Original article

Iron chelate applications improve productivity and fruit quality at harvest and during cold storage of *Actinidia chinensis* var. *chinensis* ('Hort16A') kiwifruit growing in high-pH calcareous soils

T.G. Thorp¹, A.M. Barnett², C. Civolani³, R. Spinelli⁴, N. Lallu⁵ and J. Burdon⁵

¹ Plant & Food Research Australia Pty Ltd., Albert Park, Australia

² The New Zealand Institute for Plant and Food Research Ltd., Te Puke Research Centre, Te Puke, New Zealand

³ Eurofins Agrosience Services, San Giorgio di Piano, Italy

⁴ Zespri Fresh Produce Italy, Cisterna di Latina, Italy

⁵ The New Zealand Institute for Plant and Food Research Ltd., Mt Albert Research Centre, Auckland, New Zealand

Summary

Kiwifruit (*Actinidia* spp.) are known to be sensitive to iron (Fe) deficiency in alkaline and calcareous soils with low organic matter. Symptoms most commonly observed on Fe-deficient vines are leaf chlorosis in spring and sometimes fruit chlorosis at harvest. 'Hort16A' is a yellow-fleshed cultivar of *A. chinensis* var. *chinensis* which appears to be especially sensitive to Fe deficiency-induced leaf chlorosis. Sets of 'Hort16A' vines with high and low rates of chlorosis were established by applying additional Fe chelate during summer and autumn, in addition to the current standard practice of applying Fe chelate only during spring and early summer. Both spring and summer growth flushes exhibited leaf chlorosis, and fruit chlorosis was observed, especially in fruit harvested from distal parts of vines. Additional Fe chelate applied in late summer and autumn increased the chlorophyll concentration of leaves in the following spring but not in summer and increased the concentrations of carotenoid and chlorophyll pigments in the flesh of fruit. Vine productivity was increased by 56% and 23% in the two years following treatment with additional applications of Fe chelate in late summer and autumn. 'Hort16A' fruit change from green to yellow during the final stages of maturation and ripening; additional Fe chelate applications tended to promote earlier de-greening compared with that of control fruit. Average fruit size, dry matter, soluble solids content and flesh firmness at harvest were similar in fruit on control and treated vines, but these results were confounded by treatment-induced differences in crop load. Fe chelate treatments did not affect the incidence of chilling injury after 12 weeks' cold storage, or the incidence of fruit chlorosis. While there were significant benefits from Fe chelate applications, it is regarded as expensive and not sustainable. The development of kiwifruit rootstocks tolerant of high pH soils remains the best and most sustainable solution for growers.

Keywords

Fe deficiency, leaf chlorosis, fruit chlorosis, maturation, yield, Italy

Significance of this study

What is already known on this subject?

- Several fruit crops, including kiwifruit, develop leaf chlorosis when Fe is deficient and/or uptake from alkaline and/or calcareous soils is limited. Severe leaf chlorosis left untreated can cause major reductions in flower number and yield.

What are the new findings?

- Research reported here is the first to demonstrate the cumulative effect of Fe deficiency-induced leaf chlorosis on reduced vine productivity, fruit quality and storage of a yellow-fleshed kiwifruit cultivar of *A. chinensis* var. *chinensis*.

What is the expected impact on horticulture?

- Since most of the global production of kiwifruit is now in regions with alkaline and/or calcareous soils, it is important that growers are aware of the real cost of not adequately controlling Fe deficiency, including the potential financial impacts of reduced yields, poor flesh colour, delayed de-greening and increased risk of chilling damage during cold storage.

Introduction

Originally from China, kiwifruit (*Actinidia* spp.) were first commercialised in New Zealand early last century (Ferguson and Bollard, 1990). A single green-fleshed cultivar 'Hayward' (*A. chinensis* var. *deliciosa*) became dominant in global trade. Over the last 40 years new producing regions have been established in both northern and southern hemispheres and markets are now supplied with fresh product for 12 months of the year. While China is the largest producer of kiwifruit, it exports little, whereas Italy, New Zealand and Chile together account for ~80% of global trade (Belrose, 2016). Average orchard yields of Class 1 'Hayward' fruit in New Zealand were 27 t ha⁻¹ in 2005 (Anon., 2008) and yields over 70 t ha⁻¹ are now possible (Thorp et al., 2011). Yield of 'Hayward' kiwifruit in Italy saw production increase from 4.8 t ha⁻¹ in 1984 to 20.1 t ha⁻¹ in 2006 (Testolin and Ferguson, 2009).

The expansion of production into different growing environments, along with a wider range of cultivars and species

FIGURE 1. Iron deficiency-induced leaf chlorosis in August (summer) 2011 on *Actinidia chinensis* var. *chinensis* 'Hort16A' kiwifruit vines growing at Orchard 1. Leaves with chlorosis are on secondary canes as a result of the strong summer growth flush produced by this cultivar in warm climates. Darker green leaves are on primary canes produced during the first growth flush in spring; these leaves also showed severe chlorosis in spring.

now being grown, has not been without its problems (Thorp et al., 2007). Iron (Fe) deficiency and associated leaf and fruit chlorosis is a major constraint to kiwifruit productivity in regions with high pH, calcareous soils with low organic matter, such as occurs in the main production regions in China (Wang et al., 2019a), Greece (Loupassaki et al., 1997) and northern Italy (Rombola and Tagliavini, 2006; Civolani, 2006). Previous studies with 'Hayward' kiwifruit (and other fruit crops) have demonstrated negative effects on plant productivity when leaf chlorosis is not remedied (Rombola and Tagliavini, 2006; Álvarez-Fernández et al., 2006). The newer yellow-fleshed cultivars of *A. chinensis* var. *chinensis* appear to be especially sensitive to high pH calcareous soils (Wang et al., 2019a). It is common in regions with these cultivars and soil type to observe severe leaf chlorosis in spring, when conditions are cold and wet. Symptoms also appear during summer in leaves on new, vigorous cane growth induced by warm summer temperatures (Figure 1; Snelgar et al., 2010). At this stage, symptoms have much reduced on the spring flush leaves. No new symptoms develop in autumn apart from normal leaf senescence.

Biochemical responses related to Fe deficiency chlorosis are well known across a number of crops (for reviews see Abadía et al., 2011, and Briat et al., 2015). Research with peach has associated the effects of Fe deficiency chlorosis with delayed fruit maturation and ripening, decreased red skin colour and poor eating quality from higher organic acids, phenolic compounds and vitamin C (Álvarez-Fernández et al., 2003, 2006, 2011). While previous studies with green and yellow-fleshed kiwifruit have examined changes in root, stem and leaf physiology in response to Fe deficiency, they provided little information on the effects of Fe deficiency on fruit development and ripening (Rombola et al., 2002; Wang et al., 2019a, b). The flesh of *A. chinensis* var. *chinensis* 'Hort16A' kiwifruit changes from green (~115 °h) to yellow (~100 °h) during maturation and ripening (Minchin et al., 2003; Richardson et al., 2011). It is therefore possible that Fe deficiency may also delay maturation and the timing of flesh colour change of 'Hort16A' fruit and thus delay timing of commercial harvest. Delayed harvests of 'Hort16A' fruit may increase the risk of chilling damage to fruit while they are still on the vine from early frosts, or induction of rapid softening as daytime temperatures decrease (Burdon et al., 2014, 2017). Also significantly, the development of chilling injury

symptoms during cold storage largely depends on the maturity of the fruit at harvest (Burdon and Lallu, 2011). Chilling symptoms that develop during storage of 'Hort16A' fruit are similar to those described for low temperature breakdown in 'Hayward' (Lallu, 1997), with a granular appearance in the outer pericarp just under the skin and water-soaked tissues in the inner and/or outer pericarp, but also with the possibility of skin discoloration at the distal (stylar) end of the fruit (Burdon and Lallu, 2011). While clearance for harvest is largely based on flesh colour, the fact that fruit flesh colour is not tightly associated with other aspects of maturation in 'Hort16A', including fruit soluble solids content (SSC) and firmness, means that even if flesh degreening has occurred, other factors associated with chilling sensitivity may not have changed in step.

