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Genetic and environmental influence on foliar carbon isotope composition, nitrogen availability and fruit yield of 5-year-old mango plantation in tropical Australia

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Abstract

Purpose The aim of this study was to quantify the effect of different varieties, planting densities, tree training systems and canopy aspect (north and south) on tree water use efficiency and nitrogen (N) availability in relation to mango fruit yield and fruit size as well as soil fertility (particularly total carbon (C) and total N as well as C and N isotope compositions) in a 5-year-old mango plantation of tropical Australia.

Material and Methods Mango foliar samples were collected from a 5-year-old, factorial field experiment, where we tested the effects of two mango varieties (Calypso vs Keitt); two planting densities (medium vs high); two training systems (single leader vs conventional); and two sampling canopy aspects (north vs south) on foliar total C (%), total N (%), and stable C and N isotope compositions (δ^{13}C and δ^{15}N). The 0–10 cm of surface soils were also assessed for total C, total N, and δ^{13}C and δ^{15}N of different varieties, planting densities, and training systems. In addition, mango fruit yield, and fruit size were measured.

Results There were significant genetic effects on foliar total N, tree water use efficiency (WUE) as reflected by foliar δ^{13}C, N availability as indicated by foliar total N and δ^{15}N, mango fruit yield, and fruit size in 5-year-old mango trees in tropical Australia. Overall, Keitt had higher foliar δ^{13}C and N availability (higher total N and lower δ^{15}N) as well as higher mango yield and greater fruit size, compared with those of Calypso. There were also significant environmental influences on foliar δ^{13}C and N availability. In particular, high planting density had higher N availability (higher total N), and lower foliar δ^{13}C as well as higher N loss (higher δ^{15}N), compared with those of medium planting density. High planting density treatment also had higher soil total N, compared with that of medium planting density treatment. The conventional training system had higher N availability and foliar δ^{13}C, compared with those of the single leader training system. The northern side of tree canopy (sunny side) had lower fruit number, compared with that of the southern side (shady side) of tree canopy.

Conclusion There were significant genetic and environmental influences on tree WUE and N availability as well as mango fruit yield and fruit size in the 5-year-old mango trees. Among them, Keitt's fruit was significantly larger than Calypso and had higher foliar δ^{13}C (higher WUE). Although high planting density increased soil total N, it also resulted in lower foliar δ^{13}C and more N loss. Our results highlighted the significant potential for improvement of foliar δ^{13}C and N availability as well as fruit yield and soil fertility with both genetic selection and site management regimes.

Keywords Mango variety · Water use efficiency · N availability · Planting density · Training system · Environmental influence

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1 Introduction

There are increasing demands and opportunities for developing soil and food security in the context of the growing world population and rapid global urbanization. Against the backdrop of unprecedented climate change (McDonald et al. 2011; Xu et al. 2014; King et al. 2017; Lewis et al. 2017), water restrictions (Steduto et al. 2012; Gorelick and Zheng 2015) and increasing threats to soil, food, and water security, we are faced with the major problem of maintaining and improving agricultural productivity in Australia and elsewhere. As a result, there is an urgent need for the integration and transformation of agricultural production systems to address the challenges for the global sustainability (Liu et al. 2015; Wigboldus et al. 2016; Martin et al. 2018). Understanding how orchard trees respond to different management practices may help us identify ways to navigate through these challenges. With increasing populations and a need for soil and food security, there is a trend for orchards to move to intensification (planting trees at high density). However, there is little understanding of the effects of intensification on soil and water use. As production costs and environmental pressures (especially global warming and decline in freshwater supply) continue to increase, it may be more and more important to select varieties with higher water use efficiency (WUE) and the application of water-saving strategies in agricultural production. Mango (*Mangifera Indica*) is known for its excellent exotic flavor and is often referred to as the king of fruits. At the same time, mango is also one of the most important commercial fruit crops in Queensland, Australia. It is second only to bananas in terms of yield, planting area, and popularity (Belton et al. 1993; Gil et al. 2000).

Moisture, nutrients, and light are important for plant growth and critical to high productivity. Plant cells use moisture during growth and expansion (McElrone et al. 2013; Robbins and Dinneny 2015). Most of the water in plants is lost through transpiration. External factors such as illumination and moisture, which influence plant photosynthesis and transpiration, can also affect plant $\delta^{13}C$ values (Cernusak et al. 2007; Diefendorf et al. 2010). The $\delta^{13}C$ of the leaves is used as an indicator of the long-term WUE of plants (Warren et al. 2001; Nie et al. 2014; Dong et al. 2015). Meanwhile, $\delta^{13}C$ of plants is also affected by many factors, such as competition between plants, different parts of plants and their surrounding environments, such as temperature, light, CO_2 concentration, and soil nutrients (Xu et al. 2000; Sun et al. 2003; Wang et al. 2008; Xu et al. 2009; Li et al. 2017). Most studies have shown that $\delta^{13}C$ of terrestrial plant organic matter is different between different types of plants, and plants are grown in different environments, hence it is possible to select plant varieties with improved WUE, based on specific site management factors (Afonso et al. 2017; Fang et al. 2018; Saha 2018; Mangalassery et al. 2019). Many technologies can be used to improve WUE and productivity in orchards. These technologies range from site management to the assessment of genetics to improve plant WUE and increase productivity (Xu et al. 2000; Xu et al. 2009; Pascual et al. 2016; Zheng et al. 2017).

