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Research Paper

Diverse patterns in dormancy progression of apple buds under variable winter conditions

Nigel C. Cook[a,1], Frederick J. Calitz[b], Laura A. Allderman[c], Willem J. Steyn[a,c], Esmé D. Louw[a,*]

[a] Dept. of Horticultural Science, Stellenbosch University, Stellenbosch, South Africa
[b] Agricultural Research Council Biometry-Unit, Pretoria, South Africa
[c] HORTGRO Science, Welgevallen Experimental Farm, Stellenbosch, South Africa

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ABSTRACT

Apple trees that do not receive adequate winter chill show poor bud break, uneven and delayed blooming that impact negatively on tree architecture and fruit production. Previous research indicates that the endodormancy progression of such trees differs from trees grown under adequate winter chill condition. This study aims to produce dormancy progression models for the diverse South African apple growing regions, including areas with inadequate winter chill. One-year-old ‘Granny Smith’ and ‘Royal Gala’ shoots were harvested from 24 farms across South Africa for five consecutive seasons and subjected to standard forcing conditions while monitoring the time to budbreak. A two linear joint line model was fitted producing 11 variables for each farm. Principle component and cluster analysis were used to further interpret the data. The results indicate a very diverse dormancy progression pattern across the South African apple growing regions. Three different dormancy progression clusters were identified. The clusters separate well according to maximum depth of dormancy and rate of dormancy release and could be partially explained by altitude. High laying areas showed a dormancy progression similar to that expected from areas with adequate winter chill and lower laying areas portraying significantly lower levels of endodormancy with protracted release periods. The results also indicated that the Utah chill model is not a reliable indicator of chill accumulation under these climatic conditions. Characterising the South African apple growing regions in terms of dormancy progression is not just a helpful tool for local orchard planning but also contributes to a better understanding of the impact of warmer winter conditions on apple production in general.

1. Introduction

Dormancy is defined as the temporary suspension of any visible signs of growth in any plant structure containing a meristem (Lang 1987). Bud dormancy is an adaptation of temperate zone trees enabling survival to unfavourable winter conditions and synchronisation of budbreak the following spring. The progression of bud dormancy is a continuum that starts after growth cessation and budset (completion of bud formation) in summer, increases to a maximum state and then decrease until budbreak in the following spring (Vegis 1963; Saure 1985). Lang et al. (1985) created dormancy terminology based on the site responsible for the growth inhibition. The prefixes eco-, para- and endo indicate that the inhibition can move from outside the plant (ecodormancy), to inside the plant but outside the bud (paradormancy) and to inside the bud itself (endodormancy). Although many factors can affect para- and ecodormancy it is believed that end odormancy is regulated by low temperature quantifiable as “chilling units” (CU) according to the Utah model and its derivates (Crabbé and Barnola, 1996; Fishman et al., 1987; Richardson et al., 1974; Shaltout and Unrath, 1983). Only once a certain amount of CU has accumulated will the so called ‘chill requirement’ be met and the bud will start growing once the spring temperatures become favourable.

The dormancy status of a bud can be quantified in a growth chamber by placing one-year old shoots collected from the orchard under controlled forcing conditions (constant 25 °C and continuous illumination) and monitoring the time needed for the buds to start spouting (Cook and Jacobs, 2000; Couvillon and Hendershott, 1974; Hauagge and Cummins, 1991a, 1991b;). The longer the time to budbreak, the deeper the dormancy level. Using this method to quantify dormancy, Hauagge and Cummins (1991b) reported that the dormancy progression curve (from budset in summer to budbreak the next spring) of an apple bud, follows a “bell-shaped” curve. Dormancy starts to

* Corresponding author at: Dept. of Horticultural Science, Private Bag X1, Stellenbosch University, Stellenbosch, South Africa.
E-mail address: esmelouw@sun.ac.za (E.D. Louw).
[1] Current address: Prophyta (Pty) Ltd., Elgin, South Africa.

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intensify soon after bud formation and reaches a maximum level at leaf fall/senescence and low temperature (1.5 °C to 12.4 °C according to Utah model) is responsible for the induction and the release of dormancy (Hauagge and Cummins, 1991b; Richardson et al., 1974).

In warm climates with insufficient winter cold (i.e. chill requirement not met), as is typical of the low-latitude (28–34°S) apple growing regions of South Africa, dormancy symptoms persist after winter and consequently protracted, decreased and uneven budbreak occurs (Jacobs et al., 1981). Delayed foliation, as it is commonly referred to, results in decreased yields, reduced fruit quality (Jacobs et al., 1981; Saure 1985) and impedes the full development of acrotony and subsequent apical control (Cook and Jacobs, 1999). To determine if delayed foliation could be the result of a different dormancy progression pattern caused by warm climates, Cook and Jacobs (2000) used the method of Hauagge and Cummins (1991a) to produce dormancy curves for 'Golden Delicious' and 'Granny Smith' (*Malus x domestica* Borkh.) from both a warm area (Elgin) and a colder area (Bokkeveld) in South Africa. The dormancy patterns in the two areas were found to be different. Both cultivars in the Bokkeveld rapidly entered dormancy and reached a maximum level early in the winter when less than 100 CU (Utah model) had accumulated. Thereafter, dormancy release was initially slow but increased in late winter. Entrance into dormancy for both cultivars in the warm area was gradual and maximum dormancy was only attained late in the winter when 600 CU (Utah model) had already accumulated. Neither of these patterns resembled the normal curve that typifies progression of dormancy in cold climates as described by Hauagge and Cummins (1991b). Cook and Jacobs (2000) also indicated that the Utah chill model is inadequate when considering warm winter conditions suggesting that the entrance into dormancy (autumn period) could possibly play a larger role in dormancy progression. The purpose of this study was to produce a robust data set of apple bud dormancy curves spanning five years and representing the diverse geographic and climatic apple growing regions of South Africa in order to quantify and describe the progression of dormancy of apple buds grown under conditions of inadequate chilling.