Current methods to reduce the impact of high pH soils on plant growth and productivity mainly rely on Fe chelate treatments (Rombola and Tagliavini, 2006; Tagliavini and Rombola, 2001). These are expensive, and applications made in one year do not prevent chlorosis in the next (Tagliavini et al., 2000). With 'Hayward', Fe chelate is applied as one or more foliar sprays in spring, before flowering, when soil temperatures are low and root uptake of Fe is limited (Baldi et al., 2009). Post-flowering treatments are soil-applied and watered in using irrigation, to avoid staining of fruit from foliar sprays. Treatments are usually continued every 2–3 weeks until mid-summer, 3–4 months before harvest. Although Rombola and Tagliavini (2006) demonstrated that late-season Fe chelate treatments reduced chlorosis in 'Hayward', there was a perceived risk with 'Hort16A' and other yellow-fleshed cultivars of *A. chinensis* var. *chinensis* that late-season applications would delay flesh colour change from green to yellow and delay fruit ripening.

In this project, sets of vines with high and low rates of chlorosis were established by applying additional Fe chelate to 'Hort16A' vines during summer and autumn, in addition to the current standard practice of applying Fe chelate only during spring and early summer. In a different orchard we also selected vines with severe and less severe symptoms of leaf chlorosis in spring (*i.e.* the worst and best vines in the selected orchard), thus taking advantage of the natural variation present in the orchard. Treatment differences were assessed in terms of leaf chlorosis, flowering, fruit yield and quality, pigment and nutrient analyses and the postharvest

performance of fruit during cold storage. Our hypothesis was that extended applications of Fe chelate would reduce the severity of leaf and fruit chlorosis on 'Hort16A' kiwifruit vines, leading to increased flowering and yield in the subsequent season, along with improvements in fruit quality at harvest and during cold storage.

Materials and methods

Experiments were established at two *Actinidia chinensis* (Planch.) var. *chinensis* 'Hort16A' orchards with sandy loam soils in the Emilia Romagna region of northern Italy. Orchard 1 was located near Brisighella at 126 m a.s.l. (44.206875° Lat., 11.740809° Long.). Orchard 2 was located near Faenza at 43 m a.s.l. (44.265074° Lat., 11.895885° Long.). Vines at Orchard 1 were planted in 2004 and at Orchard 2 in 2005 as grafted plants with tissue-cultured 'Hayward' rootstocks. Vines were trained on to T-bar support structures with 4.6 m between rows and 3.0 m between vines along the rows and a total fruiting canopy of 10.8 m² per vine. Both orchards used overhead netting (approx. 15% shade) during the growing season to protect canopies and fruit from hail damage. Vines were irrigated using drip irrigation with two drippers per vine. A herbicide strip, 2.0 m wide, was maintained along each row using the glyphosate herbicide Roundup® (Monsanto). All vines received a standard fertiliser programme including Fe chelate applied as a single foliar spray with Basafer® FL (Compo Expert, Italia) before flowering and then via irrigation from flowering until mid-summer (July) using Sequestrene® NK 138Fe (Syngenta Italia). Each vine received a total of 45 g of Fe per annum.

At Orchard 1, 20 pairs of vines were tagged in July 2009, avoiding low cropping and obviously weak vines. All vines were within two adjacent rows in the orchard with guard vines at the ends of each row and in adjacent rows. One vine in each pair received the standard fertiliser programme described previously (Control), including 45 g per vine of Fe chelate. The second vine received additional Fe chelate treatments (Treated) using Sequestrene® NK 138Fe applied to the soil beneath each irrigation dripper (8 g per vine) every two weeks from August until November to give an additional 56 g per vine per annum (total of 101 g of Fe per annum). The Fe chelate was covered with soil after application and the irrigation turned on. Treatments were repeated to the same vines in 2009, 2010 and 2011.

Prolonged periods of freezing temperatures in January 2010 (before budbreak) damaged flower buds at Orchard 1 so there were insufficient fruit on some vines to harvest for storage trials; postharvest assessments of fruit from vines with mild and severe rates of chlorosis were undertaken using fruit from Orchard 2 (refer following section for details).

Vine productivity and flowering

Total fruit counts per vine were recorded at Orchard 1 in 2011 and 2012 (severe frost had damaged flowering in spring 2010). Total flower counts per vine were recorded in 2012, along with flowering and percentage budbreak data from one cane per vine. The numbers of flowers pre- and post-anthesis were counted when vines were at 50–90% full bloom, to indicate any treatment differences in time of flowering.

Fruit quality

Fruit were collected from Orchard 1 in 2009, 2010 and 2011 for assessment of fruit size, dry matter (DM) concentration, flesh colour development (hue angle), firmness

(kgf) and soluble solids content (SSC). Monitoring samples of 30 fruit from Control and Treated vines (1–2 fruit per vine) were collected at approximately 10-day intervals from September until November of each year, with a larger replicated sample of 12 fruit per vine collected at commercial harvest in October. Individual fresh weight of fruit was recorded, and then one slice (3 mm thick) was cut from the middle of each fruit for DM determination: slices were weighed before and after oven-drying at 60°C to a constant weight to determine percentage dry weight. The distal (stylar) and proximal (stem) ends of each fruit (10 mm thick) were used to determine SSC using a hand-held Atago N20 refractometer (Atago Co. Ltd., Japan). A single drop of juice was squeezed from each slice onto the refractometer and then averaged to give one value per fruit. Flesh firmness (kgf) was also measured at the midpoint on the flat side and edge of each fruit, with skin removed to a depth of 1–2 mm, using a HortPlus Quickmeasure penetrometer with a 7.9-mm probe (HortPlus, Hastings, New Zealand). Finally, flesh colour (hue angle) was measured at the midpoint on the flat side and edge of each fruit opposite to the firmness measurements, with skin removed to 2–3 mm depth, using a Minolta CR300 Chromameter (Osaka, Japan).

Fruit pigments

Flesh samples were taken from fruit at Orchard 1 in 2011 for analysis of the pigments lutein, β -carotene, chlorophylls *a* and *b* by the commercial laboratory Pedonlab (Latina, Italy). Vines were grouped into three replicates, with 6–7 vines each, and a 30-fruit sample (4–5 fruit per vine) collected from each replicate for analyses. Three plugs of flesh tissue (excluding seeds and skin) were taken from an equatorial slice (5 mm thick) from each fruit and combined to give three replicate samples per treatment. Samples were snap-frozen in liquid nitrogen and stored at -80°C prior to analysis. Carotenoids and chlorophylls were extracted with methanol and dichloromethane (2:1) from homogenized tissue, concentrated, then brought to a known volume before being filtered and quantified using high performance liquid chromatography (HPLC) with a UV-VIS detector (Montefiori et al., 2009).