Plant growth and development depend to some degree on the availability of nutrients in the soil (Xu et al. 2000; Xu et al. 2009; Morgan and Connolly 2013; Razaq et al. 2017). Among all nutrients required for plant growth, nitrogen (N) is a key component of proteins and nucleic acids, which are essential for organisms. N also influences the development of leaf area and helps to maintain photosynthetic efficiency, thereby affecting the formation of plant organs, root crown development, and photosynthesis (Chun et al. 2005; Dordas and Sioulas 2008). The lack of N inhibits crop growth and photosynthesis, which affects crop yield, quality, and orchard profitability (Shangguan et al. 2000). From a soil science perspective, any mechanism of N losses (e.g., ammonia volatilization, nitrate leaching, and denitrification) preferentially take the lighter isotope (^{14}N) and leaves the heavier N isotope (^{15}N) (Högberg 1997). Craine et al. (2009) found that soil rich in ^{15}N showed an increase in N-cycle acceleration and microbial activity or N loss processes. Studies have shown factors such as microbial activity, temperature, vegetation, precipitation can influence N cycling (Craine et al. 2009; Ibell 2014; Craine et al. 2015). Therefore, the dynamics of N cycling in plants and soils can be measured using soil and plant $\delta^{15}N$ (Kahmen et al. 2008; Craine et al. 2009; Reverchon et al. 2014).

Orchard management options such as increasing or decreasing planting density can be used to affect the overall health and yield of plants by regulating plant growth and photosynthesis (Ciampitti and Vyn 2011; Díez et al. 2016; Hecht et al. 2016; Valleser 2018). Some studies have shown that crop planting density can affect soil fertility (Pavan et al. 1999; Rangel et al. 2008). Among them, planting density has been shown to significantly affect root growth (Loades et al. 2010), soil flora (Wang et al. 2018), and soil nutrient content (Li et al. 2008). Too low planting density may make fruit trees more susceptible to weeds, and excessive planting density may force fruit trees to compete for scarce nutrients and water to reduce photosynthesis of plants, leading to poor growth and development of fruit trees (He and Bazzaz 2003; Saha 2018). In addition to the tree planting spacing, the training system (i.e., tree height and crown shape) can also significantly affect the way that light is distributed and intercepted by canopies. In previous experiments, the response of mango trees to canopy management was quite different (Das and Jana 2012; Asrey et al. 2013). Proper pruning methods can increase the probability of light passing through the canopy and increases the efficiency of photosynthesis (Shalini and Sharma 2006; Yue et al. 2018). Sometimes, pruning promoted bud overgrowth or bud growth at the wrong time, thereby inhibiting flowering and fruiting (Ledesma et al. 2017).

Therefore, effective tree canopy management is essential if high-density orchards are to be planted. At the same time, the two treatments (planting density and training system) may have significant impacts on soil C and N dynamics, which in turn leads to changes in δ^{13}C and δ^{15}N in the soil and foliage.

This research aimed to investigate how orchard intensification using two training systems (single leader and conventional) and planting densities (medium and high) influenced the C and N cycling (total C, total N, δ^{13}C, and δ^{15}N) in the plant-soil interface using two varieties (Keitt and Calypso) grown under similar conditions. In this experiment, the main sources of N studied in the mango trees resulted from the soil and its management. As a result, soil N may be one of the factors affecting the δ^{15}N value in mango leaves, as well as indicating important relationships between N cycling processes in the plant-soil interface (Ibell et al. 2013; Bai et al. 2015; Wang et al. 2015; Zhang et al. 2018). Therefore, it is hypothesized that orchard intensification and its management including training systems (single leader and conventional), variety (Keitt and Calypso), and planting densities (medium and high) will influence (1) δ^{15}N in the orchard trees, as well as indicating important relationships between N cycling processes in the plant-soil interface; and (2) canopy total C, total N, and δ^{13}C and δ^{15}N in the leaves to better understand the C and N cycling processes in the tropical mango plantations.

2 Material and method

2.1 Study area and experiment design

Soil and mango foliage samples tested in the experiment were collected at the Walkamin Research Station of the Queensland Department of Agriculture and Fisheries, Mango Planting System Experiment (17° 8′ 17″ S 145° 25′ 41″ E; elevation 599 m). Soil types are a Yellow to Brown Ferrosol under the Australian Soil classification (Enderlin et al. 1997). Soils are generally deeply motteled yellow-brown pedal clay with a neutral pH and ferromagniferous nodules accumulated through the profile.

