



# > The development of red-skinned apples adapted to the warm climates of South European countries

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Many red-skinned apple cultivars grown under warm summer conditions do not redden as much as those grown in locations with cooler summer temperatures. Reflective films and over-tree sprinkler irrigation have been used to mitigate the issue. However, the most efficient strategy is to breed new cultivars that have a high genetic potential for fruit colour development under warmer climates. New cultivars selected for their adaptation to such climates are being bred by a joint Institut de Recerca i Tecnologia Agroalimentàries-Plant & Food Research (IRTA-PFR) breeding programme. Understanding the physiological and genetic control of the response to warm orchard temperature is crucial for developing new tools for more efficient breeding of red-skinned apple cultivars. We manipulated fruit skin temperature by heating and cooling 'Royal Gala' fruit in orchards in New Zealand and Spain and measured the expression of the genes regulating red pigmentation. Evidence of down-regulation of the main activator of red pigmentation (*MYB10*) was demonstrated, and this gene is linked to a locus controlling the red-skinned phenotype. A marker based on *MYB10* was developed and is now used for marker-assisted breeding of new apple cultivars suited to warm conditions.



## Introduction

Apple skin colour contributes to the appeal of the fruit, and as each cultivar has a characteristic colouration, it aids consumer recognition. A lack of red skin colouration can result in a reduced commercial value associated with poor consumer acceptance (Baughner et al., 1990). Along with fruit size, the intensity and quality of red skin colour provide the basis for the grading standards used by European Union (EU) countries.

Red skin colouration in apple is due to the presence of anthocyanins, primarily cyanidin-3-galactoside or idaein (Lancaster, 1992). The development of anthocyanin is partly regulated by temperature (Lin-Wang et al., 2011; Palmer et al., 2012; Iglesias et al., 2016). The skin of red apple cultivars grown in warm climates often has poor reddening because of lower anthocyanin production under warm summer temperatures. One practice for optimising apple fruit colouration in commercial orchards is to increase light exposure of the fruit by using reflective films (Iglesias and Alegre, 2009), while another involves the indirect modification of temperature by the use of over-tree sprinkler irrigation (Williams, 1993; Iglesias et al., 2000). However, these techniques are expensive and alternatives are thus required. Planting new cultivars and/or strains with enhanced fruit

colouration is a more cost-effective strategy. In the last decades, red sports of traditional bicoloured cultivars such as 'Gala', 'Red Delicious', 'Jonagold' and 'Fuji' have been widely planted in the main apple-producing areas of the world as they can achieve a more characteristic colouration in regions with hot summers (Iglesias et al., 1999, 2008, 2012; Iglesias and Echeverría, 2009). In addition, apple breeding programmes worldwide focus on developing new cultivars with superior fruit characteristics (including red colouration and eating quality) that are adapted to a range of environments (Janick et al., 1996; Fellman et al., 2000; Sansavini et al., 2005, 2012; Batlle et al., 2008; Cantin et al., 2015). The use of genetic markers linked to red colouration in marker-assisted breeding (MAB), and a better understanding of the molecular and physiological control of red skin colouration will contribute to developing new apple cultivars with high colouration that are adapted to a range of environments (Espley et al., 2007; Lin-Wang et al., 2011; Iglesias et al., 2016).