Leaf chlorophyll

Leaf chlorophyll content was estimated at Orchard 1 in May (spring) and October (autumn) 2011 using a Minolta SPAD-502Plus chlorophyll meter (Konica Minolta Optics Inc., Osaka, Japan). Data are presented as SPAD (single-photon avalanche diode) units. In May, measurements were made on 20 mature, fully expanded leaves on primary canes per vine. In October, 10 leaves were collected from primary canes and 10 from secondary canes per vine. Primary canes are produced during spring, while secondary canes are produced during summer as lateral branches on the primary canes. Leaves were collected from exposed positions in the canopies, thus avoiding any shaded leaves and leaves that were already senescent. Leaf blades were cut on the diagonal to enable measurements to be made at 4 points across the leaf, these values were then averaged to give one value per leaf.

Soil and nutrient analyses

Soil samples were taken 25 cm away from the irrigation emitters at each vine, to a depth of 20 cm, with two samples per vine and all vines combined into a single sample per treatment for physical and chemical analysis by APHA standard methods (PedonLab, Latina, Italy). Leaf and fruit sam-

ples were collected from Orchard 1 in May and October 2011 for standard nutrient analyses (N, P, K, Ca, Mg, Fe and Mn) by ICP-OES (PedonLab, Latina, Italy) with N determined using the Kjeldahl method. Leaf samples (excluding petioles) collected in May were taken from primary canes only, while in October samples were collected from primary and secondary canes. In May, leaf samples were replicated with 6–7 vines each per replicate (as described in previous section) and included 4 leaves per vine and cane type (24 leaves per replicate). In October, leaf samples were combined to give one sample of 40 leaves (2 leaves per vine) per treatment and cane type. Fruit samples included 4–5 fruit per vine (30 fruit per replicate). Three plugs of flesh tissue (excluding seeds and skin) were taken from an equatorial slice (5 mm thick) from each fruit and combined to give one sample per replicate.

Postharvest performance (Orchard 2)

In spring 2010, before flowering, 20 vines with severe leaf chlorosis and 20 vines with mild chlorosis were identified in a similar area at Orchard 2. All vines at this orchard showed some leaf chlorosis. The two groups of vines were identified as exhibiting the most and least severe symptoms for vines at this site. Fruit were collected from two positions within each vine, from proximal canes (close to the trunk) and distal canes (canes at the ends of leaders distal to the trunk). A sample of 90 fruit per treatment and position on the vine was collected for assessment of fruit size, DM, flesh colour, firmness and SSC as previously described. At the same time 15 fruit from proximal canes and 15 fruit from distal canes were harvested from each vine for storage trials. All fruit from the same treatment and vine position (300 fruit) were combined and then divided equally into six lots of 50 fruit each. Each lot of fruit was then placed in 5-kg cardboard modular bulk packs with perforated polyliner bags for cold storage. Three packs from each treatment and vine position were stored at 0.5°C and 3 packs were stored at 1.5°C. Fruit were assessed after 12 weeks of storage followed by 7 days at 20°C for external and internal symptoms of storage disorders (chilling damage) and chlorosis of the flesh.

Statistical analysis

Statistical comparisons of vine averages were made using paired *t*-tests (Minitab® R 15.1) with a 95% simultaneous confidence interval. Comparisons of combined samples were made using ANOVA with means separation by the Tukey-Kramer method using a family error rate of 0.05. A two-factor ANOVA was performed for fruit quality data with respect to severity of chlorosis and position on vine. Binomial generalised linear models were fitted for storage temperature, severity of chlorosis and position on vine with each factor or interaction adjusted for all the other factors and interactions of similar complexity.

Results

Vine productivity and flowering

No yield data were collected in 2009, and a prolonged period of freezing temperatures in late-winter 2010 damaged flower buds and so there were substantially reduced numbers of fruit per vine in that year. In 2011, the third year of treatment, Treated vines produced 56% more fruit than Control vines and in 2012 the number of fruit per vine was 23% higher on the Treated vines than Control vines (Table 1). Budbreak (%) and flowers per winter bud were similar on Control and Treated vines, but there were more flowers per shoot on Treated vines (Table 2). Full bloom each year occurred in the last week of April. Although significant ($p=0.031$), there were only slight differences in time of flowering recorded between treatments, with flowering delayed by less than one day (data not shown).

Fruit quality

Commercial harvest was completed at Orchard 1 on 28 October in each year (2009, 2010 and 2011) which was 180, 179 and 185 days after 90% full bloom, respectively. Flesh colour change tended to be more advanced in fruit from Treated than fruit from Control vines during the final period of maturation in each of the three years of this trial (Figure 2). This difference was greatest in 2010 when fruit from Treated vines at commercial harvest had lower flesh colour values (less green colour) and higher SSC and DM than fruit from Control vines (Table 3). However, this was an unusual year with low yields as a consequence of frost damage during spring. Flesh firmness values were similar for fruit from Treated and Control vines across all seasons.

TABLE 1. Effect of iron (Fe) chelate fertiliser on the number of fruit per vine in 2011 and 2012 on *Actinidia chinensis* var. *chinensis* 'Hort16A' kiwifruit vines growing at Orchard 1. Control vines received Fe fertiliser each year during spring and early summer (45 g per vine per annum). Treated vines received the same standard applications plus additional applications in late-summer and autumn (101 g per vine per annum). Values are vine averages $\pm$ SE ($n=20$ vines).

Treatment	Crop load (fruit per vine)	
	2011	2012
Control	243 $\pm$ 22	395 $\pm$ 22
Treated	378 $\pm$ 14	486 $\pm$ 26
Significance	***	**
<i>p</i> -values	<0.001	0.004

Significance: ** = $p<0.01$; *** = $p<0.001$.

TABLE 2. Effect of iron (Fe) chelate fertiliser on budbreak (%), flowers per winter bud and flowers per shoot in 2012 on *Actinidia chinensis* var. *chinensis* 'Hort16A' kiwifruit vines growing at Orchard 1. Control vines received Fe fertiliser each year during spring and early summer (45 g per vine per annum). Treated vines received the same standard applications plus additional applications in late-summer and autumn (101 g per vine per annum). Values are vine averages $\pm$ SE ($n=20$ vines).

Treatment	Budbreak (%)	Flowers per winter bud	Flowers per shoot
Control	63.2 $\pm$ 1.5	1.99 $\pm$ 0.11	3.29 $\pm$ 0.11
Treated	66.0 $\pm$ 1.6	2.19 $\pm$ 0.09	3.54 $\pm$ 0.14
Significance	NS	NS	(*)
<i>p</i> -values	0.253	0.148	0.089

Significance: (*) = $p<0.10$; NS = not significant.

Fruit pigments

At commercial harvest in October 2011, fruit from Treated vines had higher concentrations of the carotenoid pigments lutein and β -carotene than fruit from Control vines (Table 4). Fruit from Treated vines had higher concentrations of chlorophyll *b* than fruit from Control vines, indicating a fundamental change in chlorophyll concentration rather than different rates of de-greening.