The experiment included three experimental factors, two mango varieties (Calypso^{TM} and Keitt), two planting densities (medium-416 tree/ha and high-1250 tree/ha), and two training systems (conventional and single leader). Each combination of variety, planting density, and training system was replicated in 6 complete blocks. Each sub-sub-plot consisted of three datum rows with two outer guard rows, and each row comprised five trees which included a guard at either end and three datum trees in the middle. Any sampling in the experiment did not include the guard row to prevent root extension between the blocks and affect the accuracy of the experimental data. The high-density trees were irrigated with (8 L/h drippers) in a continuous wetted pattern along the row while the medium-density trees were irrigated with (35 L/h) sprinklers at the base of each tree. Both high- and medium-density trees were subjected to the same rates of fertilizer (rates according to age by Meurant et al. 1999).

Foliage samples and the related soil samples were collected and analyzed for total C, total N, δ^{13}C, and δ^{15}N from two mango varieties, Keitt (Florida USA) and Calypso (Australia) in one experiment under similar soil conditions. Total C, total N, δ^{13}C, and δ^{15}N were determined in the samples by using a mass spectrometer connected to an elemental analyzer (EA-IRMS). Analysis of total C, total N, δ^{15}N, and δ^{13}C by mass spectrometry is a highly accurate method (Asche et al. 2003).

2.2 Soil and foliage sampling

In this experiment, soil and foliage were sampled in January 2019. The foliage samples were taken from each of the two varieties (Calypso^{TM} and Keitt) in both the conventional and single-leader trained trees from the medium and high planting densities (96 samples). Foliage samples were taken from the most recently matured leaves, at the ends of shoots in the upper canopy of the trees in the northern and southern aspects. Soil samples were collected from under the canopy in the north and south aspects of the canopy using a 5-cm diameter auger to collect 0–10-cm soil samples.

2.3 Chemical analysis

The leaf samples were oven dried at 65 °C for 48 h, while the soil samples were oven dried at 40 °C for 48 h. The dried soil and foliage samples were ground to a fine powder by a Rocklabs^{TM} ring grinder (Mixer Mill MM301; Retsch, Austria). Approximately 6–7 mg of foliage samples and 30–40 mg of soil samples were then transferred into tin capsules. The powders were burned to N_2 in the presence of O_2 in a CN analyzer (Roboprep-CN; Europa Scientific, Crewe, UK) and transported by interface to a mass spectrometer (Tracermass; Europa Scientific, Crewe, UK). Relative to international standards (Vienna-Pee Dee Belemnite for δ^{13}C and air for δ^{15}N), these values are expressed as δ‰ (Camin et al. 2009). The ratio of the heavy and light isotopes in the sample (R_{sample}) was measured by mass spectrometry as the deviation from the isotope ratio of the standard (R_{std}); where R represents the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$, expressed in δ notation, such as:

$$\delta^{13}C(‰) = \left(\frac{R_{\text{sample}}}{R_{\text{std}}} - 1\right) \times 1000 \quad (1)$$

The R_{sample} and the R_{std} are the $^{13}C/^{12}C$ ratios in the sample and the Pee Dee Belemnite standard respectively.

The high value of this parameter indicates the enrichment of ^{13}C or ^{15}N with its heavy isotopes.

2.4 Tree crop measurements

Tree crop yield was collected in January 2016 for Calypso and Keitt as the combination of total fruit count multiplied by average fruit weight. Fruits were counted and weighed in the field. Total yield per hectare (ha) was calculated as the tree yield multiplied by tree number planted per ha. Biological fruit yield refers to the fruit that was harvested from each tree as well as the count of those on the ground at harvest. In comparison, tree yield was only those fruits on the tree at harvest. Average fruit weight was calculated as the total fruit weight on a tree divided by the total count of fruits on the tree.

2.5 Statistical analysis

Analysis of variance was performed using SPSS 23.0 software (SPSS Institute Inc., Chicago, USA). The means were tested using the least significant difference in $P < 0.05$ level (LSD 0.05). Linear regression was performed by SPSS 23.0 software to identify the relationship between total N and δ^{13}C in the foliage and soil samples and to calculate regression equations. Multivariate analysis of variance (ANOVA) model was used to determine whether mango varieties, training systems, planting density, and canopy aspect had significant effects on the values of total C, δ^{13}C, total N, and δ^{15}N in the surface soil and mango foliage samples, as well as fruit yields.

3 Results

3.1 Foliar C and N in varieties, planting densities, and training systems

There was also a significant difference in foliage δ^{13}C between the two varieties ($P = 0.0001$). δ^{13}C for Keitt (−28.29‰) was significantly higher than that of Calypso (−29.50‰) (Table 1). Foliage δ^{15}N was also significantly different between the two varieties ($P = 0.0002$). The δ^{15}N of Calypso (2.83‰) was significantly higher than δ^{15}N of Keitt (1.93‰) (Table 1). Foliage total N was significantly higher in Keitt than in Calypso ($P = 0.0003$) (Table 1).

