

## Relative Contribution of Avoidance and Tolerance to Dehydration Resistance in Kiwifruit (*Actinidia* species)

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*The mechanisms of a plant to face water stress can be composed of either avoidance and/or tolerance. However, reliable and rapid methods for measuring these components have not been established in kiwifruit. Therefore, we qualitatively evaluated the avoidance and tolerance abilities in fruit of Actinidia deliciosa (Hayward-Green) and Actinidia chinensis (Hort16A-Gold) by continuously measuring their gravimetric water contents corresponding with the ionic strength under dehydration stress across 24 hours. Fruit and leaf traits were also evaluated in this study. A. deliciosa had significantly higher leaf surface area and lower fruit dry matter than A. chinensis. Fruit volume was remarkably higher in A. deliciosa than in A. chinensis. Higher moisture content and lower total soluble solids as well as ionic strength were observed in A. deliciosa compared to A. chinensis. Regardless of species, the moisture content decreased and both total soluble solids and ionic strength increased across time. The two species showed contrasting patterns of response to dehydration stress. A. deliciosa had lower avoidance and higher tolerance than A. chinensis. The combinations of these two components in both the species resulted in different degrees of resistance. A. deliciosa had higher water*

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*loss during short-term dehydration stress than A. chinensis. This study demonstrated the importance of avoidance and tolerance to dehydration resistance in the Actinidia species.*

*KEYWORDS* dehydration stress, ionic strength, kiwifruit, water footprint

## INTRODUCTION

Emission of greenhouse gasses change the environment in many ways, e.g., increased drought and salinization caused mainly by low precipitation, which can adversely affect plant performance and results in significant reductions in crop yield and quality worldwide. The exposure of plants to such environmental stresses as low or high levels of water, light, air temperatures and nutrients, and certain air pollutants can result in the production of plant secondary metabolites (Taiz & Zeiger 2006). Plants adopt various mechanisms to resist environmental stress. These mechanisms can be divided into two components: avoidance and tolerance (Levitt 1972). Avoidance represents the ability to alleviate effects of external stress conditions whereas tolerance represents the ability to maintain growth and survival under the influence of stress conditions. Tolerance to dehydration stress reflects the abilities of cells to protect themselves against mechanical stress caused by dehydration (Oliver 1996). The ability of dehydrated cells to tolerate mechanical injury results from the morphological properties of plant cells (Bewley & Krochko 1982) and from the physiological adjustment by accumulation of compatible solutes (Hoekstra, Golovina, & Buitink 2001). Solute accumulation is a recognized physiological response to water stress, and has been demonstrated for a number of crops, including peach (Steinberg et al. 1989), cherry (Ranney, Bassuk, & Whitlow 1991), tomatoes (Mitchell et al. 1991), strawberry (Zhang & Archbold 1993), and apple (Wang & Stutte 1992; Mills et al. 1994). Leaf water potential, stomatal conductance, sap flow, and water-use efficiency are well-established parameters to identify plant drought-stress tolerance in plants (Green & Clothier 1988; Heschel & Riginos 2005; Greven et al. 2009). The activity of solute substances in a solution depends on the product of its concentration and the activity coefficient in that solution. The activity coefficient depends on the ionic strength of the solution. Ohyashiki, Taka, and Mohri (1985) hypothesized that the membrane surface charge is one of the important elements controlling membrane fluidity and protein structure in biological membrane systems. Theory predicted that intracellular ionic strength might play an important role in regulating the expression of genes encoding osmolyte-accumulating molecules. Neuhofer et al. (2002) observed that the effect of intracellular ionic strength

on the expression of osmotic stress protein (*osp94*) was modulated by additional factors such as cell volume, and that its effect on the pathways regulated heat shock protein (*hsp70*). It is, therefore, necessary to investigate dehydration resistance by observing the changes of ionic strength with time.