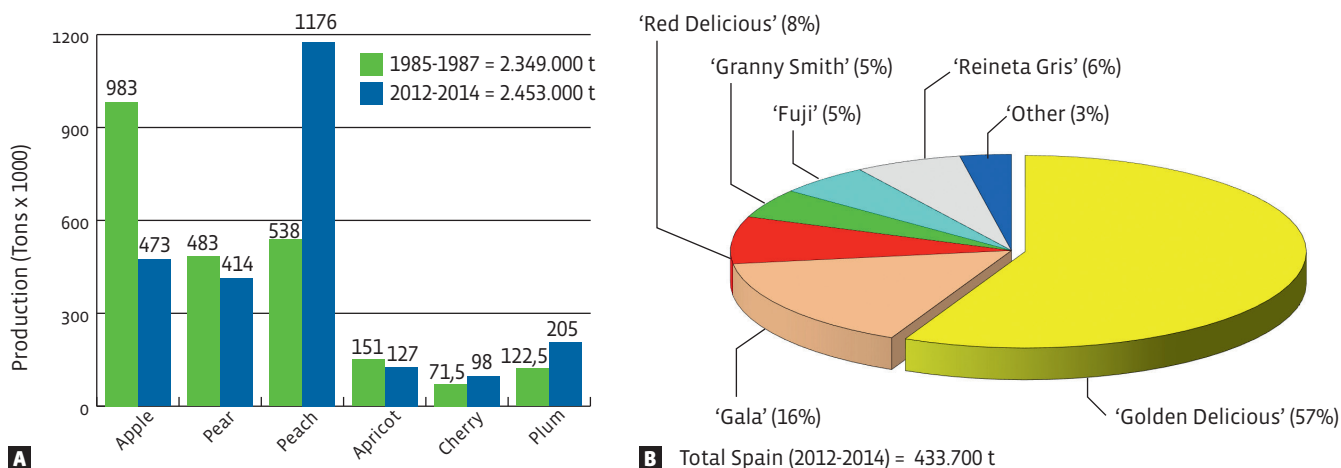
## Current situation and trends of apple production in Spain

Spain is the fifth largest apple producer in the EU after Poland, Italy, France and Germany, with an average production of 430,000

tons year<sup>-1</sup>. Apple production is located mainly in the low altitude areas of the Ebro Valley, which typically has a warm summer (July and August) climate, with maximum daily temperatures frequently reaching over 35°C and minimum temperatures ranging from 15 to 20°C. These conditions have a negative effect on the overall apple quality, significantly reducing growers' returns because of a lack of fruit colour development, an increase in the incidence of sunburn, and decreases in flesh firmness and storage potential.

As a result of the lower fruit quality produced in these adverse environmental conditions, and strong competition in European markets, apple production in Spain has reduced by half since the 1985-1987 period (Figure 1A). In comparison, peach production has doubled over the same period, partly because of the better adaptation of this species to warm and dry climates, which result in high fruit colour and good eating quality.

Currently, apple production in Spain is dominated by 'Golden Delicious' (57% of the total production), followed by 'Gala' and 'Red Delicious' (Figure 1B). 'Golden Delicious' is widely planted because the yellow skin of this cultivar is not adversely affected by hot temperatures. Over the period of 1985-1987, 'Golden Delicious' was also the dominant cultivar, followed by 'Red Delicious', with



■ Figure 1. (A) Pipfruit and stonefruit production during the 1985-1987 and 2012-2014 periods in Spain. (B) Apple production in Spain by cultivar during the 2012-2014 period.

the major change over time having been the substitution of 'Red Delicious', mainly with 'Gala' and 'Fuji'. Highly coloured red sports of 'Elstar' and 'Jonagold' are not adapted to the warm conditions of the main apple-growing areas of Spain.

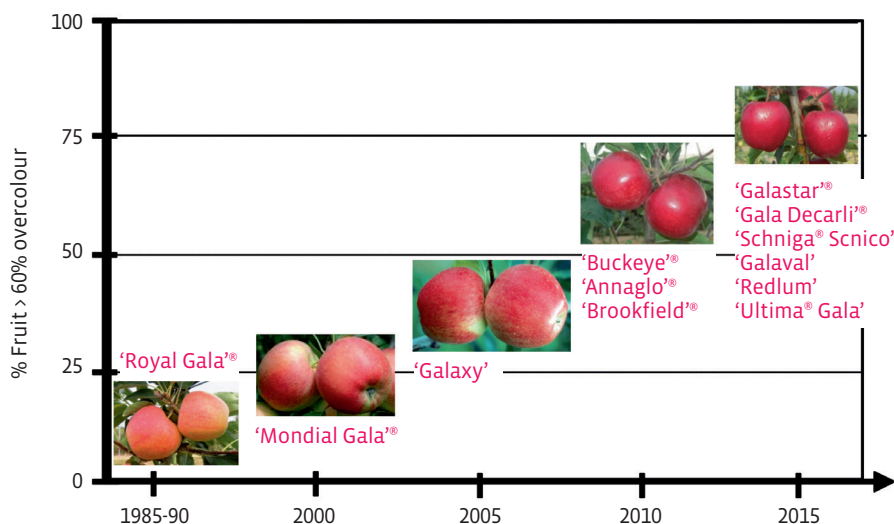
### Improving fruit colour by selection of new red sports

