Scientia Horticulturae 130 (2011) 357–372

Contents lists available at ScienceDirect

Scientia Horticulturae

journal homepage: www.elsevier.com/locate/scihorti

Review

Dormancy in temperate fruit trees in a global warming context: A review

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ARTICLE INFO

Article history:
Received 16 November 2010
Received in revised form 22 June 2011
Accepted 5 July 2011

Keywords:
Adaptation
Chilling requirements
Climatic change
Dormancy
Phenology
Temperate fruit

ABSTRACT

Dormancy is the mechanism that plants use to protect sensitive tissue from unfavourable climatic conditions. In a changing global environment, temperate fruit crop adaptation might be at risk due to changes in temperature cues. A complete picture of dormancy is shown in this review, using results from the early, pioneering work to the molecular basis, also emphasising dormancy modelling and measurement and their implication in temperate fruit production. This description is completed by the variability that climatic change might induce in plants through direct or indirect changes in dormancy. Future avenues for the correct adaptation of temperate fruit crops are proposed that span basic questions, from temperate fruit distribution to more-applied questions of dormancy, such as application of rest-breaking agents, depth-of-dormancy markers, breeding strategies, cross-pollination and host–pest interaction. In the context of global climate change, a linkage among the cited fields is intended in this review in order to raise awareness in the scientific community.

Contents

1. A brief introduction to dormancy

Dormancy in temperate-zone deciduous fruit trees is a phase of development that allows trees to survive unfavourable conditions during the winter (Faust et al., 1997). Diverse factors can lead to meristem inactivity. For example, unfavourable environmental conditions, such as chilling temperatures or short photoperiod, generally induce this inactivity. Temperatures or day lengths below a certain threshold impede the processes that lead to growth and prevent any external indication of activity. Nonetheless, physiological activity does not subside altogether. Activity during the dormancy season affects future potential development and growth. Processes that inhibit the development of other vegetative

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Abbreviations: ABA, abscisic acid; CO/FT, constant/flowering locus T module; CA, chilling accumulation; CR, chilling requirements; CU, chill units; DMO, 5,5-dimethyl-oxazolidine-2,4-dione; DAM genes, dormancy-associated MADS-box genes; FLC, flowering locus C; GA, gibberellins; HR, heat requirements; PHY, phytochrome; TDZ, thidiazuron.

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doi:10.1016/j.scienta.2011.07.011

meristems are well known. These processes are catalogued as apical dominance or inhibition, such as that imposed by leaves on axillary buds. For example, in peach, earlier defoliation in summer can result in forced bloom (Lloyd and Couvillon, 1974). Globally, these processes are known as correlative inhibition. Correlative inhibition is external and usually occurs at a distance from the inhibited meristem. This inhibition mechanism generally operates in all woody plants, independent of their origin or adaptation areas, and frequently has substantial implications for the morphogenetic factors that determine tree structure (Champagnat, 1983). At the beginning of the 20th century, Coville (1920) pointed out an unusual phenomenon that equally affected both native shrubs and trees from cold, northern areas. Coville (1920) found that trees kept in greenhouse conditions for breeding purposes during winter also stopped their growth in autumn, shed their leaves and entered into dormancy without the progressive effect of low temperatures. Equally unusual was the fact that the plants grown in greenhouse conditions were unable to flower in spring. This finding suggested a type of growth inhibition and developmental phase characteristic of the woody species specifically grown in temperate zones with well-defined seasons. This type of inhibition confers endurance in unfavourable winter conditions and, most importantly, delays the reproductive processes, i.e., flowering and fruit set, ensuring the survival and reproduction of the individual.

Unlike the characteristics of apical dominance and dormancy associated with unfavourable environmental conditions, this inhibition seemed to be caused by an endogenous factor of the meristem, present in both vegetative and reproductive buds. Chouard (1956) attempted to classify the different causes of the growth inhibition observed in woody, temperate species. He defined the following groups: quiescence, which is inhibition determined by environmental conditions; correlative inhibition, which is inhibition mediated through dominance between different parts of the plant; and dormancy, which is inhibition controlled by a mechanism that resides in the inhibited structure itself. Subsequently, Saure (1985) defined these inhibitions as imposed dormancy, pre-dormancy and true dormancy. Lang et al. (1987) proposed the classification scheme that is most often used today. They classified the inhibitions as ecodormancy, which is found in late winter and spring and imposed by temperatures unfavourable to growth; paradormancy, which is equivalent to correlative inhibition or apical dominance; and endodormancy, which is deep dormancy or winter dormancy. The last is the genuine dormancy that characterises woody plants in temperate zones and has been the subject of many studies that have shown the enormous complexity of this phenomenon (Fig. 1).