Foliage δ^{13}C was significantly different between the two planting densities ($P = 0.0138$), with an average of − 28.69‰ for medium planting density and − 29.10‰ for high planting density (Table 1). In addition, foliage δ^{15}N was also significantly different between two planting densities ($P = 0.005$), with the average δ^{15}N under medium planting density to be 2.16‰, and the average δ^{15}N under high planting density to be 2.59‰ (Table 1). Foliage total C was significantly different between the two planting densities ($P = 0.0209$). Foliar total C was significantly higher in the high planting density (Table 1). However, foliar total C, total N, δ^{13}C, and δ^{15}N from the different aspects (north and south) were not statistically significantly different ($P > 0.05$) (Table 1). Foliar total C was significantly different between the training systems where foliar total C was higher in the conventionally trained trees ($P = 0.0059$) (Table 1). However, foliar total C, total N, δ^{13}C, and δ^{15}N from the different orientations (north and south) were not statistically significantly different ($P > 0.05$) (Table 1).

Table 1 Effect of mango variety, planting density, training system, and canopy aspect on the concentrations of total C and total N as well as stable C and N isotope composition (δ^{13}C and δ^{15}N) in the middle canopy of a mango plantation of tropical Australia

Main effects	Total C (%)	Total N (%)	δ^{13}C (‰)	δ^{15}N (‰)
Variety				
Calypso	44.2 A	1.21 b	− 29.50 b	2.83 a
Keitt	44.4 A	1.40 a	− 28.29 a	
Planting density				
Medium	44.1 b	1.30 A	− 28.69 a	2.16 b
High	44.5 a	1.31 A	− 29.10 b	2.59 a
Training system				
Single leader	44.0 b	1.28 B	− 29.02 B	2.40 A
Conventional	44.6 a	1.33 A	− 28.77 A	2.35 A
Canopy aspect				
North	44.3 A	1.30 A	− 28.85 A	2.35 A
South	44.2 A	1.31 A	− 28.94 A	2.41 A

For each pair of entries, means followed by the same upper-case letter are not significantly different at $P < 0.10$, and those followed by the same lower-case letter are not significantly different at $P < 0.05$

There was a significant interaction between the planting densities and the training systems for foliage total C, as well as between the varieties and training systems ($P < 0.05$). When foliage data were pooled and analyzed for the interaction of planting density and training systems, total C was higher at the high planting density; however, total C under the high planting density was only significantly higher than the medium density, single-leader trained trees ($P = 0.027$) (Fig. S1). In addition, the Calypso with the single leader training system had significantly lower foliar total C compared to that of the conventional training system ($P = 0.035$) (Fig. S2). However, for the Keitt variety, the difference in foliar total C between different training systems was not significant ($P = 0.950 > 0.05$) (Fig. S2).

3.2 Mango fruit yield under different mango varieties, planting densities, training systems, and canopy orientation

Mango yield was significantly affected by different planting densities ($P < 0.05$; Table 2) where total yield per ha

Table 2 Effects of mango varieties, planting density, training systems, and canopy aspect on mango fruit yield and size in the middle canopy an orchard of a mango plantation of tropical Australia

Main effects	Total fruit count (tree and ground)	Tree fruit count	Average fruit weight (g)	Yield per tree (kg)	Yield per ha (tons)
Variety					
Calypso	88.1 A	72.6 A	472 B	39.7 A	31.2 A
Keitt	89.0 A	79.8 A	513 A	44.5 A	34.2 A
Planting density					
Medium	103.8 a	86.9 a	510 A	47.8 a	19.9 b
High	73.3 b	65.4 b	475 A	36.4 b	45.4 a
Training system					
Single leader	95.6 A	78.8 A	480 A	44.2 A	34.2 A
Conventional	81.5 A	73.6 A	505 A	40.0 A	31.2 A

For each pair of entries, means followed by the same upper-case letter are not significantly different at $P < 0.10$, and those followed by the same lower-case letter are not significantly different at $P < 0.05$

under the high planting density was higher than that of the medium planting density ($P < 0.05$). However, at high planting densities, the yield per tree was significantly lower than that of medium density. Average fruit weight was higher in Kiett than in Calypso ($P < 0.10$; Table 2), but neither planting density nor training system significantly affected average fruit weight.

3.3 Relationships between foliage total N and δ^{13}C

When pooling data from all foliage samples, there was a significant, positive correlation between foliage total N and δ^{13}C ($R^2 = 0.208$, $P < 0.001$, $n = 96$) (Fig. 1). However, when we looked at the different treatments, the linear relationship between foliage total N and foliage δ^{13}C was steeper for the high planting density ($R^2 = 0.321$, $P = < 0.001$, $n = 48$) (Fig. 2), compared to that of the medium-density planting ($R^2 = 0.155$, $P = < 0.01$, $n = 48$) (Fig. 2). While for the training systems, the linear relationship between foliage total N and foliage δ^{13}C was steeper for the conventional training system ($R^2 = 0.341$, $P = < 0.001$, $n = 48$) (Fig. 3), compared to that of the single leader training system ($R^2 = 0.084$, $P < 0.05$, $n = 48$) (Fig. 3).

