Spur variables such as leaf area, total soluble carbohydrates (TSC), starch concentration, winter survival and return bloom were collected and analyzed with generalized linear mixed models and structural equation models. Starch concentration in non-fruiting spurs (excluding de-fruited spurs) was twice as high as starch concentration of fruiting spurs. Similarly, in the following season, the probabilities of survival and bloom in non-fruiting spurs were 55% and 61% higher than fruiting spurs, respectively. Structural equation modeling suggests that starch concentration in a spur is correlated with spur leaf area, number of fruits, fruit weight, and TSC. Thus, this work improves our understanding of return bloom and winter spur survival.

1. Introduction

In mature almonds (*Prunus dulcis* [Mill] DA Webb.), spurs (short proleptic shoots that can have both leaves and flowers) are the main reproductive structure. Spurs are considered semi-autonomous in terms of carbon assimilation and, therefore, in the accumulation of starch, survival and flowering (Heerema et al., 2008; Lampinen et al., 2011; Saa et al., 2017; Tombesi et al., 2015; Valdebenito et al., 2017b). According to Lampinen et al. (2011), the probability of survival and return bloom for fruiting spurs is 54% and 14%, respectively. Lampinen et al. (2011) and Tombesi et al. (2015) demonstrated that these low rates are associated with the leaf area of the spur during the previous season. Lampinen et al. (2011) found that a spur leaf area of at least 28 cm² is necessary for the survival of the spur into the following season, and an area of at least 45 cm² is necessary for the spur to bloom. However, spur leaf area is negatively affected by the fruit presence in the same season at the spur level (Heerema et al., 2008; Saa and Brown, 2014; Tombesi et al., 2015). The presence of fruits on spurs also significantly reduces

spur leaf area due to preferential use of carbohydrates and nutrients by fruits during their development (Tombesi et al., 2015). Evidence from Tombesi et al. (2015) indicates that the hierarchy between fruit and the vegetative parts of a spur is of such a great magnitude that leaf area of spurs with four fruits is 75% less than leaf area of those non-fruiting spurs. Along the same lines, Saa and Brown (2014) demonstrate that the presence of two almond fruits significantly reduces CO₂ assimilation starting 55 days after full bloom (DAFB). This reduction, is explained because the fruits compete for resources to the detriment of source capacity throughout the season. This not only diminishes the leaf area of the fruiting spurs, but also the nitrogen concentration of their leaves (Heerema et al., 2009; Saa and Brown, 2014; Saa et al., 2017; Valdebenito et al., 2017b).

CO₂ assimilation occurs in plant leaves, which are considered source organs of carbohydrates for the rest of the organism when they reach physiological maturity (Marchi et al., 2008; Naschitz et al., 2010). These carbohydrates could be used immediately or stored as Starch. Starch is the main reserve carbohydrate in vascular plants (Bahaji et al.,

* Corresponding author.

E-mail address: sebastian.saa@pucv.cl (S. Saa).

2014). Previous studies have shown the contribution of starch as an energy source during flowering, budding, pollination, and fruit setting in both perennial and deciduous species (Boldingh et al., 2016; Guerra and Rodrigo, 2015; Klein et al., 2016; Tixier et al., 2017). Similarly, starch hydrolysis provides soluble carbohydrates that allow the survival of perennial structures (Dietze et al., 2014), or support periods of stress (Martinez-Vilalta et al., 2016). Specifically, in the genus *Prunus*, as flowering occurs before the emergence of leaves (or when they are immature), starch consumption must be utilized as an important energy source (Kuhn, 2006).

Independent of the origin of the carbohydrates (whether they are produced in leaves of the same season or whether they come from the stored reserves of the plant from the previous season) they are transported to the organs of the plant that cannot satisfy their energy requirement by themselves. These organs, known as sinks, are principally wood growth of the main stem and vegetative growth of twigs, flowers, fruits and roots (Berman and Dejong, 2003). These organs are structures that require carbohydrates to achieve their development potential (Erel et al., 2016; Haouari et al., 2013). If, however, the supply of carbohydrates is limited (i.e., low leaf area), or the demand is excessive (i.e., high fruit demand) there is a hierarchy of preferential supply to developing parts that is spatially and temporally dynamic among sinks (Reyes et al., 2016). This hierarchy results in a differential carbohydrate distribution that depends on the dynamic demand of each of these organs (Bihmidine et al., 2013; Marcelis, 1996). The dynamic demand depends on the number of sinks of the same type, the size of each of them, and their activity among other factors.

Manipulation of source/sink relationships has been studied before in several plant species. For example, in citrus plants, Martinez-Alcantara et al. (2015) recorded 2.4 times more shoots in trees without a crop load than trees with fruits. Similarly, in sweet cherry (*Prunus avium* L.) Usenik et al. (2010) showed an improvement in final fruit soluble sugars and fruit size when leaf:fruit ratio went from 0.7:1 (control treatment) to 3:1. On the other hand, Saa et al. (2017) reported an increase of 2.1 times in spur leaf area and an increment of 0.6% in leaf nitrogen concentration in two-fruiting almond spurs when soil nitrogen rate went from 140 to 392 UN ha⁻¹. This, could mean an important increase in source capacity of these spur types (Saa and Brown, 2014).