Leaf chlorophyll

Primary cane leaves on Treated vines were visibly greener than those on Control vines in May (spring) 2011 following two years of treatment with additional Fe chelate fertiliser. This result was confirmed by estimates of chlo-

rophyll content made with a Minolta SPAD 502 instrument showing significantly higher chlorophyll content in primary cane leaves from Treated vines than those from Control vines (Table 5). Measurements were repeated in October (autumn) using leaves from primary canes produced during spring and leaves on secondary canes produced during summer (Figure 1). Primary cane leaves on both Control and Treated vines had similar chlorophyll content in October, with values equivalent to those recorded in primary cane leaves collected in May from Treated vines (Table 5). Likewise there was no treatment effect on leaf chlorophyll content on secondary cane leaves in October; however, both Treated and Control leaves on secondary canes had less chlorophyll content than leaves on primary canes at the same time.

Soil and nutrient analyses

1. Soil. Soil at Orchard 1 was a sandy loam with 57% sand, 26% loam and 17% clay (data not presented). The soil was alkaline (pH 8.0) with 2.0% organic matter (Table 6). There were no substantial differences in mineral nutrients between soils collected from beneath Treated and Control vines. Most major minerals were within normal ranges expected for other kiwifruit soils in this region (Mauro Sbaraglia, PedonLab, Latina, Italy), except that Ca and P were relatively high and Mg was relatively low compared with industry norms.

2. Leaves. Leaves collected from primary canes in May (spring) 2011, following two years of treatment with additional Fe chelate fertiliser, had higher N and K concentrations on Control vines than on Treated vines (Table 7). Leaf Fe concentrations were similar on both Control and Treated vines. Nutrient concentrations in primary cane leaves collected in October (autumn) were mostly within normal ranges expected for 'Hort16A' orchards in Italy (Mauro Sbaraglia, PedonLab, Latina, Italy); only K concentrations were relatively high. Although no statistical comparisons were possible with leaf analyses from samples collected in October as there was just a single combined sample, the data indicated that Ca, Fe and Mn concentrations were higher in leaves from Control than in leaves from Treated vines, and that concentrations were higher in primary than in secondary cane leaves.

FIGURE 2. Effect of iron (Fe) chelate fertiliser treatments on flesh colour during maturation of *Actinidia chinensis* var. *chinensis* 'Hort16A' kiwifruit grown at Orchard 1. Control vines received Fe fertiliser each year during spring and early summer (45 g per vine per annum). Treated vines received the same standard applications plus additional applications in late-summer and autumn (101 g per vine per annum). Values are treatment averages $\pm$ SE ($n = 30$ fruit).

TABLE 3. Effect of iron (Fe) chelate fertiliser on fruit quality (fresh weight, soluble solids content, flesh firmness, flesh colour and dry matter) at commercial harvest of *Actinidia chinensis* var. *chinensis* 'Hort16A' kiwifruit grown at Orchard 1. Control vines received Fe fertiliser each year during spring and early summer (45 g per vine per annum). Treated vines received the same standard applications plus additional applications in late-summer and autumn (101 g per vine per annum). Values are vine averages $\pm$ SE ($n = 20$ vines with 12 fruit per vine).

Year	Treatment	Fresh weight (g)	Soluble solids content (%)	Flesh firmness (kgf)	Flesh colour (°h)	Dry matter (%)
2009	Control	92.1 $\pm$ 1.4	10.6 $\pm$ 0.3	5.4 $\pm$ 0.1	108.9 $\pm$ 0.4	nd ¹
	Treated	89.1 $\pm$ 2.3	11.2 $\pm$ 0.3	5.3 $\pm$ 0.1	108.1 $\pm$ 0.5	nd
	Significance	NS	NS	NS	NS	
	p-values	0.277	0.107	0.324	0.198	
2010	Control	100.8 $\pm$ 3.1	11.8 $\pm$ 0.3	3.6 $\pm$ 0.2	105.6 $\pm$ 0.4	16.3 $\pm$ 0.3
	Treated	107.6 $\pm$ 2.7	13.2 $\pm$ 0.3	4.1 $\pm$ 0.3	102.8 $\pm$ 0.4	18.1 $\pm$ 0.3
	Significance	NS	**	NS	***	***
	p-values	0.102	0.001	0.161	<0.001	<0.001
2011	Control	91.8 $\pm$ 1.3	13.5 $\pm$ 0.2	5.6 $\pm$ 0.1	106.6 $\pm$ 0.4	18.7 $\pm$ 0.2
	Treated	88.6 $\pm$ 1.3	13.5 $\pm$ 0.2	5.6 $\pm$ 0.1	106.0 $\pm$ 0.4	18.6 $\pm$ 0.2
	Significance	(*)	NS	NS	NS	NS
	p-values	0.058	0.937	0.923	0.273	0.730

¹ nd = no data.

Significance: (*) = $p < 0.10$; ** = $p < 0.01$; *** = $p < 0.001$; NS = not significant.

3. Fruit. Additional applications of Fe chelate over the previous two years increased the Fe concentration of fruit in May (spring) 2011 from Treated vines compared with those from Control vines (Table 8). This difference in Fe was no longer apparent at commercial harvest in October (autumn), by which time there had been a reduction in the concentration of all fruit minerals measured since May. Otherwise, fruit mineral concentrations were similar on Treated and Control vines in May and October.

Postharvest performance

The effect of Fe deficiency on the postharvest performance of fruit was evaluated in 2010 using fruit sampled from Orchard 2 on 28 October (179 days after full bloom).

Overall, there was no effect of prior leaf chlorosis severity on the fruit flesh colour at harvest, with the flesh colour

of fruit from all treatments being between 103 and 104 °h, although the fruit from vines with more severely affected leaves did have higher DM and SSC at harvest (Table 9). More consistent effects were recorded in relation to cane position, with fruit from distal canes having on average lower DM, lower SSC and firmer fruit than fruit from proximal canes. Overall, these observations suggested that the fruit from the distal canes were slightly less advanced than the fruit from the proximal canes.

The incidence of fruit displaying flesh chlorosis was strongly associated with fruit that came from distal canes rather than proximal canes (Table 10; Figure 3). The high incidence of chlorosis affected fruit found in the '1.5°C/Mild chlorosis/Distal canes' sample appears anomalous within this overall trend. Examples of severe fruit chlorosis ("white flesh") were observed early in summer on parts of vines se-

TABLE 4. Effect of iron (Fe) chelate fertiliser on fruit pigments (lutein, β -carotene and chlorophyll *a* and *b* content) at commercial harvest in 2011 of *Actinidia chinensis* var. *chinensis* 'Hort16A' kiwifruit grown at Orchard 1. Control vines received Fe fertiliser each year during spring and early summer (45 g per vine per annum). Treated vines received the same standard applications plus additional applications in late-summer and autumn (101 g per vine per annum). Values are treatment averages $\pm$ SE ($n = 3$ replicates of 30 fruit each).

Treatment	Pigment (mg kg ⁻¹ FW)			
	Lutein	β -carotene	Chlorophyll <i>a</i>	Chlorophyll <i>b</i>
Control	5.02 $\pm$ 0.2	0.68 $\pm$ 0.04	2.86 $\pm$ 0.5	1.26 $\pm$ 0.2
Treated	6.55 $\pm$ 0.6	0.91 $\pm$ 0.09	3.68 $\pm$ 0.3	1.64 $\pm$ 0.1
Significance	*	*	NS	(*)
<i>p</i> -values	0.040	0.041	0.197	0.083

Significance: (*) = $p < 0.10$; * = $p < 0.05$; NS = not significant.