High-colour strains of cultivars such as 'Gala', 'Red Delicious', 'Jonagold' and 'Fuji' are grown around the world. Compared with the original cultivar, high-coloured strains develop a more precocious and intense colour at commercial harvest (Figure 2) even in warm climates. Agronomic performance parameters such as bloom and harvest time, fruit size, eating quality, yield and postharvest performance are not different in high-colour strains (Walsh and Volz, 1990; Kappel et al., 1992; Iglesias et al., 1999; Iglesias and Echeverría, 2009). However, some of the highly coloured and blushed strains of 'Delicious' (Warrington et al., 1990) and 'Fuji' (Iglesias et al., 2012) were reported to be less aromatic than the original cultivars.

Conversely, highly coloured strains such as 'Buckeye® Gala', 'Brookfield® Gala' and 'Gala Decarli' can have excessive skin colour intensity when planted in cooler environments such as New Zealand or in mountain areas. This can negatively affect fruit market value, as the appearance differs significantly from the characteristic colouration of the original cultivar, and consumers are unable to recognise them (Sansavini et al., 2012; Iglesias and Ruiz, 2015).

### Breeding new highly coloured apple cultivars adapted to a warm climate

The alternative to selecting highly coloured red sports is to develop new cultivars



■ Figure 2. Fruit percentage overcolour (>60%) across the period 1985-2015 for newly developed red sports of 'Gala' apple in Spain, from less to more colour development.

by breeding. For example, the scab-resistant cultivar 'Liberty' was used as a parent for the selection of the new cultivar 'Modí' (CIVG198) by the Consorzio Italiano Vivaisti (CIV), Italy, which has high red colour in warm South European environments. Unfortunately, most apple cultivar breeding programmes are located in temperate climatic areas and therefore most of the new cultivars bred in the last two decades do not fulfil their potential for fruit colour, appearance, or eating quality in these warm climates. The most efficient solution to this issue was to establish a breeding programme that selected new cultivars in the same climatic conditions in which they will be grown.

A joint Institut de Recerca i Tecnologia Agroalimentàries-Plant & Food Research (IRTA-PFR) apple scion breeding programme was initiated in Lleida (Catalonia, Spain) in 2002 with this objective (Batlle et al., 2008; Cantin et al., 2015). The programme has used high quality

parents from PFR's New Zealand apple breeding programme, selected under cool climate conditions, to generate progeny that have been grown and evaluated in Catalonia.

Over the last 12 years, 258 controlled crosses have been made (Table 1) and a total of 202,493 apple seedlings raised from 2002 to 2014 and planted in the selection plots, with 17,063 fruiting seedlings currently being evaluated. In 2014, 42 (44%) progeny with overcolour greater than 60% out of the 96 fruiting Stage 2 selections were identified as having commercial cultivar potential. To better determine their commercial potential, in 2013 and 2014 six selections were introduced into Stage 3 evaluation trials, with five of these having high fruit colour as well as good agronomic performance and fruit quality.

For breeding populations developed specifically for creating high red-coloured apple cultivars, a wide range in red skin colour

■ Table 1. Summary table of the IRTA-PFR apple and pear breeding programme over the period 2002- 2014.