Growth regulators have also shown to have an effect in source/sink relationships. Specifically, antigibberellins such as paclobutrazol have been used to manipulate flower and fruit set status in avocado (*Persea Americana* Mill.) (Whiley et al., 1991; Wolstenholme et al., 1990) and in mango (*Mangifera indica* L.) (Blaikie et al., 2004; Upreti et al., 2013; Winston, 1992). In avocado paclobutrazol has been applied at flowering to improve fruit set by stopping shoot growth and thus reducing the competition between fruit and shoots early in the season (Whiley et al., 1991). In mango, paclobutrazol has been applied prior to bloom to induce flowering and thus reduce alternate bearing (Upreti et al., 2013). Among other effects, the application of paclobutrazol positively increased the carbon to nitrogen ratio and the cytokinin content (another growth regulator) of the treated buds, which promoted higher flowering in the following year (Upreti et al., 2013). In cherry trees, however, trunk painting of paclobutrazol reduced shoot growth and tree height, with no benefit on flower initiation, but promoted an earlier bloom (Jacyna, 2007).

Cytokinins are growth regulators mainly synthesized in root meristems, and to a lesser extent by shoot meristems and seed embryos (Lynch et al., 2012). Cytokinins have shown to improve return bloom in lychee (*Litchi chinensis* L.) (Chen, 1991), apples (*Malus domestica* Borkh) (Ramirez and Hoad, 1981) and pecan (*Carya illinoensis*) (Wood, 2011). In young apple trees, applications of cytokinin (zeatin) improved flowering in long shoots (Skogerbo, 1992). In mature apple trees, zeatin applications on individual spurs significantly promoted flower initiation (Ramirez and Hoad, 1981). In pecan, applications of the cytokinin 6-benzylaminopurine in conjunction with an auxin

transport inhibitor prior to kernel filling improved return bloom compared to the control trees (Wood, 2011). In kiwifruit (*Actinidia arguta*), the use of cytokinin (forchlorfenuron) is widely used to improve fruit size (Kim et al., 2006), but no current literature has reported positive effects of forchlorfenuron applications on return bloom.

In almond trees var. Nonpareil, flower bud initiation occurs approximately 150–180 days after full bloom (DAFB) (Lamp et al., 2001). This phenological stage coincides with the presence of newly matured seeds (kernels) that might inhibit return bloom through hormone production or through negatively affecting nutrient and/or carbohydrate demand (Tombesi et al., 2011). In almonds, spur leaf area is defined in spring and no further growth occurs after that period. Therefore, a foliar spray of paclobutrazol during the period of kernel filling (summer) may induce flower initiation by inhibition of the endogenous production of gibberellins from the seed, while an application of cytokines might promote bloom at the following season. Foliar nitrogen sprays in summer may mitigate the nitrogen competition that occurs at the spur level during the period of kernel fill (Saa and Brown, 2014) and thus improve spur survival or return bloom.

2. Materials and methods

2.1. Selection of the site, plant material and experimental design

A commercial orchard of mature almond trees (thirteen-year-old ‘Nonpareil’ trees grafted onto nemaguard rootstock) in the sixth region of Chile (34° S, 70° W) was used for a two season experiment. Ninety-six homogeneous trees were selected from the orchard. In each tree, four spurs were chosen of each spur type. The spur types were: F(0) (non-fruiting spurs); F(1/40) (one fruiting spurs, de-fruited at 40 DAFB); F(1/70) (one fruiting spurs, de-fruited at 70 DAFB); F(1) (one fruiting spurs); and F(2) (two fruiting spurs). In the first season, a total of 1920 spurs were tagged (spring of 2016), of which 480 were destructively sampled in the summer of 2017. Of the remaining 1440 spurs, 1366 spurs were recovered in the second season. F(0) spurs were labeled at green tips while the other spur types were at “pink bud” phenological state in winter of 2016, while the other categories were labeled after the first natural fruit drop occurred, in October of 2016. The fruits of F(1/40) and F(1/70) spurs were manually removed at 40 DAFB and 70 DAFB, respectively. Spurs were marked on the north and south sides of the tree (between rows) at a height of 1.5 to 3.0 m, on the outside of the canopy. Spurs were monitored from winter 2016 (season 2016–2017) to spring 2017 (season 2017–2018) to record survival and return bloom probabilities by visually inspecting each tagged spur.

The experimental layout used a completely random block design, with a split-split plot factorial structure. The experiment consisted of the following three factors: foliar nitrogen (two levels), as the main plot; application of growth regulators (four levels), as a sub plot; and type of spur (five levels), as a sub plot. The levels of each factor were: foliar application of nitrogen (N) (N + indicates 3 applications of Urea-Triazone, in doses of 3600 ppm; N- indicates no application of foliar N); foliar application of growth regulators (Ck + indicates 3 applications of 6-benzyladenine, in doses of 25 ppm; Un + indicates 3 applications of uniconazole-P, in doses of 281 ppm; CU + indicates 3 applications of Ck + plus 3 applications of Un +; H- was the control, without application); and type of spur (F(0); F(1/40); F(1/70); F(1); F(2)). Six blocks of 16 trees each were used. The application factor for N was randomized to a group of 8 trees, while the application factor for growth regulators was randomized to a group of two trees, and finally, the spur type factor was randomized at the tree level. In each tree was selected four spurs per category.

2.2. Measurements of vegetative variables

Total length, current season spur growth, and number of leaves of each spur were measured non-destructively before Hull Split. The total

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