TABLE 5. Effect of iron (Fe) chelate fertiliser on chlorophyll content (SPAD units) of leaves collected in May (spring) and October (autumn) 2011 from primary and secondary canes on *Actinidia chinensis* var. *chinensis* 'Hort16A' kiwifruit vines growing at Orchard 1. Control vines received Fe fertiliser each year during spring and early summer (45 g per vine per annum). Treated vines received the same standard applications plus additional applications in late-summer and autumn (101 g per vine per annum). Values are vine averages $\pm$ SE ($n = 20$ vines).

Leaf sampling (month)	Treatment	Chlorophyll content (SPAD units)			
		Leaves from primary canes	Leaves from secondary canes		
May	Control	35.1 $\pm$ 1.6	–		
	Treated	41.2 $\pm$ 0.3	–		
	Significance	**			
	<i>p</i> -value	0.001			
October	Control	43.4 $\pm$ 0.5	33.3 $\pm$ 0.9	***	<0.001
	Treated	43.7 $\pm$ 0.5	31.2 $\pm$ 1.2	***	<0.001
	Significance	NS	NS		
	<i>p</i> -values	0.627	0.175		
				Significance	<i>p</i> -values

Significance: ** = $p < 0.01$; *** = $p < 0.001$; NS = not significant.

TABLE 6. Organic matter, pH and nutrient content of soil samples (20 cm subsoil) collected in October (autumn) from beneath Control and Treated *Actinidia chinensis* var. *chinensis* 'Hort16A' kiwifruit vines growing at Orchard 1. Control vines received Fe fertiliser each year during spring and early summer (45 g per vine per annum). Treated vines received the same standard applications plus additional applications in late-summer and autumn (101 g per vine per annum). Values are for a combined sample taken from below 20 vines per treatment.

Treatment	Organic matter (%)	pH	N (%)	P K Ca Mg Fe Mn					
				(ppm)					
Control	1.9	8.0	0.13	34	418	1,450	300	9.0	2.2
Treated	2.1	8.0	0.12	30	442	1,500	260	8.6	1.7

TABLE 7. Effect of iron (Fe) chelate fertiliser on nutrient content of leaves collected in May (spring) and October (autumn) 2011 from primary and secondary canes on *Actinidia chinensis* var. *chinensis* 'Hort16A' kiwifruit vines growing at Orchard 1. Control vines received Fe fertiliser each year during spring and early summer (45 g per vine per annum). Treated vines received the same standard applications plus additional applications in late-summer and autumn (101 g per vine per annum). Samples collected in May were replicated ($n=3$ replicates of 6–7 vines); October samples were combined into a single sample per treatment and cane type. Values are treatment/cane type averages $\pm$ SE.

Leaf sampling (month)	Treatment	Cane type	N (%)	P (%)	K (%)	Ca (%)	Mg (%)	Fe (ppm)	Mn (ppm)
May	Control	Primary	3.0 $\pm$ 0.03	0.37 $\pm$ 0.04	3.2 $\pm$ 0.24	2.6 $\pm$ 0.23	0.37 $\pm$ 0.01	66 $\pm$ 12.9	47 $\pm$ 6
	Treated	Primary	2.5 $\pm$ 0.04	0.23 $\pm$ 0.01	2.1 $\pm$ 0.09	2.9 $\pm$ 0.22	0.37 $\pm$ 0.01	70 $\pm$ 7.5	56 $\pm$ 15
	Significance		*	NS	(*)	NS	NS	NS	NS
<i>p-values</i>									
October	Control	Primary	0.022	0.123	0.071	0.546	1.000	0.698	0.694
	Treated	Primary	1.4	0.26	1.9	7.1	0.48	92	72
	Treated	Primary	1.3	0.20	1.8	4.3	0.40	74	42
Control	Control	Secondary	1.7	0.21	2.3	2.9	0.30	80	27
	Treated	Secondary	1.3	0.19	1.8	2.8	0.30	56	21

Significance: (*) = $p < 0.05$; * = $p < 0.05$; NS = not significant.

TABLE 8. Effect of iron (Fe) chelate fertiliser on nutrient content of fruit collected in May (spring) and October (autumn) 2011 from *Actinidia chinensis* var. *chinensis* 'Hort16A' kiwifruit vines growing at Orchard 1. Control vines received Fe fertiliser each year during spring and early summer (45 g per vine per annum). Treated vines received the same standard applications plus additional applications in late-summer and autumn (101 g per vine per annum). Values are treatment averages $\pm$ SE ($n=3$ replicates of 6–7 vines).

Leaf sampling (month)	Treatment	N (%)	P (%)	K (%)	Ca (%)	Mg (%)	Fe (ppm)	Mn (ppm)
May	Control	2.80 $\pm$ 0.07	0.35 $\pm$ 0.01	3.20 $\pm$ 0.01	0.45 $\pm$ 0.03	0.18 $\pm$ 0.01	23 $\pm$ 0.9	6.7 $\pm$ 0.9
	Treated	2.65 $\pm$ 0.10	0.32 $\pm$ 0.01	2.97 $\pm$ 0.07	0.49 $\pm$ 0.03	0.19 $\pm$ 0.01	27 $\pm$ 0.6	8.0 $\pm$ 1.2
	Significance	NS	NS	(*)	NS	NS	**	NS
<i>p-values</i>								
October	Control	0.380	0.157	0.073	0.635	0.529	0.008	0.508
	Treated	0.93 $\pm$ 0.05	0.17 $\pm$ 0.01	1.78 $\pm$ 0.09	0.09 $\pm$ 0.01	0.07 $\pm$ 0.01	19 $\pm$ 2.0	2.0 $\pm$ 0.5
	Treated	0.96 $\pm$ 0.02	0.17 $\pm$ 0.01	1.77 $\pm$ 0.04	0.07 $\pm$ 0.01	0.08 $\pm$ 0.01	17 $\pm$ 1.4	1.5 $\pm$ 0.2
Control	Control	NS	NS	NS	NS	NS	NS	NS
	Treated	0.683	0.856	0.867	0.140	0.396	0.397	0.341

Significance: (*) = $p < 0.10$; ** = $p < 0.01$; NS = not significant.

verely affected by leaf chlorosis; symptoms were less obvious at harvest in October. Examples of fruit chlorosis were also observed in fruit after 12 weeks of storage (Table 10; Figure 4).

The incidence of chilling injury (CI) was generally, but not always, higher when fruit were stored at 0.5°C than at 1.5°C (Table 10; Figure 4). In addition, there was a greater incidence of chilling injury in fruit from distal canes than in fruit from proximal canes. This positional difference may be associated with at-harvest compositional differences detailed in Table 9.

Discussion

This research is the first description of the cumulative effect of Fe deficiency-induced leaf chlorosis on vine productivity and fruit quality of a yellow-fleshed kiwifruit. Fruit of 'Hort16A', whose flesh colour changes from green

to yellow during the final stages of maturation and ripening (Richardson et al., 2011), appear to be especially sensitive to Fe deficiency, either directly through lack of Fe to support early fruit development in spring, or indirectly through Fe deficiency-induced leaf chlorosis with reduced leaf chlorophyll content and lower vine productivity. Both the spring and summer growth flushes exhibited leaf chlorosis. In extreme examples, fruit chlorosis was also observed, especially in fruit harvested from distal parts of vines, where Fe supply from the roots would be expected to be most limiting. Field observations were that leaf chlorosis was also more prevalent in leaves sampled from these distal positions. This is consistent with chlorosis being caused by impaired Fe uptake and transport within the plant (Tagliavini et al., 2000).