3.4 Soil properties under different planting densities

For all soil samples collected in this experiment, soil δ^{13}C ranged from − 17.98 to − 17.16‰, soil δ^{15}N from 2.99 to 3.34‰, total soil C from 2.17 to 2.36%, and

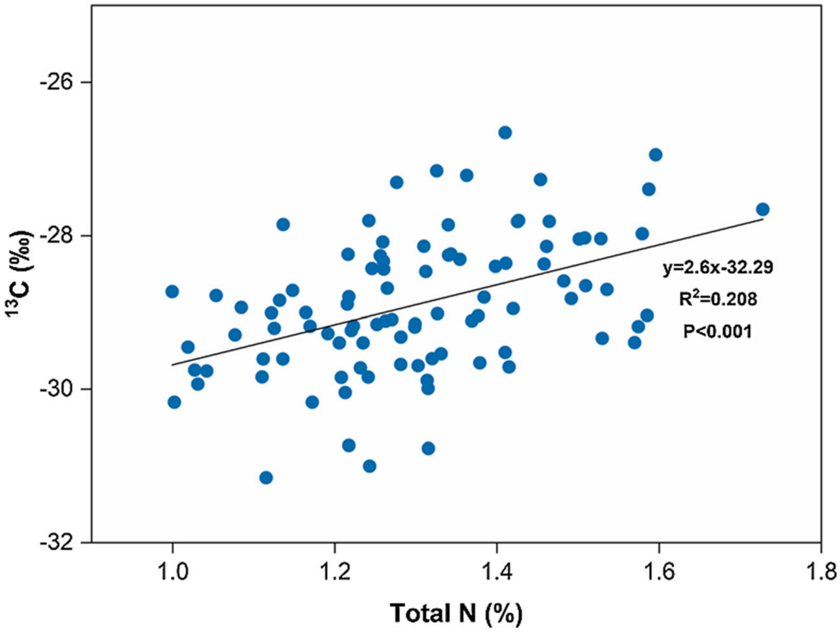
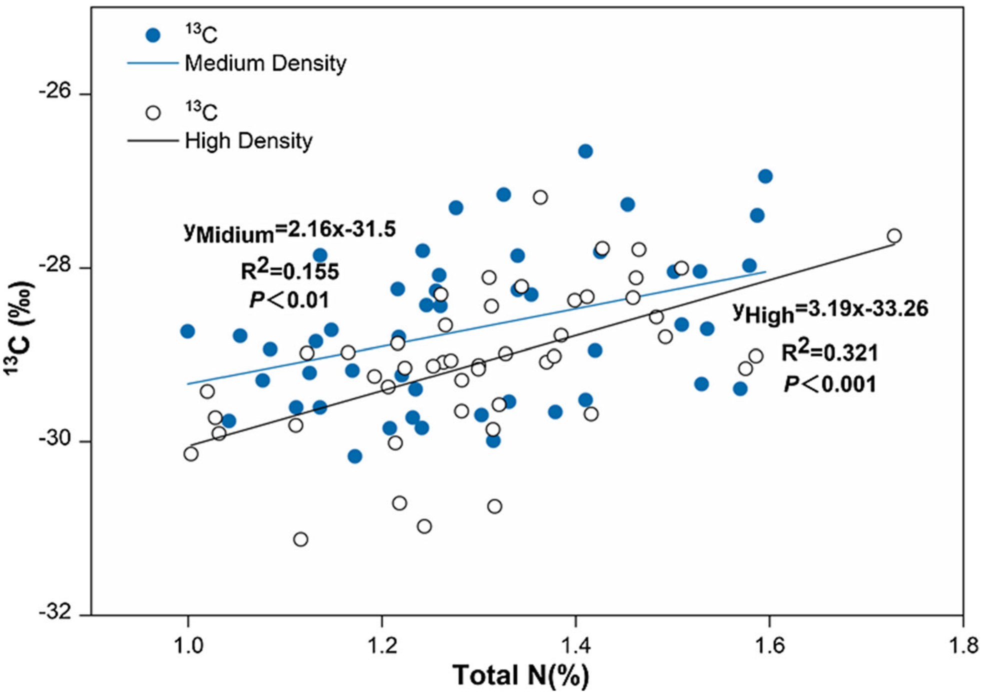


Fig. 1 The relationship between foliar total nitrogen concentration (TN, %) and stable carbon isotope composition (δ^{13}C, ‰) of a mango plantation with different varieties, planting densities, training systems and canopy sampling positions in tropical Australia.

Fig. 2 The relationship between foliar total nitrogen concentration (TN, %) and stable carbon isotope composition (δ^{13}C, ‰) for medium and high density of a mango plantation with different varieties, training systems, and canopy sampling positions in tropical Australia



total soil N from 0.159% to 0.176%. Among them, only total soil N was significantly different between planting densities (P = 0.0207), with soil total N under the high planting density (0.174%) being significantly higher than that of the medium planting density (0.161%). Soil total C, δ^{13}C, and δ^{15}N were not significantly different between the treatments (Table 3).