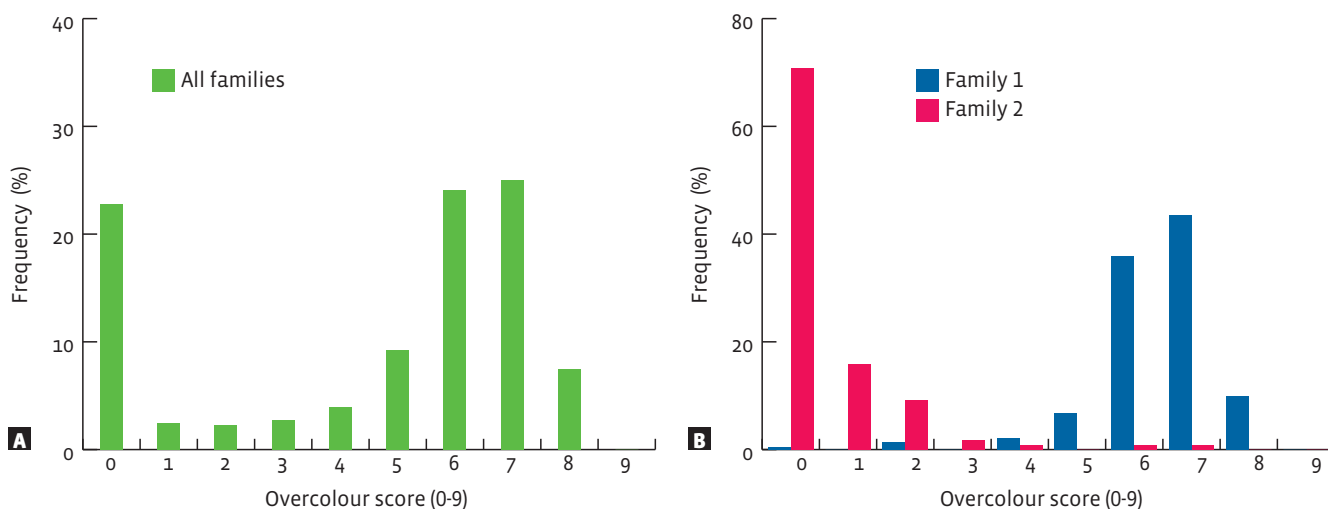
| IRTA-PFR apple programme (period 2002-2014)                        |         |
|--|---------|
| N° of crosses made   | 258     |
| N° of seeds obtained   | 202,493 |
| N° seedlings evaluated in the 1 <sup>st</sup> Stage                | 59,817  |
| N° seedlings evaluated in 2014                                     | 17,063  |
| N° Stage 2 selections  | 241     |
| N° Stage 2 selections evaluated in 2014                            | 96      |
| N° Stage 2 selections evaluated in 2014 with overcolour $\geq$ 60% | 42      |
| N° Stage 3 selections  | 6       |
| N° Stage 3 selections with overcolour $\geq$ 60%                   | 5       |

## Physiological and genetic control of red skin colour in apples in warm climates

Improvements in the efficiency of breeding for high red colour in warm climates can be brought about by a greater understanding of high colour phenotypes and the genetic control of anthocyanin production.

To this end, understanding the effect of temperature on anthocyanin pigmentation and relative RNA expression of the genes regulating anthocyanin content is crucial. Anthocyanin concentration and gene expression in the apple fruit skin were measured using ‘Royal Gala’ grown in different environmental conditions (Spain and New Zealand) and by in situ modification of the temperature.

The anthocyanin concentration in the skin of ‘Royal Gala’ apple increased progressively



■ Figure 3. Variation in red skin colour development at harvest (A) across 10,000 apple seedlings and (B) for seedlings from a high (Family 1) and a low (Family 2) performing family in the IRTA-PFR apple breeding programme on fruit assessed from 2007-2014. (Overcolour score 0-9 = 0-100% red colour coverage over the fruit surface).

■ Table 2. Apple skin anthocyanin content ( $\pm$ SE) of ‘Gala’ apples grown in Havelock North, New Zealand and Lleida, Spain, over the last nine weeks before eating ripe in 2008. DAFB = days after full bloom.

| New Zealand |                                      | Spain |                                      |
|-------------|--------------------------------------|-------|--------------------------------------|
| DAFB        | Anthocyanin (nmol cm <sup>-2</sup> ) | DAFB  | Anthocyanin (nmol cm <sup>-2</sup> ) |
| 86          | 27.0 $\pm$ 2.1                       | 75    | 9.9 $\pm$ 0.3                        |
| 100         | 40.1 $\pm$ 1.0                       | 96    | 9.2 $\pm$ 0.1                        |
| 114         | 59.4 $\pm$ 2.3                       | 110   | 10.0 $\pm$ 0.1                       |
| 128         | 99.0 $\pm$ 3.2                       | 124   | 22.5 $\pm$ 0.4                       |
| 141         | 107.0 $\pm$ 2.8                      | 138   | 26.9 $\pm$ 0.6                       |

development in the progenies has been observed. Nevertheless, over 30% of the seedlings have developed high red colour coverage (overcolour score of 7 or greater; Figure 3A) from which selections as potential

commercial cultivars and/or future breeding parents have been made. The significant among-family variation in red colour (Figure 3B) demonstrates its strong genetic component under warm growing conditions.

towards harvest in both New Zealand and Spain, with higher concentrations in New Zealand than in Spain (Table 2). Under the same conditions in both locations, the red sport ‘Brookfield Gala’ contained between 2 and 3 times more anthocyanins than ‘Royal Gala’. The average daily minimum and maximum temperatures for this period were 12.8 and 24.5°C (New Zealand) and 18.5 and 33.2°C (Spain), respectively.