There are some negative relations between avoidance and tolerance abilities in grass species. This trade-off implies that there is a limit to the creation of a single 'super' resistant line having both maximal avoidance and tolerance abilities. Although a trade-off between avoidance and tolerance has been reported among desiccation-tolerant species exposed to rapid dehydration stress (Farrant et al. 1999), it is not certain whether this trade-off is widely found in other plants species. The eco-physiological understanding of mechanisms underlying the difference in avoidance and tolerance abilities is essential to determine the mechanisms by which vines adapt to water stress and improve resistance to drought. Broadly, avoidance is best under conditions of mild or short duration of stress, whereas tolerance is advantageous under conditions of severe or prolonged stress (Riga & Vartanian 1999). Olive (*Olea europaea* L.) is a drought-tolerant species. Greven et al. (2009) evaluated the effects of drought on the water use, fruit development, and oil yield from young olive trees. They concluded that irrigation was required in dry years for economic production of olives at the study area. In hydroponic solutions with elevated salt concentrations, *Actinidia deliciosa* and *Actinidia arguta* rapidly accumulated myo-inositol in leaf tissue and rapid declined with stress relief (Klages, Boldingh, & Smith 1999). Sabreen and Sugiyama (2008) evaluated the trade-off between cadmium tolerance and relative growth rate in 10 grass species. Fruit cell turgor may additionally be controlled by active regulation of the level of solutes in the fruit apoplast, as suggested by Matthews and Shackel (2005). Hallett and Sutherland (2005) studied the structure and development of kiwifruit skins. They observed that the skins of both *A. chinensis* and *A. deliciosa* had a more complex structure than other fruits. All the above encouraged us to draw the conclusion that the relative resistance abilities of kiwifruit could be different than those of other economic fruit crops under various stress conditions. However, there have been few studies on the avoidance and tolerance to dehydration resistance in kiwifruit. Information on the relationships between the resistance, avoidance, and tolerance is also lacking in kiwifruit species. Such information may be of great importance to better understanding the economics and sustainability of kiwifruit production in relation to water footprint. Therefore, we tested the hypothesis that relative resistance ability would differ between *A. deliciosa* (Hayward-Green) and *A. chinensis* (Hort16A-Gold) species grown under a conventional system on Allophanic soil in New Zealand.

## MATERIALS AND METHODS

### Study Site and Growth Conditions

The experiment was conducted during the 2007–2008 growing season in Te Puna, located in the Bay of Plenty region of the North Island of New Zealand with the latitude of 37°39'S and longitude of 176°11'E. The Bay of Plenty region covers 12,200 km<sup>2</sup> of land and 9,500 km<sup>2</sup> of coastal marine area and is one of the warmest in New Zealand, particularly along the coastline, with most areas experiencing at least 2,000 hours of sunshine per annum. Average temperatures in the growing season studied ranged from 19.3°C in February to 9.8°C in July, while precipitation ranged from 74 mm in January to 128 mm in both March and June. April and May 2008 received 105 mm and 91 mm of rain, respectively. We selected two orchards (Hayward Green and Hort16A Gold) representative of many kiwifruit orchards in Bay of Plenty, New Zealand. Both orchards have sandy loam soils and are at an altitude of 24 meters above sea level. Both Hayward Green and Hort16A Gold, have been under conventional management since establishment of vines [*Actinidia deliciosa* (A. Chev.) C.F. Liang and A.R. Ferguson var. *deliciosa*] in 1981. In Gold, *A. chinensis* Planch. was grafted on *Actinidia deliciosa* [(A. Chev.) C.F. Liang and A.R. Ferguson var. *deliciosa*] rootstock in 1999. The study sites were adjacent to one another and had the same general soil characteristics (viz., soil texture, moisture-holding capacity, three-phase distribution). Thirty soil and leaf samples were collected in May and December, respectively. Samples were analyzed for physico-chemical properties (soil) and macro- and micronutrients (leaf). Based on the results of soil and leaf tests, fertilizers were applied from August to December. Annual nutrient inputs were typical for the industry, with 109 kg N, 52 kg P, 184 kg K, 66 kg Mg, 148 kg Ca, and 4 kg B applied per hectare to the Hayward Green, and 124 kg N, 40 kg P, 205 kg K, 67 kg Mg, 238 kg Ca, and 3 kg B applied per hectare to the Hort16A Gold. The study sites received split applications of pesticides, insecticides, and fungicides according to the kiwifruit industry standard during kiwifruit growth.