4 Discussion

4.1 Effects of variety on foliar δ^{13}C, δ^{15}N, and total N

The change of plant δ^{13}C is caused by both genetic and environmental factors and depends largely on genetic factors (Donovan and Ehleringer 1994; Damesin et al. 1998;

Fig. 3 The relationship between foliar total nitrogen concentration (TN, %) and stable carbon isotope composition (δ^{13}C, ‰) for single leader and conventional training system of a mango plantation with different varieties, planting densities, and canopy sampling positions in tropical Australia

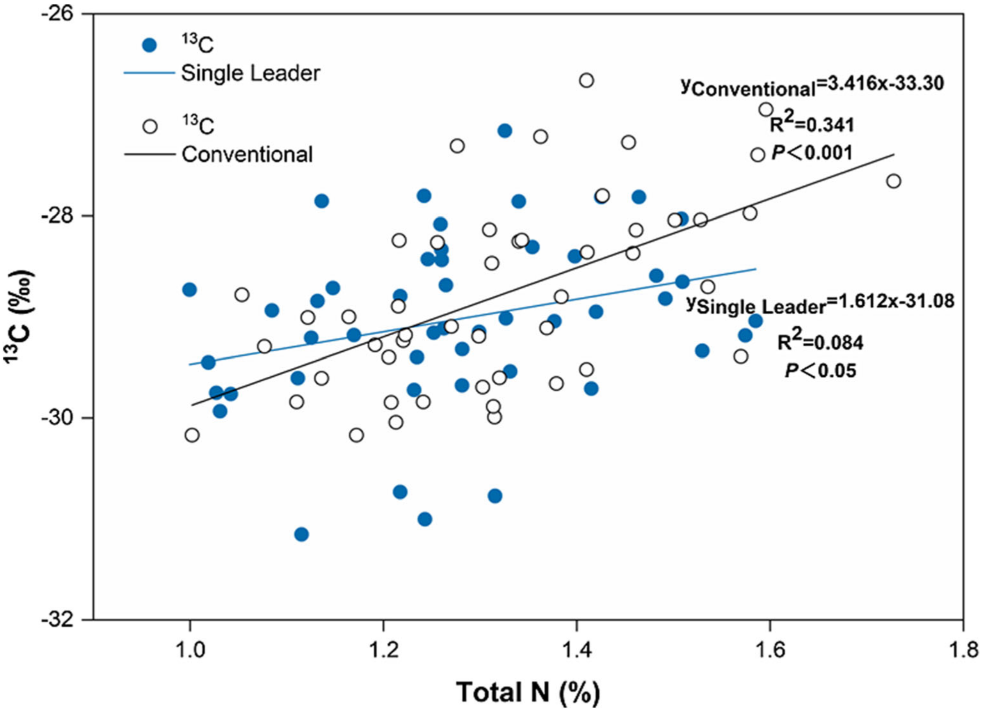


Table 3 Effect of mango variety, planting density, and training system on the concentration of soil total C and total N concentration as well as stable C and N isotope composition ($\delta^{13}C$ and $\delta^{15}N$) in a mango plantation of tropical Australia

Main effects	Total C (%)	Total N (%)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Variety				
Calypso	2.25 A	0.167 A	− 17.43 A	3.21 A
Keitt	2.28 A	0.168 A	− 17.70 A	3.13 A
Planting density				
Medium	2.18 B	0.161 b	− 17.13 A	3.17 A
High	2.35 A	0.174 a	− 18.01 A	3.17 A
Training system				
Single leader	2.26 A	0.169 A	− 17.41 A	3.23 A
Conventional	2.27 A	0.166 A	− 17.73 A	3.10 A

For each pair of entries, means followed by the same upper-case letter are not significantly different at $P < 0.10$, and those followed by the same lower-case letter are not significantly different at $P < 0.05$

Johnsen et al. 1999; Xu et al. 2014; Fu et al. 2020). For the two mango varieties evaluated in this study, the key variables explaining the change of foliar $\delta^{13}C$ were planting density and mango varieties, especially mango varieties ($P < 0.001$) (Table 1). The effects of variety on foliage $\delta^{13}C$ have been widely reported, in other species, and each variety usually has inconsistent results (Marshall et al. 2007; Chaves et al. 2010; Bota et al. 2016; Famula et al. 2019). According to the experimental data (Table 1), Keitt's average leaf $\delta^{13}C$ was more positive than that of Calypso, indicating that it exhibited a higher WUE.

The reasons that affect the variation of $\delta^{13}C$ in plants are obviously complex. Many factors such as plant development (Geber and Dawson 1990; Isabel et al. 2008; Yang et al. 2015), spatial gradient in the canopies (Garten and Taylor 1992; Véronique et al. 2005), altitude (Hultine and Marshall 2000), and rainfall (Miller et al. 2001) can explain the variation of plant $\delta^{13}C$. A large number of studies have confirmed that based on the positive correlation between plant $\delta^{13}C$ and WUE, foliar $\delta^{13}C$ can be used as an indicator of plant WUE (Marshall and Zhang 1994; Bai et al. 2008; Song et al. 2008). For C3 plants, $\delta^{13}C$ varies between − 20 and − 35‰, while in C4 plants $\delta^{13}C$ is between − 7 and − 15‰ (O'leary et al. 1992; Shim et al. 2008). WUE can represent the performance of crops grown under any environmental constraints (Howell 2001). ^{13}C is a surrogate feature of WUE with high heritability; as a result, this has led to selection of varieties with improved WUE among different plant genotypes (Farquhar and Richards 1984; Anyia et al. 2007). Therefore, we have assumed that by analyzing the changes in $\delta^{13}C$ of mango leaves under the same site management, it is feasible to reveal the water use strategies of different varieties of mango trees.