Genes from the anthocyanin biosynthetic pathway such as *chalcone synthase (CHS)*, *chalcone isomerase (CHI)* and *leucoanthocyanidin dioxygenase (LDOX)* were significantly more highly expressed in New Zealand than in the warmer Spanish conditions (Figure 4). Similarly, the expression of the transcription factor *MYB10* (Espley et al., 2007) responsible for activating the anthocyanin biosynthetic pathway genes listed above, was higher in New Zealand than in Spain, and increased during fruit development (Figure 4).

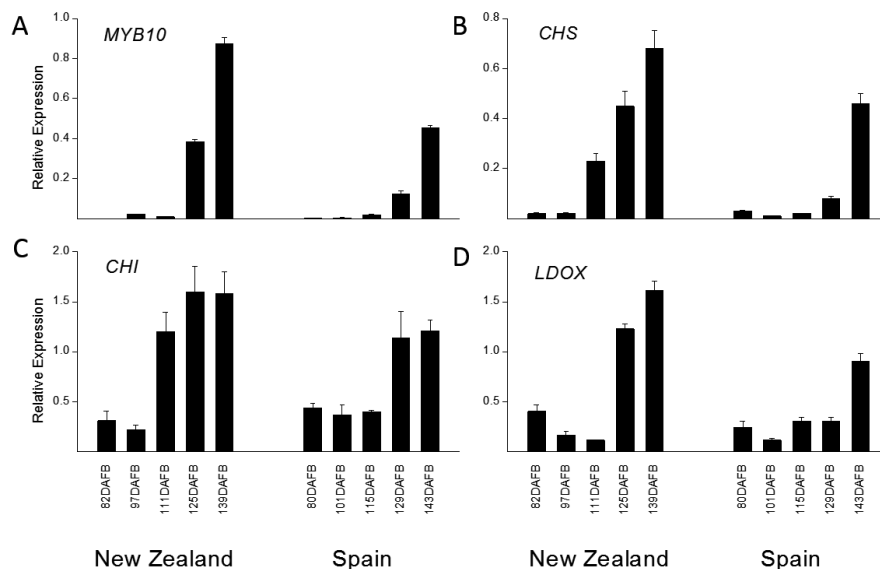
Heating and cooling experiments were carried out in situ on ‘Royal Gala’ fruit to alter the fruit skin temperature. The cooling trial in Spain decreased the mean fruit skin temperature by between 5.5°C (night) and 7.2°C (day). To mimic the temperature conditions in Lleida, the heating trial in New Zealand increased mean minimum night-time temperature by 6 to 8°C compared with that of the unheated fruit. Over the seven days of the treatment, the minimum fruit skin temperature of the unheated fruit was 7.3°C compared with 17.0°C for the heated fruit. The unheated fruit skin temperature was similar to the screen air temperature at night, but did show some increase over air temperature during the day caused by solar heating. Apple skin anthocyanin concentrations increased in the unheated fruit within seven days, but heating resulted in a much smaller increase in anthocyanins because the temperature also had a direct effect on either the regulation of genes coding the enzymes or the regulation of the *MYB* genes (Espley et al., 2007). Temperature can also affect the catabolism of anthocyanin compounds (Curry, 1997; Lin-Wang et al., 2011; Palmer et al., 2012).

In ‘Royal Gala’, the relative expression levels of all the anthocyanin synthesis genes from *CHS* to *UFGT* and the transcription factor *MYB10* were determined. Expression was down-regulated by heating in New Zealand, and up-regulated by cooling in Spain (Figure 5). Accordingly, the relative expression of some MYB repressors such as *MYB15* and *MYB17* increased in hot climates with high day-night temperatures. In contrast, *MYB10* gene expression was reduced in these conditions.