### Sampling and Analyses

A set of fruit and leaf samples (each set of 30 individuals) were collected at pre-harvest time on May 2, 2008, for measuring avoidance and tolerance to dehydration resistance as well as fruit and leaf morphology. Full bloom dates were 18 October 2007 for the gold and 25 November 2007 for the green, respectively. These dates meant that fruit samples were collected 197 days after full bloom (DAFB) from the gold and 159 days after full bloom from the green. While these differences in DAFB were not ideal, it was decided it was preferable to pick both the gold and green fruit on the same date to ensure that they had both experienced the same climatic

conditions immediately before harvest. In further work, it may be possible to evaluate the effect that differences in DAFB have on avoidance and tolerance to moisture stress. In this study, we chose 30 samples in each orchard as from experience—the kiwifruit industry has found these numbers to give reliable data. The sampling technique for dry matter test in kiwifruit The nine vine positions namely: trunk base (TB), trunk middle (TM), trunk end (TE), mid base (MB), mid middle (MM), mid end (ME), end base (EB), end middle (EM), and end end (EE) are suitable for sampling kiwifruit. In this study samples were collected at 8:30 A.M. from the identical position (mid middle) on vines to eliminate bias from the results. The fresh weight of fruit, leaf, and petiole were recorded. Leaf surface area was calculated according to Boase, Wright, and McLeay (1993), and petiole length was measured. The fruit volume was determined by the amount of water displaced when fruit was immersed in water. The fruit and leaf samples were placed in a vacant plastic container to hold in phase. Fruit samples were then kept in an incubator at a constant temperature of 22°C and humidity of ~60%. The fruit water content was continuously measured gravimetrically at 0, 1, 2, 3, 4, 5, 7, and 24 h exposed to water stress. Corresponding with time, total soluble solids (TSS) and electrical conductivity (EC) of fruits were measured with a pocket refractometer (Atago Co. Ltd. Japan) and EC/TDS/Salt tester (Oakton Ltd., Malaysia), respectively, at temperature 22°C. Debye & Hückel first proposed a method to calculate ion activities in 1923, and it was more recently modified by Griffin & Jurinak (1973). Here, we estimated ionic strength according to the modified method outlined by Griffin & Jurinak (1973). Fruits and leaves were dried at 60°C for 24 h using a ventilated oven (Ezidri Ultra 1000FD, Hydraflow Industries Ltd., New Zealand), and the dry weight of each sample was determined.

### Experimental Design, Calculation and Statistical Analysis

The experiment was conducted in the randomized block design with three replications. We collected fruit according to a systematic sampling design across the S-shaped transect (Rahman & Sugiyama 2008) from each orchard and tested destructively. For calculation of resistance, avoidance, and tolerance, the slopes of the linear regressions of fruit ionic strength against time, water content against time, and ionic strength against water content after exposure to dehydration stress, respectively, were used. Intraspecific differences for avoidance, tolerance, and resistance were tested using heterogeneity of slopes between regression equations (Sokal & Rohlf 1995). To assess differences between species for the total variation among 60 fruits including two species, the total sum of squares (SS) was partitioned in SS due to common slope and SS attributable to heterogeneity of regressions between species. A two-way analysis of variance (ANOVA) was employed to determine whether time/species affected the parameters (moisture content,

total soluble salt, and ionic strength). The two-way ANOVA model included time and species as the main sources of variation: time  $\times$  species interaction. The least significant differences (LSD) test was used to determine whether differences between means were statistically significant ( $p < 0.05$ ). Means were compared using Duncan's multiple range test (DMRT) at 5% level of significance (Gomez & Gomez 1984). Pearson correlation coefficients between attributes and intercorrelation among attributes were performed. All statistical analyses were conducted using JMP 4.0 (SAS Institute, Cary, NC, USA).

## RESULTS AND DISCUSSION

### Variations in Fruit and Leaf Traits

Being able to predict the morphological traits of *Actinidia* species would be helpful in developing improved cultivars. On the day of harvest, fruit traits (fruit volume, fruit moisture, fruit dry weight) and leaf traits (leaf surface area, leaf moisture, leaf let dry matter, petiole length, petiole moisture, and petiole dry matter) were recorded (Table 1). Fruit volume and moisture content were slightly higher in *A. deliciosa* than those in *A. chinensis*. Fruit dry matter was significantly lower in *A. deliciosa* than in *A. chinensis*. Fabbroni et al. (2007) observed clear increases in fruit size throughout the growing season. This increase in fruit size was reflected in a clear and reproducible increase in fresh weight as well as dry weight for both species. Xylem as well as phloem inflow and transpiration are believed to be the driving forces behind fruit enlargement. In apples and grapes, fruit enlargement depends on phloem unloading (Lang 1990), but in kiwifruit phloem contribution to fruit volume is negligible, and xylem provides an important contribution to daily fresh matter gain both at cell division and expansion (Morandi et al.