Standard applications of Fe chelate in spring and early summer were not sufficient to eliminate chlorosis in the leaves and fruit. While applications of additional Fe chelate

TABLE 9. Effect of leaf chlorosis severity on fruit quality (fresh weight, soluble solids content (SSC), flesh firmness, flesh colour and dry matter) at commercial harvest in October (autumn) 2010 of *Actinidia chinensis* var. *chinensis* 'Hort16A' kiwifruit grown at Orchard 2. Fruit were selected from vines with mild or severe leaf chlorosis in the previous spring (May) and from fruiting canes located in proximal or distal positions relative to the vine trunk. Values are treatment averages $\pm$ SE ($n = 90$ fruit). Values within a column not sharing a common letter are significantly different ($p < 0.05$).

Leaf chlorosis	Position	Fresh weight (g)	SSC (%)	Flesh firmness (kgf)	Flesh colour ($^{\circ}$ h)	Dry matter (%)
Mild	Proximal	102.0 $\pm$ 1.8 a	12.7 $\pm$ 0.1 b	4.0 $\pm$ 0.1 a	103.6 $\pm$ 0.2	17.3 $\pm$ 0.1 b
	Distal	96.2 $\pm$ 1.8 b	12.6 $\pm$ 0.2 b	4.3 $\pm$ 0.1 a	103.9 $\pm$ 0.2	17.3 $\pm$ 0.1 b
Severe	Proximal	97.7 $\pm$ 1.7 ab	13.7 $\pm$ 0.1 a	3.4 $\pm$ 0.1 b	103.5 $\pm$ 0.2	17.9 $\pm$ 0.1 a
	Distal	100.9 $\pm$ 1.8 ab	12.5 $\pm$ 0.1 b	4.9 $\pm$ 0.1 a	104.0 $\pm$ 0.2	17.4 $\pm$ 0.1 b
<i>Statistical analyses</i>						
Main effects	Chlorosis	0.923	0.001	0.934	0.964	0.012
	Position	0.467	<0.001	<0.001	0.074	0.026
Interaction	Chlorosis $\times$ Position	0.010	<0.001	<0.001	0.859	0.033

TABLE 10. Effect of leaf chlorosis severity on incidence of flesh chlorosis and chilling injury after 12 weeks of storage at either 0.5°C or 1.5°C in *Actinidia chinensis* var. *chinensis* 'Hort16A' kiwifruit grown at Orchard 2. Fruit had been harvested at commercial harvest in October (autumn) 2010 from vines that had mild or severe leaf chlorosis in the previous May (spring) and from fruiting canes located proximal or distal to the vine trunk. Values are treatment averages $\pm$ SE ($n = 3$ packs, each of 50 fruit). Values within a column not sharing a common letter are significantly different ($p < 0.05$).

Storage temperature	Leaf chlorosis severity	Cane position	Incidence (%)	
			Flesh chlorosis	Chilling injury
0.5°C	Mild	Proximal	0.9 ± 0.9 b	20.2 ± 2.8 a
		Distal	6.6 ± 2.3 ab	18.6 ± 3.5 a
	Severe	Proximal	2.6 ± 0.1 b	10.5 ± 1.6 ab
		Distal	10.6 ± 4.5 ab	12.8 ± 3.2 ab
1.5°C	Mild	Proximal	0.0 ± 0.0 b	12.2 ± 2.5 ab
		Distal	14.1 ± 2.4 a	3.6 ± 0.7 b
	Severe	Proximal	2.2 ± 1.2 b	17.9 ± 2.1 a
		Distal	5.9 ± 3.2 ab	4.6 ± 2.6 b
Statistical analyses				
Main effects	Temperature		0.666	0.003
	Chlorosis		0.884	0.393
	Position		<0.001	0.004
Interactions	Temperature × Chlorosis		0.136	0.012
	Temperature × Position		0.754	<0.001
	Chlorosis × Position		0.104	0.722
	Temperature × Chlorosis × Position		0.241	0.587

FIGURE 3. Iron deficiency-induced leaf and fruit chlorosis in July (summer) 2010 on *Actinidia chinensis* var. *chinensis* 'Hort16A' kiwifruit vines growing at Orchard 2. Leaves and fruit on left show severe symptoms compared with no symptoms on right.

from summer through autumn increased leaf chlorophyll content in the following spring, the summer growth flush on these vines still showed significant leaf chlorosis, indicating that the vines did not have sufficient Fe to support this new growth (Briat et al., 2015; Tagliavini et al., 2000). The summer growth flush on 'Hort16A' vines in Italy is typically very vigorous compared with that of 'Hayward' vines (Snelgar et al., 2010).

The combined effect of leaf chlorosis on 'Hort16A' vines in spring and again in summer clearly had a negative effect on vine productivity. Although it was not possible to make worthwhile yield comparisons in 2010 because flowering across all vines was reduced by severe winter frosts, treatment effects on productivity were obvious in 2011 and 2012, with a 56% and 23% increase in average fruit number per vine on Treated and Control vines, respectively.

Leaf yellowing can also be caused by photoinhibition. Kiwifruit leaves are known to be highly sensitive to photoinhibition during spring when temperatures are low and irradiance is high (Greer, 1995). It is likely that there is a significant energy cost to the plant in simply repairing this damage (Losciale et al., 2010). It would be interesting in future studies to compare the energy deficit from photoinhibition with that created by leaf chlorosis and to determine if there is an interaction between the two.

Treatment-induced differences in fruit yield may have accounted for the differences in leaf nutrient concentrations recorded at the end of the growing season (Buwalda and Smith, 1990). High crop loads on Treated vines appeared to reduce leaf concentrations of the less mobile elements Fe, Mn and Ca. Higher crop loads did not appear to affect fruit nutrient concentrations.

Timing of harvest of 'Hort16A' fruit is largely determined by flesh colour change from green to yellow, with flesh colour decreasing by 1.0 °h approximately every 3 days during the period of rapid colour change prior to commercial harvest (Figure 1; Minchin et al., 2003). However, it should also be noted that flesh colour, firmness and SSC are not tightly associated and may be dissociated depending on growing conditions (Burdon et al., 2014). The additional Fe chelate treatments in this study advanced the rate of flesh colour change slightly and increased fruit DM, although this result was confounded by treatment-induced differences in crop load. 'Hort16A' fruit from vines with high crop loads generally have delayed colour change and lower DM than fruit from low cropping vines (Boyd and Barnett, 2011). In 2010 it was estimated that the additional applications of Fe chelate advanced flesh colour change by 9 days (102.8 °h compared with 105.6 °h at harvest) and increased fruit DM by 1.8 percentage units (from 16.3% to 18.1%). Treated vines in 2011 were carrying considerably more fruit, and treatment effects on flesh colour change and DM were less pronounced. There was no evidence that treatment affected the subsequent time of flowering. Future research to determine the full effect of Fe deficiency on fruit quality would need to maintain equivalent crop loads on treated and untreated vines.