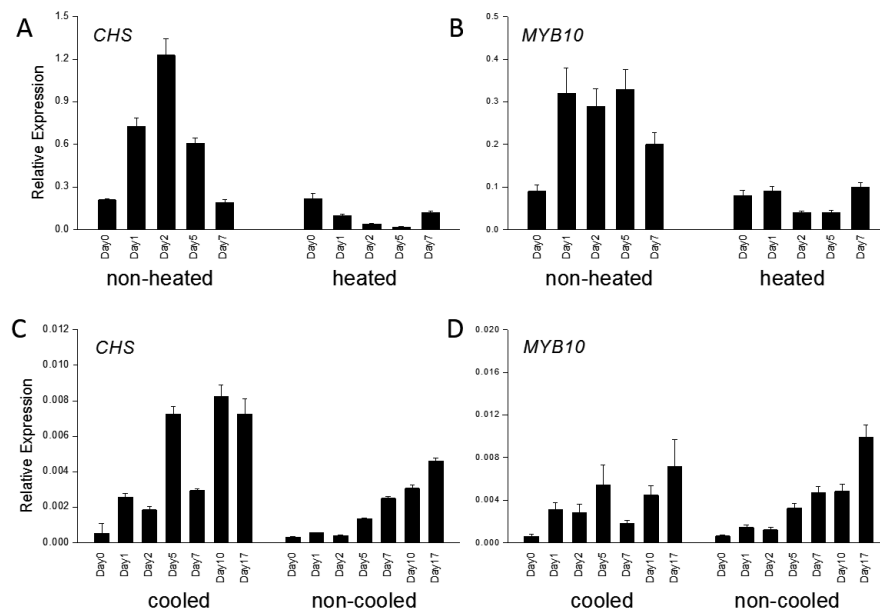
Relative gene expression and regulation are affected by the fruit temperature in attached apples. We propose that temperature-induced down-regulation of fruit anthocyanin biosynthesis is primarily due to down-regulation of the anthocyanin regulatory complex and that the genes encoding the complex are useful loci for the development of MAB of new apple cultivars tolerant to warm conditions (Lin-Wang et al., 2011).

### Selecting highly coloured apples using marker-assisted selection

MAB is an efficient strategy for selecting new cultivars faster by determining which parents are the best combination to be crossed, followed by selecting those seedlings that carry the traits of interest. The prerequisite for MAB is to develop genetic markers linked to the trait of interest. Genetic mapping was used to identify a major locus controlling red skin colouration at the bottom of chromosome 9, by screening genetic markers covering the apple genome at high density over a population segregating for red skin colour. Interestingly, the locus linked to red skin colouration on



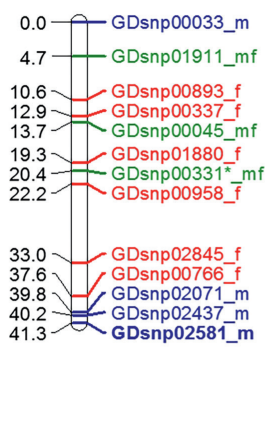
■ Figure 4. Relative RNA expression levels of (A) *MYB10*, (B) *CHS*, (C) *CHI* and (D) *LDOX* genes detected by Real-Time qPCR analysis in ‘Royal Gala’ apple skin grown in Havelock North (New Zealand) and Mollerussa (Spain), over the last nine weeks before fruit were eating ripe. Histograms represent the averages and bars represent ±SE of three biological replicates. This figure is reprinted as follows from Lin-Wang et al. (2011), with permission from John Wiley and Sons (License No. 3770460757384): A is part of Figure 2, B and D are part of Figure 1 and C is included in Supplementary Information.