**TABLE 1** Fruit and Leaf Traits of Kiwifruit Grown in Conventional Management System

Different traits	Kiwifruit		
	<i>A. deliciosa</i>	<i>A. chinensis</i>	LSD <sup>1</sup>
Fruit volume (cc)	128.25	119.50	11.79
Fruit moisture (%)	84.04	81.20	3.08
Fruit dry matter (%)	15.96	18.80	1.92
Leaf surface area (cm <sup>2</sup> )	306.06	186.55	22.46
Leaf moisture (%)	66.80	65.75	2.22
Leaf let dry matter (%)	33.20	34.25	1.22
Petiole length (cm)	10.09	10.12	1.05
Petiole moisture (%)	85.81	85.13	1.14
Petiole dry matter (%)	14.19	14.87	1.14

<sup>1</sup>Least significant difference (LSD) at  $P < 0.05$  among the values within rows.

2007). Lang and Thorpe (1989) found that net volume growth more or less ceased in the later stages of fruit development in grapes. They attributed this to the strong inflow of sugary water through the phloem being closely balanced by transpiration water loss through the skin and backflow of xylem water to the parent vines. It seems the mechanisms involved in fruit growth differ depending on the plant genus and species. There were no significant differences in leaf moisture and dry matter as well as petiole length, moisture, and dry matter between *A. deliciosa* and *A. chinensis*. Leaf surface area was significantly lower in *A. deliciosa*. In this study, higher leaf surface area was observed in low fruit dry matter species (*A. deliciosa*). Higher specific leaf area may be associated with higher stomatal conductance (Clearwater et al. 2007). Higher stomatal conductance means higher rate of passage of carbon dioxide through the stomata into internal spaces within the leaf. This carbon dioxide then diffuses into mesophyll cells where it becomes available for photosynthesis, a metabolic pathway that converts carbon dioxide into organic compounds. In recent studies, Pima cotton (*Gossypium barbadense*) and bread wheat (*Triticum aestivum*) have shown a remarkable positive correlation between yield increases and increases in stomatal conductance (Lu et al. 1998). Increases in stomatal conductance in crops grown at high temperatures have valuable implications for the development of models to predict the effect/consequences of global climate changes in horticulture, which are expected to occur because of known increases in atmospheric CO<sub>2</sub> due to global warming. These models must take into consideration the effect of higher temperatures on the stomatal control of evapotranspiration in kiwifruits. Many research reports have suggested that dry matter varied with internal and external environmental components as well as kiwifruit species and the environmental factors appeared to have a greater impact on *A. deliciosa* than on *A. chinensis* (Mowat & Kay 2007; Mowat & Maguire 2007; Throp et al. 2007).

#### TEMPORAL CHANGES IN MOISTURE CONTENT, TOTAL SOLUBLE SOLIDS AND IONIC STRENGTH

Environmental stress affects plant performance with significant reductions in crop yield and quality. Tolerance to dehydration stress reflects the abilities of plant cells to protect themselves against mechanical stress caused by dehydration. The ability of dehydrated cells to tolerate mechanical injury results from physiological adjustment by accumulation of compatible solutes and/or ions (Levit 1972; Taiz & Zeiger 2006). Therefore, in the laboratory, we monitored moisture, total soluble solids, and ionic strength in kiwifruit across time. The ionic strength refers to activities rather than concentration of ions of a solution. Changes in moisture content, total soluble solids, and ionic strength of kiwifruit exposed to dehydration stress across time are shown in Table 2 and Table 3. The moisture content of kiwifruit was

**TABLE 2** Summary of ANOVA Test for Moisture Content, Total Soluble Solids, and Ionic Strength of Kiwifruit Exposed to Extreme Dehydration