Flesh colour change from green to yellow involves a reduction in chlorophyll content of fruit, exposing the underlying carotenoid pigments (Montefiori et al., 2009). Although the additional applications of Fe chelate either directly or indirectly appeared to increase the chlorophyll concentrations in fruit, which could be expected to delay flesh colour change, this did not occur, because the underlying carotenoid concentrations were also increased.

FIGURE 4. Iron deficiency-induced chlorosis in *Actinidia chinensis* var. *chinensis* 'Hort16A' after 12 weeks of cold storage. Fruit were from Orchard 2. The two fruit on the left have severe chlorosis, the fruit on the right has very mild chlorosis. All fruit are showing typical symptoms of chilling injury.

Fe deficiency and leaf chlorosis did not have a severe negative effect on the postharvest performance of 'Hort16A' fruit, apart from the obvious fruit chlorosis. This chlorosis was most obvious in spring and was clearly visible without needing to cut fruit open. External symptoms of fruit chlorosis were less obvious by summer and at commercial harvest in autumn, so it would not be feasible to visually segregate these fruit at harvest. This would be more effective if done during commercial early-summer fruit thinning.

The lack of a storage temperature effect on fruit chlorosis merely reflected the fact that fruit chlorosis developed prior to harvest and was not a storage disorder, unlike chilling injury. The strong overall positional effect on postharvest quality was largely driven by the chilling expression among fruit stored at 1.5°C, as indicated by the significant interaction effect between storage temperature and cane position (Table 10). The interaction effect between storage temperature and prior leaf chlorosis may also be a reflection of the compositional differences in the fruit associated with the prior leaf chlorosis. That chilling injury incidence was greater in fruit at the lower storage temperature is not surprising, but it may be that at the slightly higher storage temperature, differences in the populations of fruit in different treatments were more obvious than at the harsher lower storage temperature.

In this study we more than doubled the application of Fe chelate compared with current standard orchard recommendations. While this led to improvements in vine yields and fruit quality it was not sufficient to eliminate leaf chlorosis. A rough calculation from our data shows that the amount of Fe removed annually through crop removal was approximately 1 g Fe per vine, compared with the 45 and 101 g Fe per vine we applied to our Control and Treated vines, respectively. Clearly, adding more Fe chelate would not be economically or environmentally sustainable, considering its additional cost and the risk of excess Fe leaching into the groundwater (Tagliavini et al., 2000). Various more sustainable solutions have been suggested for kiwifruit, including intercropping rows of vines with grass and non-grass plants that secrete phytosiderophores into the soil and assist uptake of Fe by the vine (Briat et al., 2015). However, the development of rootstocks tolerant of high pH soils might offer the best and most sustainable solution to prevent Fe deficiency-induced leaf and fruit chlorosis in kiwifruit (Viti et al., 1990; Rombola et al., 2002; Rombola and Tagliavini, 2006).

Acknowledgments

We thank Maurizio Savorani and Renato Cantagalli for access to their orchards; Sauro Graziani and Mauro Marchetti for assistance in setting up the trials; Adamo Rombola, Christos Xiloyannis, Bartolomeo Dichio and Mauro Sbaraglia for their very useful discussions on Fe deficiency in kiwifruit in Italy; and Mirco Montefiori for advice on pigment analyses. We thank Duncan Hedderley for statistical analyses in Tables 9 and 10, Robert Lamberts for assistance with Figure 3, and Ann Smith for assistance with formatting. We also thank Simona Nardoza for her critical reading of the manuscript. This work was funded by Plant & Food Research's KRIP programme 'Actinidia in a Global Environment'.

References

Abadía, J., Vázquez, S., Rellán-Álvarez, R., El-Jendoubi, H., Abadía, A., Álvarez-Fernández, A., and López-Millán, A. (2011). Towards a knowledge-based correction of iron chlorosis. *Plant Physiol. Biochem.* 49(5), 471–482. <https://doi.org/10.1016/j.plaphy.2011.01.026>.

Álvarez-Fernández, A., Paniagua, P., Abadía, J., and Abadía, A. (2003). Effects of Fe deficiency chlorosis on yield and fruit quality in peach (*Prunus persica* L. Batsch). *J. Agric. Food Chem.* 51, 5738–5744. <https://doi.org/10.1021/jf034402c>.

Álvarez-Fernández, A., Abadía, J., and Abadía, A. (2006). Iron deficiency, fruit yield and fruit quality. In *Iron Nutrition in Plants and Rhizospheric Microorganisms*, L.L. Barton, and J. Abadía, eds. (Dordrecht: Springer), p. 85–101. https://doi.org/10.1007/1-4020-4743-6_4.

Álvarez-Fernández, A., Melgar, J.C., Abadía, J., and Abadía, A. (2011). Effects of moderate and severe iron deficiency chlorosis on fruit yield, appearance and composition in pear (*Pyrus communis* L.) and peach (*Prunus persica* (L.) Batsch). *Environm. Exp. Bot.* 71, 280–286. <https://doi.org/10.1016/j.envexpbot.2010.12.012>.

Anon. (2008). Horticulture and arable monitoring report. (Wellington, New Zealand: MAF Policy, Ministry of Agriculture and Forestry), SOPI@mpi.govt.nz (accessed August, 2020).

Baldi, E., Amadei, P., Pelliconi, F., and Marangoni, B. (2009). Efficacia dell'epoca di somministrazione del chelato di ferro nella prevenzione della clorosi ferrica in piante di actinidia (*A. deliciosa*). *Italus Hortus* 16(5), 189–191.

Belrose, Inc. (2016). World Kiwifruit Review, 2016 Edn. <https://www.e-belrose.com/world-kiwifruit-review> (accessed August, 2020).

Boyd, L.M., and Barnett, A.M. (2011). Manipulation of whole-vine carbon allocation using girdling, pruning, and fruit thinning affects fruit numbers and quality in kiwifruit. *HortScience* 46(4), 590–595. <https://doi.org/10.21273/HORTSCI.46.4.590>.

Briat, J.-F., Dubos, C., and Gaymard, F. (2015). Iron nutrition, biomass production, and plant product quality. *Trends Plant Sci.* 20(1), 33–40. <https://doi.org/10.1016/j.tplants.2014.07.005>.

Burdon, J., and Lallu, N. (2011). Kiwifruit (*Actinidia* spp.). In *Postharvest Biology and Technology of Tropical and Subtropical Fruit*, Vol. 3, Cocona to Mango, E.M. Yahia, ed. (U.K.: Woodhead Publishing Ltd.), p. 326–360. ISBN 978-1-84569-735-8.

Burdon, J., Pidakala, P., Martin, P., McAtee, P.A., Boldingh, H.L., Hall, A., and Schaffer, R.J. (2014). Postharvest performance of the yellow-fleshed 'Hort16A' kiwifruit in relation to fruit maturation. *Postharvest Biol. Technol.* 92, 98–106. <https://doi.org/10.1016/j.postharvbio.2014.01.004>.

Burdon, J., Pidakala, P., Martin, P., and Billing, D. (2017). Softening of 'Hayward' kiwifruit on the vine and in storage: The effects of temperature. *Sci. Hortic.* 220, 176–182. <http://dx.doi.org/10.1016/j.scienta.2017.04.004>.