Nitrogen is the basis for the growth and development of fruit trees and a key factor in determining the growth and productivity of fruit trees (Zhao et al. 2008). The N deficiency reduces the photosynthetic capacity of plant leaves and can have significant impact on the plant C skeletons, plant productivity, and crop yield (Lam et al. 1996; Zhao et al. 2005; Rogers and Wszelaki 2012). Various studies have reported that crop yields are significantly positively correlated with leaf photosynthetic capacity (Richards 2000). Compared with the situation with $\delta^{13}C$, the understanding of the influence of environmental variables on $\delta^{15}N$ is still insufficient in previous studies (Houlton et al. 2006). The main reason for the change in $\delta^{15}N$ is that almost all N cycling processes (e.g., nitrification, denitrification, leaching, and ammonia volatilization) preferentially favors lighter ^{14}N and against heavier ^{15}N (Mariotti et al. 1981; Högberg 1997). The $\delta^{15}N$ in plants can serve as an indicator of N cycling activity and be more sensitive than total N in the soil (Johannisson and Högberg 1994). Because the formation of soil organic matter (SOM) largely retains the isotopic signal of plants, it also carries some microbial isotope discrimination (Hobbie 2005).

The $\delta^{15}N$ variation among different plant species may also be due to differences in different species in isotope fractionation, differences in plant preference for N forms, and differences in rooting depth or density (Emmerton et al. 2001; Miller and Bowman 2002). However, plants generally absorb "light" forms of ^{14}N, leaving the "heavier" forms of ^{15}N behind in the soil. Leaf total N of the mango variety Keitt was significantly higher than that of Calypso, but $\delta^{15}N$ of the Keitt foliage samples was significantly lower than that of Calypso. Our results show that Keitt retained more N in the leaves but had a lower $\delta^{15}N$ from the soil. While Keitt has been shown to have a stronger photosynthetic capacity (Ibell et al. in press), it may also have a greater N availability resulting in higher N uptake and lower N losses in the soil. From a long-term perspective, the Keitt may be more productive than Calypso.

4.2 Effects of management on foliar C and N

Crop management practices such as planting density, irrigation, and training systems have impacts on the productivity and sustainability of food production systems. In this study, foliage $\delta^{13}C$ was also significantly different under different planting density management ($P < 0.05$). Different soil moisture conditions under different management can result in plants having different WUE. High-density plants (1250 trees per hectare) had higher yields than traditional planting densities (208 trees per hectare). This could enable faster recovery of initial costs of establishing and maintaining orchards and increase economic efficiency (Khan et al. 2015). However, trees planted at close range may compete for light, resulting in poor plant growth (He and Bazzaz 2003). Foliar $\delta^{13}C$ was significantly lower under high planting densities compared to the medium-density planting. This indicates that the trees from the high planting densities had a significant lower long-term WUE. However, more effectively drip irrigation was used at higher planting densities in the experiment, but mango trees had lower foliar $\delta^{13}C$ (less efficient in WUE) with relatively less water stress under the high planting density, compared to that of the medium planting density due to the efficient drip irrigation system, which may be the cause of the low foliar $\delta^{13}C$ of high planting density trees.

Foliar $\delta^{15}N$ was also significantly different between different planting densities. Higher foliar $\delta^{15}N$ occurred in trees planted at high density compared to those planted at medium density. The $\delta^{15}N$ can change during the transfer of isotopes from soil to plants which may be due to assimilation and metabolic processes (Dawson et al. 2002). More effectively drip irrigation at high-density planting may result in more N losses (high $\delta^{15}N$) by increasing N leaching and denitrification, resulting in more N loss in areas of inherent soil fertility (Mmolawa and Or 2000; Pu et al. 2001; Peter et al. 2003). Therefore, in this experiment, foliar $\delta^{15}N$ under high-density planting was higher, indicating a trade-off between reducing water stress and the maintaining high N availability under the high planting density.