Sources of variations	Moisture content		Total soluble solids		Ionic strength	
	F ratio	Pr > F	F ratio	Pr > F	F ratio	Pr > F
Time	321.76	<.0001	2353.64	<.0001	966.42	<.0001
Species	113.82	<.0001	979.43	<.0001	236.60	<.0001
Time × Species	0.31	0.9483	44.95	<.0001	5.70	<.0001

affected by time ( $F$  ratio: 321.76;  $Pr > F$ : <0.0001) and species ( $F$  ratio: 113.82;  $Pr > F$ : <0.0001), accounting for 28.71% and 71.24% of total sum of squares, respectively (Table 4). Total soluble solids were influenced by time ( $F$  ratio: 2353.64;  $Pr > F$ : <0.0001) and species ( $F$  ratio: 979.43;  $Pr > F$ : <0.0001), accounting for 27.71% and 71.99% of total sum of squares, respectively. Ionic strength was also influenced by time ( $F$  ratio: 966.42;  $Pr > F$ : <0.0001) and species ( $F$  ratio: 236.60;  $Pr > F$ : <0.0001), accounting for 36.30% and 62.21% of total sum of squares, respectively. It can be concluded that the species effect was more pronounced than the time effect relative to the changes in moisture content, total soluble solids, and ionic strength in kiwifruit grown in a conventional system. For total soluble solids and ionic strength, the time × species interaction was significant, indicating that the species exhibited variable effect on both attributes due to time duration.

The moisture content was significantly higher, and total soluble solids and ionic strength were significantly lower in *A. deliciosa* than *A. chinensis* at all times (Table 3). The reason for higher moisture level in *A. deliciosa* may be lower total soluble solids content. The differences in total soluble solids between *Actinidia* species may be derived from the variation in activity of invertase and sucrose synthase (Matsui & Kitagawa 1998). Remorini et al. (2007) and Maguire, Spinelli, and Nicolai (2007) observed that canopy position markedly influenced total soluble solids in fruits of *Actinidia* species. Moisture content decreased and total soluble solids and ionic strength increased across time for both the species (Table 3). From Table 3 it can be seen that moisture content decreased in both *A. deliciosa* and *A. chinensis* after 24 hours of exposure to dehydration stress, and both total soluble solid and ionic strength correspondingly increased. Our results corroborate those of Marsh and Stowell (1993) who also observed a sharp increase in total soluble solids across time in *A. deliciosa* stored at 0°C. Cicco et al. (2007) observed that the total soluble solids content in *A. deliciosa* increased 70% within 21 days of storage at 10°C. Kim et al. (2007) stated that ethylene production by *A. rufa* 'Awaji' and *A. rufa* 'Nagano' increased with time of incubation, which has changed the color in fruits of *Actinidia* (Montefiori et al. 2007). Color changes may be associated with the synthesis

**TABLE 3** Temporal Changes in Physical and Chemical Characteristics of Kiwifruits Under Extreme Dehydration Stress

Property	Species	Time										LSD <sup>5</sup>
		0 hr	1 hr	2 hr	3 hr	4 hr	5 hr	7h r	24 hr			
Moisture content <sup>1</sup>	<i>A. deliciosa</i>	83.5a <sup>4</sup>	82.9a	82.7a	82.6a	82.2a	81.9a	81.6a	78.2a			0.232
	<i>A. chinensis</i>	81.2b	81.1b	80.5b	80.4b	80.3b	80.1b	79.5b	76.6b			0.212
	Av.	82.4	82.0	81.6	81.5	81.3	81.0	80.6	77.4			
Total soluble solids <sup>2</sup>	<i>A. deliciosa</i>	4.3b	4.6b	4.9b	5.0b	5.1b	5.2b	5.4b	7.2b			0.124
	<i>A. chinensis</i>	5.3a	5.6a	5.8a	5.9a	6.1a	6.3a	6.7a	9.5a			0.184
	Av.	4.8	5.1	5.4	5.5	5.6	5.8	6.1	8.4			
Ionic strength <sup>3</sup>	<i>A. deliciosa</i>	6.8b	7.3b	7.4b	7.9b	8.1b	8.7b	9.1b	9.8b			0.143
	<i>A. chinensis</i>	7.8a	8.5b	8.7a	9.0a	9.4a	10.1a	10.8a	12.0a			0.188
	Av.	7.3	7.9	8.1	8.5	8.8	9.4	10.0	10.9			

<sup>1</sup>Percent in oven dried basis.<sup>2</sup>Degrees Brix, a measurement of soluble solids concentration.<sup>3</sup>Mol/l at 22°C, ionic strength multiplied by 10<sup>-2</sup>.<sup>4</sup>Values within the columns and parameters for each variable with same letters are not significantly different at  $P < 0.05$ .<sup>5</sup>Least significant difference (LSD) at  $P < 0.05$  among the values within rows.