2. Materials and methods

2.1. Plant material and trial sites

Over five consecutive years (2005–2009) shoots from mature, bearing, 'Granny Smith' (GS) and 'Royal Gala' (RG) apple trees on either seedlings rootstock or M793 rootstocks were sourced from 24 commercial farms representing the diverse geographic and climatic apple growing regions of South Africa (Table 1). Fourteen, one-year-old shoots (35 cm) of both GS and RG were randomly harvested from each of the orchards at regular intervals throughout each of the seasons. Shoot collection commenced at budset and terminated when either rest breaking agents (0.5% H-cyanamide and 3% mineral oil mixture) were applied or, in most cases, natural budswell occurred the following spring. To prevent dehydration, the shoots were defoliated, placed in sealed plastic bags and transported to the laboratory. All collection dates were recorded together with the latitude and altitudes of each farm site (Table 1). Temperature data was obtained by placing loggers in each study site recording the hourly temperature for the duration of the trial. The classical chilling requirements, according to the North Carolina model, for GS and RG are very similar at 1064 CU and 1049 CU respectively (Hauagge and Cummins, 1991c).

2.2. Forcing experiments

Within 72 h of harvest, the shoots were cut to 30 cm by removing the excess proximal shoot piece. The fourteen shoots were bundled, labelled and placed in 5 dm^3 white plastic buckets containing 5 cm^3 of household bleach (3.5% sodium hypochlorite) in 1 dm^3 of water. The dormancy level of the buds was determined by forcing the shoots in a growth chamber that maintained a constant 25 °C and continuous illumination (ca. 200 μmol m^{-2} s^{-1} photosynthetically active radiation). The water was replaced every two to three days and 10 mm of the basal part of each shoot was cut off weekly to prevent blockage of the xylem. The number of days to 50% budburst was recorded by monitoring the buds every two to three days until a single bud (either terminal or lateral) on seven of the fourteen shoots had reached green tip stage. The time interval between the shoots being subject to forcing conditions and 50% budburst was used as an indication of the depth of dormancy (Cook and Jacobs, 2000; Hauagge and Cummins, 1991a).

2.3. Data handling and modeling

Progression of bud dormancy for each cultivar, farm and year was determined by plotting individual scatter graphs of the depth of dormancy (days to 50% budburst) and the collection dates (day of year) (See dots in Fig. 1). A typical dormancy progression curve contained a period where the dormancy levels increases (entrance into dormancy), reaches a maximum and then decrease (exit from dormancy). In cases where the initial or last data points in the progression did not show an increase or decrease in the depth of dormancy i.e. the buds had not yet started entering or had already exited dormancy, the data points were classified as tail points and were removed from the data set. The number of days to bud break for the tail points varied between zero and five days. The scatterplots were then modelled by fitting a two linear joint line model which represented the entrance into and exit from dormancy with the join point signifying the maximum depth of dormancy (Fig. 1).

The model can be described as two converging straight lines:

$$\text{Dormancy Entrance} = a_1 + b_1(\text{Day of Year})$$

$$\text{Dormancy Exit} = a_2 + b_2(\text{Day of Year})$$

where:

$a_2 = a_1 + (b_1\text{-}b_2)(\text{Day of Year})$

and Day of Year = Joining point

The modelling involved a univariate, nonlinear regression analysis performed with SAS statistical software (SASVersion 9.21999) using the NLIN procedure with unspecified derivatives (DUD method). In cases where the procedure failed to converge when fitting the model, the data points, lines and standardised residuals were examined and data points that influenced this were considered as outliers and consequently removed. This process was repeated until the model converged. Models that did not fit had either insufficient data points for the entrance into or exit from dormancy or the buds never actually entered dormancy (days to 50% budburst remained low throughout the winter season). These data sets were discarded. The successful models identified 11 variables (described in Fig. 1) for each cultivar on each farm for every year. These variables were used in the statistical analysis.

2.4. Statistical analysis

To compare the means of the 11 variables a three-factor (Year, Cultivar and Farm) analysis of variance (ANOVA) was performed, at the 5% significance level, using the three factor interaction as the error term (SASVersion 9.21999). Standardised residuals were examined in the univariate procedure and data points removed until the residuals were symmetric or normal distributed using Shapiro-Wilk test for non-normality (Shapiro and Wilk, 1965).

To reveal interrelationships between the farms and their respective 11 variables a Principle Component Analysis (PCA) was performed using XLSTAT (Version 18.06). The factor scores from Principle Component (PC) 1 and PC 2 were used in a multivariate cluster analysis (CA) to identify groups of farms with similar dormancy progressions. The clustering involved a hierarchical, agglomerative method using Euclidean distance for dissimilarity and Ward's method for joining of