The state of plant leaf N generally provides insight into the pattern of plant photosynthetic capacity (Reich et al. 1997; Kloeppel et al. 2000; Katahata et al. 2007). In particular, leaf N concentration (total N) and $\delta^{13}C$ have been shown to be effective indicators for comparing plant-to-resource gradient responses (Reich et al. 1997; Dawson et al. 2002). These results show a linear relationship between foliar total N and $\delta^{13}C$, which reflects a relationship between N resources and photosynthetic capacity. A positive correlation between plant $\delta^{13}C$ and leaf chlorophyll or N content has been observed previously (Hill et al. 1996; Sparks and Ehleringer 1997), consistent with the results of this experiment. From this relationship, it can be assumed that 20.8% of the variability in foliar $\delta^{13}C$ was driven by leaf N. The relationship between foliar ^{13}C and total N varied with planting density and training systems where the high planting density and the convention systems had steeper slopes, indicating that these systems have increased N availability and foliar $\delta^{13}C$ (WUE). This could reflect increased soil C (root biomass) in the high-density plantings (including conventional training systems) and thus leading to lower water stress and lower $\delta^{13}C$.

In the conventional training systems, foliar total C was significantly higher ($P < 0.05$) than that of the single leader training system. The high planting density system also had higher foliar total C than that of the medium density system. This suggests that training system and planting density may influence foliar total C. The arrangement of leaves in the different training systems influences how light is distributed through the canopy, and the single leader training system is implemented to create a more even light environment within the canopy which results in greater photosynthetic efficiency in this system. Therefore, canopy management needs to consider the effects of pruning on shoot and branch regeneration, light distribution through the canopy, and leaf loss which can support developing crops. Experiments in peach have shown that effective training systems affect the early productivity of young trees and tree growth under the high planting density is ultimately limited by the amount of light later in the orchards life (Corelli-Grappadelli and Marini 2008). These issues need to be further verified by long-term experiments.

4.3 Effects of varieties and planting density on mango yield

While Calypso had decreased fruit size, both varieties had similar amounts of fruits per tree and per ha. There was a significant effect of planting density, where the total yield per hectare was significantly higher than that under the medium planting density. Interestingly, it was the medium density trees that had increased yield per tree. This is consistent with the results of other studies that show that as planting density increases, the yield per tree tends to decline (Reddy et al. 2002; Amundson et al. 2012). In the early life of orchards, those with high planting densities are generally more productive than orchards with low planting densities (Krishna et al. 2006; Nath et al. 2007; Rajesh et al. 2014). However, trees planted under high density can begin to crowd and shade each other very quickly (Singh et al. 2013). Low light limits the quality of the fruit, such as size, color, soluble solids content, and starch content (Barritt 1987; Cherbiy-Hoffmann et al. 2012; Feng et al. 2013). Tree training and pruning have been proposed as techniques to increase light penetration and have a beneficial effect on fruit yield over time, as has been shown in other mango and apple orchards (Hampson et al. 2002; Sarkhosh et al. 2018). However, between the two training systems selected in this experiment, there was no significant difference in total yield per ha and yield per tree. This may be due to the training systems not crowding each other and being effective at their given planting densities at this early age. High planting density did influence total tree counts and yield per tree which suggest a trade-off between yield and tree size in the high-density systems. Overall it was an increase in tree planting density that has lifted yields per ha despite variety or training system.

4.4 Effects of management on soil properties

Controlling of planting density can also affect undergrowth litter and soil nutrients as a result of changes in light, temperature, and humidity in the orchard (Sheng et al. 2003). In this experiment, soil total N at 0-10-cm depth under the high-density planting was higher than that under the medium-density planting, which was consistent with other research results (Razaq et al. 2017), where high-density plantings increased and contained soil N within the area. The amount of N applied to an orchard can also affect the way in which N is used (N availability) and photosynthesis of plants. Improvement of the way in which N is applied can also have beneficial effect on the root growth of plants (Kern et al. 2004; Zhao et al. 2008). Under appropriate levels of N fertilization, root length and root surface area increase (Costa et al. 2002). In this experiment, trees at high planting density may have better access to adjacent N resources resulting in more efficient N utilization. This may have led to improved root growth. This is supported by increased soil C under the high-density trees which could have resulted from increased C inputs from vegetative or root biomass in this planting density. Under the high planting density, more N fertilizer could apply and hence more N losses under high irrigation conditions, resulting in higher δ^{15}N in the soil and subsequent plant uptake of higher δ^{15}N in the foliage.

5 Conclusion

There were significant genetic and environmental effects on foliar δ^{13}C (WUE), δ^{15}N (N availability), and yield characteristics in this 5-year-old mango orchard. Mango variety significantly affected tree WUE as reflected by foliar δ^{13}C, N availability as indicated by foliar total N and δ^{15}N where Keitt had significantly higher foliar δ^{13}C (higher WUE), and significantly larger fruit than Calypso. Some management factors also significantly affected the tree environment which has influenced foliar δ^{13}C, δ^{15}N and yield characteristics. Higher planting density led to increased N availability (increased soil total N), but the lowered foliar δ^{13}C (WUE) and increased foliar δ^{15}N indicating greater soil N losses. Despite these results, soil total N under the high planting density was still higher than that of the medium-density plantings, due to improved NUE and increased N fertilizer application. Trees trained with a single leader system had lower foliar δ^{13}C (lower WUE) and total N, compared to those of the conventionally trained trees. These results show that orchard intensification may lead to management (planting density and training system) and variety selection decisions that could improve both foliar δ^{13}C (WUE) and N availability in the tropical mango production.

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