of secondary metabolites. Research showed that the synthesis of phenolic compounds in kiwifruit was significantly lowered when the surrounding environment was poorly illuminated (Montanaro, Treutter, & Xiloyannis 2007). Miller et al. (1998) found that moderate water stress late in the season improved kiwifruit fruit quality as reflected by higher soluble solids. It is clear that the physiological properties of kiwifruit changed with environmental factors as well as developmental stages. Future experiments should concentrate on the synthesis of ethylene, actinidin, antioxidants, quinic acid, and vitamin C in kiwifruit while they are exposed to dehydration stress at different growth stages.

#### INTERSPECIFIC VARIATIONS IN RESISTANCE, AVOIDANCE, AND TOLERANCE

Avoidance represents a fundamental response of plants to conditions of water deficit. Estimation of avoidance to dehydration required simultaneous measurement of environmental and plant water conditions. This is not only difficult but also time-consuming in a field environment that experiences dynamic diurnal changes due to the influences of ambient and edaphic moisture conditions and plant traits controlling water flow within the plant. Therefore, we quantitatively estimated the abilities of kiwifruit to avoid dehydration stress by continuously measuring gravimetric water contents with changes in ionic strength under controlled conditions. There were clear differences between the species for dehydration resistance, avoidance, and tolerance as shown in Table 4. The values for resistance to dehydration stress for *A. deliciosa* and *A. chinensis* were 624.7 and 485.5, respectively: the difference was highly significant ( $p < 0.001$ ). The dehydration avoidance and dehydration tolerance also showed significant ( $p < 0.001$ ) differences between the two species (Table 4). The coefficients of the linear regression representing fruit water loss with time were  $-4.18$  and  $-5.51$  for *A. deliciosa*

**TABLE 4** Slopes of Regressions for Resistance, Avoidance and Tolerance and their Coefficients of Determination ( $R^2$ )

Species	Resistance		Avoidance		Tolerance	
	Slope	$R^2$	Slope	$R^2$	Slope	$R^2$
<i>A. deliciosa</i>	624.72	0.82	-4.18	-0.97	-133.46	-0.83
<i>A. chinensis</i>	485.48	0.84	-5.51	-0.98	-94.48	-0.86
% of SS	Resistance		Avoidance		Tolerance	
Specific-species regression	65.71		22.41		28.74	
Common regression	27.23		16.12		40.16	
<i>F</i> value for species effect	188.24*		265.73*		173.83*	

Proportion of sum of squares (SS) explained by common regression and by species-specific regression are also shown.

\*Significant different at  $P < 0.05$ .

and *A. chinensis*, respectively. On the other hand, coefficients of the linear regression representing fruit water loss with ionic strength were  $-133.5$  for *A. deliciosa* and  $-94.5$  for *A. chinensis*. It may be worth mentioning here that the *A. deliciosa* had lower avoidance and higher tolerance than *A. chinensis*, and the combinations of these two components in both the species resulted in different degrees of resistance. Although we conducted this experiment in a different agro-ecological zone, our results are consistent with the findings of Zhou (1999) and Jiang and He (2000), who observed that *A. deliciosa* had better tolerance to hot summer conditions than *A. chinensis*. We may infer from our results that *A. deliciosa* was more thixotropic than *A. chinensis*. These properties should be verified by exposing *Actinidia* species to prolonged periods of moisture deficit. In this experiment, the different degrees of resistance in two species were probably related to their genetic variations. Navaro, Dziewiatkoski, and Enyedi (1999) stated that tolerant plant species are lower metal accumulators than sensitive ones, as they inhibit translocation of metal taken up in root, and its detoxification is taken into account including binding in cell wall, chelating in cytosol, or compartmentalization in the vacuole. We can predict that *A. deliciosa* would be a lower metal accumulator than *A. chinensis*. This mechanism has not been tested in kiwifruit yet, but should be tested under various stress conditions. Givnish (1979) predicted that smaller leaves should increase fitness in dry conditions as decreased surface area to volume ratio of smaller leaves inhibits desiccation (Larcher, 1995). In our experiment, lower avoidance of *A. deliciosa* is supported by higher fruit volume, higher fruit moisture, as well as higher leaf surface area (Table 1). The results allowed us to predict that the skins of both *A. deliciosa* and *A. chinensis* were the main factors to behave differently with dehydration stress; as in *A. deliciosa*, parenchyma cells beneath the hypodermis gradually merged into the fleshy tissue that forms most of the outer pericarp. On the other hand, in *A. chinensis*, this region is separated from the outer skin by a zone containing a mixture of parenchyma and brachysclereides (stone cells) (Hallett & Sutherland, 2005).