■ Figure 5. Relative RNA expression levels of (A) *CHS* and (B) *MYB10* using real-time quantitative PCR analysis for ‘Royal Gala’ apples grown in Motueka (New Zealand) under non-heated (control-unheated) and heated conditions, and of (C) *CHS* and (D) *MYB10* in Lleida (Spain) under cooled and non-cooled conditions. The data were normalized on the basis of the *eIF1-α* housekeeping gene. Histograms represent the averages and bars represent ±SE of three biological replicates. Figures A and B are reprinted from part of Figure 4 in Lin-Wang et al. (2011), with permission from John Wiley and Sons (License No. 3770460757384).

chromosome 9 co-locates with the *MYB10* transcription factor (Figure 6), which activates the anthocyanin biosynthetic pathway and responds to warm temperatures, as shown by the heating and cooling experiments. A genetic marker linked to *MYB10* on chromosome 9 was validated in five breeding popu-

lations of the IRTA-PFR breeding programme. The genotype of this marker was compared with the phenotypic data for 403 segregating individuals assessed in 2011 and 2012. The marker predicted skin colouration well (Figure 7), as individuals homozygous for the red allele had high red colouration, while the

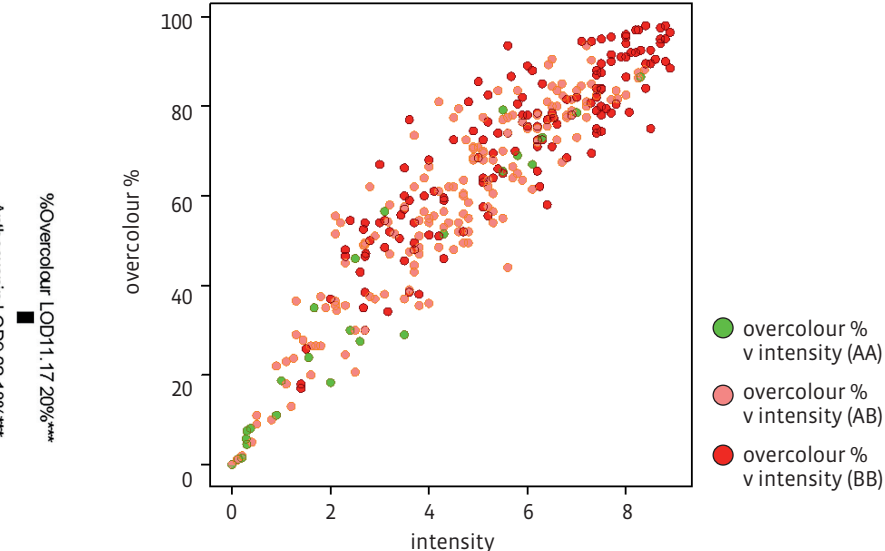


■ Figure 6. Quantitative trait loci detection for red skin colouration in a T89 × ‘Gala’ apple population.

homozygous non-red allele had low red colouration. We recommend using it for MAB in apple for selecting new cultivars with higher red skin colouration.

## Conclusions

Apple production located in the warm southern European country of Spain experienced a significant production decrease over the past two decades because of poor cultivar adaptation to warm summer conditions. Our research has demonstrated a negative effect of warm temperature on the RNA expression of the *MYB10* transcription factor and the biosynthetic genes regulated by *MYB10*. We propose that temperature-induced down-regulation of fruit anthocyanin biosynthesis is primarily due to down-regulation of the anthocyanin regulatory complex. A genetic marker developed from *MYB10* was validated in the IRTA-PFR joint breeding programme and can now be



■ Figure 7. Validation of the genetic marker linked to *MYB10* on apple chromosome 9 to select for red fruit skin, using five breeding populations. The fruit colour was measured as percentage overcolour (Y axis), and intensity (X axis) on a scale from 0 (no red colouration) to 9 (high red colouration). Individual seedlings with the AA homozygous genotype had low red colouration, while homozygous BB had high red colouration and heterozygous AB individuals had intermediate phenotypes.

used routinely to select for high red skin colouration. The genetic marker enables apple breeders to choose the best parent based on the *MYB10* genotype and to cull young seedlings that do not carry the red allele of this marker. Using MAB for the selection of high coloured apples will, in the near future, result in apple cultivars with enhanced visual appearance even when grown in areas with challenging climatic conditions.

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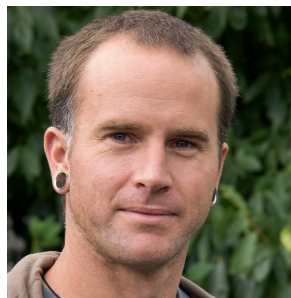
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