Buwalda, J.G., and Smith, G.S. (1990). Acquisition and utilization of carbon, mineral nutrients, and water by the kiwifruit vine. *Hortic. Rev.* 12, 307–347. <https://doi.org/10.1002/9781118060858.ch7>.

Civolani, C. (2006). Effetti di strategie agronomiche preventive della clorosi ferrica sulla dinamica dello sviluppo radicale e la produttività in *Actinidia*. Tesi di Laurea (Università di Bologna, Alma Mater Studiorum).

Ferguson, A.R., and Bollard, E.G. (1990). Domestication of the kiwifruit. In *Kiwifruit: Science and Management*, I.J. Warrington, and G.C. Weston, eds. (Auckland: Ray Richards Publisher in association with the New Zealand Society for Horticultural Science), p. 165–246.

Greer, D.H. (1995). Effect of canopy position on the susceptibility of kiwifruit (*Actinidia deliciosa*) leaves on vines in an orchard environment to photoinhibition throughout the growing season. *Austral. J. Plant Physiol.* 22, 299–309. <https://doi.org/10.1071/PP9950299>.

Lallu, N. (1997). Low temperature breakdown in kiwifruit. *Acta Hortic.* 444, 579–586. <https://doi.org/10.17660/ActaHortic.1997.444.89>.

Losciale, P., Chow, W.S., and Corelli-Grappadelli, L. (2010). Modulating the light environment with the peach “asymmetric orchard”: Effects on gas exchange performances, photoprotection, and photoinhibition. *J. Exp. Bot.* 61(4), 1177–1192. <https://dx.doi.org/10.1093/jxb/erp387>.

Loupassaki, M.H., Lionakis, S.M., and Androulakis, I.I. (1997). Iron deficiency in kiwi and its correction by different methods. *Acta Hort.* 444, 267–272. <https://doi.org/10.17660/ActaHortic.1997.444.41>.

Minchin, P.E.H., De Silva, N., Snelgar, W.P., Richardson, A.C., and Thorp, T.G. (2003). Modelling of colour development in the fruit of *Actinidia chinensis* ‘Hort16A’. *N. Z. J. Crop Hortic. Sci.* 31, 41–53. <http://dx.doi.org/10.1080/01140671.2003.9514234>.

Montefiori, M., McGhie, T.K., Hallett, I.C., and Costa, G. (2009). Changes in pigments and plastid ultrastructure during ripening of green-fleshed and yellow-fleshed kiwifruit. *Sci. Hortic.* 119(4), 377–387. <http://dx.doi.org/10.1016/j.scienta.2008.08.022>.

Richardson, A.C., Boldingh, H.L., McAtee, P.A., Gunaseelan, K., Zhi Wei, L., Atkinson, R.G., David, K.M., Burdon, J.N., and Schaffer, R.J. (2011). Fruit development of the diploid kiwifruit, *Actinidia chinensis* ‘Hort16A’. *BMC Plant Biol.* 11(182). <https://doi.org/10.1186/1471-2229-11-182>.

Rombolà, A.D., and Tagliavini, M. (2006). Iron nutrition of fruit crops. In *Nutrition in Plants and Rhizospheric Microorganisms*, L.L. Burton, and J. Abadía, eds. (The Netherlands: Springer), p. 61–83. http://dx.doi.org/10.1007/1-4020-4743-6_3.

Rombolà, A.D., Brüggemann, W., López-Millán, A.F., Tagliavini, M., Abadía, J., Marangoni, B., and Moog, P.R. (2002). Biochemical responses to iron deficiency in kiwifruit (*Actinidia deliciosa*). *Tree Physiol.* 22, 869–875. <https://doi.org/10.1093/treephys/22.12.869>.

Snelgar, W.P., Thorp, T.G., Spinelli, R., and Brun, S. (2010). We don’t know how lucky we are? *N. Z. Kiwifruit J.*, Jul./Aug., 14–18.

Tagliavini, M., Abadía, J., Rombolà, A.D., Abadía, A., Tsipouridid, C., and Marangoni, B. (2000). Agronomic means for the control of iron-deficiency chlorosis in deciduous fruit trees. *J. Plant Nutr.* 23, 2077–2022. <https://doi.org/10.1080/01904160009382161>.

Tagliavini, M., and Rombola, A.D. (2001). Review – Iron deficiency and chlorosis in orchard and vineyard ecosystems. *Eur. J. Agron.* 15, 71–92. [https://doi.org/10.1016/S1161-0301\(01\)00125-3](https://doi.org/10.1016/S1161-0301(01)00125-3).

Testolin, R., and Ferguson, A.R. (2009). Kiwifruit production and marketing in Italy. *N. Z. J. Crop Hortic. Sci.* 37, 1–32. <https://doi.org/10.1080/01140670909510246>.

Thorp, T.G., Clearwater, M.J., Barnett, A.M., Martin, P.J., Blattmann, P.J., and Currie, M.B. (2007). ‘Hort16A’ fruit beak end softening and shrivelling in California. *Acta Hort.* 753, 389–396. <https://doi.org/10.17660/ActaHortic.2007.753.49>.

Thorp, T.G., Barnett, A.M., and Blattmann, P.J. (2011). What are the productivity limits for ‘Hayward’ kiwifruit? *Acta Hort.* 913, 419–424. <https://doi.org/10.17660/ActaHortic.2011.913.56>.

Viti, R., Xiloyannis, C., Trinci, M., and Ragone, A.F. (1990). Effect of calcareous soil on vegetative growth of own rooted and grafted kiwi fruit trees. *Acta Hort.* 282, 209–216. <https://doi.org/10.17660/ActaHortic.1990.282.27>.

Wang, N., Yao, C., Li, M., Li, C., Liu, Z., and Ma, F. (2019a). Anatomical and physiological responses of two kiwifruit cultivars to bicarbonate. *Sci. Hortic.* 243, 528–536. <https://doi.org/10.1016/j.scienta.2018.09.011>.

Wang, N., Jiao, X., Guo, T., Li, C., Liu, Z., and Ma, F. (2019b). Time course of physiological responses in kiwifruit induced by bicarbonate. *Trees* 33(6), 1711–1722. <http://dx.doi.org/10.1007/s00468-019-01892-9>.

Received: Aug. 6, 2020

Accepted: Feb. 19, 2021

Addresses of authors:

T.G. Thorp^{1,*}, A.M. Barnett², C. Civolani³, R. Spinelli⁴, N. Lallu⁵ and J. Burdon⁵

¹ Plant & Food Research Australia Pty Ltd., 7 Bevan St, Albert Park VIC 3206, Australia

² The New Zealand Institute for Plant and Food Research Ltd., Te Puke Research Centre, 412 No. 1 Road, RD 2, Te Puke 3182, New Zealand

³ Eurofins Agrosience Services, Via XXV Aprile, 8/2-8/3, 40016 San Giorgio di Piano BO, Italy. Currently with CIFO S.r.l, Via Oradour 6/8, 40016 San Giorgio di Piano BO, Italy

⁴ Zespri Fresh Produce Italy, Via dei Rangers 1, Cisterna di Latina 04012, Italy

⁵ The New Zealand Institute for Plant and Food Research Ltd., Mt Albert Research Centre, Private Bag 92 169, Auckland 1142, New Zealand

* Corresponding author;

E-mail: grant.thorp@plantandfood.com.au