2. Dormancy modelling

After an initial stage, during which the adaptation problems associated with partial endodormancy release were attributed to diverse causes (Weldon, 1934), these problems progressively came to be associated with climatic conditions. As Coville (1920) indicated, there is a relationship between dormancy release and the action of low temperatures. Despite initial disagreement regarding the temperature threshold for dormancy breaking, 45 °F (7.2 °C) was finally adopted (Samish, 1954; Vegis, 1964; Weldon, 1934). By approximation, 7 °C was adopted as the useful temperature threshold with respect to overcoming endodormancy. Concomitantly, the concept of the chilling requirement (CR) needed to overcome dormancy and to flower was established. This parameter was considered to be cultivar specific and was useful because the possibility of successfully adapting a cultivar to a pre-determined environment could be known beforehand (Samish and Lavee, 1962).

However, it was soon perceived that CRs tended to be highly variable and dependent on the year and location. This variability called into question its consistency and suitability for measuring the quantity of cold required to overcome dormancy over a particular period. New approaches were developed to solve this problem. Numerous proposals have been made, indicating the notable difficulties associated with delimiting this phenomenon. An important advance was the establishment of the Utah Model by Richardson et al. (1974), which assigned chill unit values to different temperature ranges. Subsequently, models adjusted with regard to the Utah Model were developed, such as the Low Chilling Model (Gilreath and Buchanan, 1981b) and the North Carolina Model (Shaltout and Unrath, 1983). Common elements among these proposals are the consideration of temperatures noticeably higher than 7 °C as useful for overcoming dormancy and the negative effect of temperatures above a certain threshold on the chill accumulated, especially when combined with low temperatures in a daily cycle (Couvillon and Erez, 1985a; Erez et al., 1979a, 1979b; Erez and Lavee, 1971; Overcash and Campbell, 1995). Cesaraccio et al. (2004) developed a model that considered temperatures from harvest to bloom and divided this period into chill days (rest) and anti-chill days (during quiescence). This model minimised the variability between predicted and observed data by selecting the most suitable temperature thresholds. The Dynamic Model (Fishman et al., 1987a, 1987b) was developed for the warm winters in Israel and is thought to be a milestone in dormancy modelling. This model aimed to include new advances in the understanding of dormancy (i.e., the effect of temperature cycles, fixed accumulation) and to solve the inaccuracy of the Utah Model in warm-winter areas. The main distinction from the Utah Model was the fixed accumulation of chill. The Dynamic Model assumes that chill accumulates by a two-step process. The first is the accumulation of an intermediate product promoted by cold temperatures. This process is reversed by warm temperatures. However, once a sufficient amount of the intermediate product has accumulated, Chill Portions are permanently accumulated. This two-step model was based on previous, temperature-controlled experiments. Erez et al. (1979b) showed that a limited period between the application of low and high temperatures is required for a negative effect of high temperatures. However, under field conditions, this period is usually long enough; therefore, low temperatures act in a permanent way and the negative effect disappears. Another important contribution implemented in the Dynamic Model was the establishment of the synergic effect of moderate temperatures (13–15 °C) when combined with low temperatures in daily cycles. Moderate temperatures do not have a positive effect on dormancy release by themselves, but when they occur after cold treatment, they substantially augment its positive effect (Erez and Couvillon, 1987; Guerriero et al., 1985).

Several modifications to the Utah Model (Richardson et al., 1974), have been presented. These modifications have arisen from the discovery of temperature effects that were originally not considered, the application of the model in species other than peach and the application of the model in areas with climatic conditions different from those in Utah. These factors led to dormancy progressions divergent from those initially postulated by the model (Linsley-Noakes and Allan, 1994; Shaltout and Unrath, 1983). CRs are influenced by diverse cultivar responses and conditioned by the contrasting dormancy intensity of different cultivars and year-to-year variation (Saure, 1985). This influence demands studies that include a high number of cultivars and annual repetitions to obtain solid conclusions about the suitability of the models. In a posterior phase, the inclusion of the latest advances has made it possible to formulate new, more complex and more accurate models. For example, Naor et al. (2003) have shown fairly disparate results in apple compared to previous reports: temperatures close to 0 °C