### Relationships Among the Traits

In this study, correlation coefficients were calculated between the physical and chemical properties of kiwifruits across time after exposure to dehydration stress (Table 5). As expected, there were significantly positive correlations for dry matter vs. total soluble solids, dry matter vs. ionic strength, and total soluble solids vs. ionic strength in all the steps of observation time. On the other hand, significantly negative correlations were observed for dry matter vs. moisture content, moisture content vs. total soluble solids, and moisture content vs. ionic strength. Cheng et al. (2007) observed the significant positive correlation between dry matter and total

**TABLE 5** Correlation Coefficients Among Fruit Dry Matter (DM), Moisture Content (MC), Total Soluble Solids (TSS), and Ionic Strength (IS) of Kiwifruit

Traits	Time (h)							
	0	1	2	3	4	5	7	24
DM vs TSS	0.753	0.750	0.789	0.790	0.790	0.766	0.763	0.758
DM vs IS	0.685	0.551	0.505	0.481	0.573	0.517	0.659	0.671
DM vs MC	-0.957	-0.946	-0.832	-0.952	-0.786	-0.885	-0.917	-0.577
TSS vs IS	0.857	0.796	0.784	0.710	0.784	0.784	0.871	0.805
MC vs TSS	-0.663	-0.658	-0.585	-0.698	-0.609	-0.623	-0.661	-0.483
MC vs IS	-0.566	-0.429	-0.396	-0.407	-0.429	-0.392	-0.624	-0.539

Data pooled for *A. deliciosa* and *A. chinensis*; n = 48.

soluble solids content in *A. chinensis*. Sugiyama (2006) observed a negative correlation between potential growth under stress-free conditions and survival under a severe water stress condition for two ryegrass species.

Because there has been no published data on the correlations between fruit and leaf traits of kiwifruit and resistance, avoidance, and tolerance, we established correlations between fruit and leaf traits with resistance, avoidance, and tolerance. Irrespective of the species and time, fruit volume, fruit moisture, and leaf surface area showed significant positive correlation with resistance and avoidance and negative correlation with tolerance (Table 6). On the other hand, fruit dry matter showed significant negative correlation with resistance and avoidance and positive correlation with tolerance. In this study, fruit dry matter correlated negatively with fruit volume (Table 7). Fruit volume correlated positively with fruit moisture. Leaf dry matter correlated positively with petiole dry matter and correlated negatively with leaf moisture and petiole moisture. Petiole dry matter correlated negatively with petiole length and petiole moisture, while petiole length correlated positively with petiole moisture. Our results found significant negative correlation ( $r = -0.284$ ;  $p < 0.05$ ) between fruit dry matter and leaf surface area, which is inconsistent with results of Clearwater et al. (2007), who found a significantly positive correlation between fruit dry matter and leaf surface area ( $r = 0.440$ ;  $p < 0.05$ ). Earlier studies have shown that a range of vegetative traits was often correlated with plant productivity, where productivity generally refers to total biomass production. Generally leaf traits like higher specific leaf area (leaf area per unit dry weight), stomatal conductance, maximum photosynthetic rates per unit weight, and leaf nitrogen content are correlated with high productivity (Reich, Walters, & Ellsworth 1997). When species and functional types (ecotypes and/or genotypes) are compared, maximum relative growth rates correlate with high specific leaf area, high leaf area ratios (leaf area per unit plant weight), and higher specific root area (root area per unit dry weight)

**TABLE 6** Correlation Coefficients of Fruit and Leaf Traits with Resistance, Avoidance, and Tolerance

Different traits	Resistance	Avoidance	Tolerance
Fruit volume	0.275	0.284	-0.299
Fruit moisture	0.466	0.327	-0.535
Fruit dry matter	-0.466	-0.327	0.535
Leaf surface area	0.285	0.279	-0.381
Leaf moisture	0.146	-0.074	-0.107
Leaf dry matter	-0.146	0.074	0.107
Petiole length	0.074	-0.119	0.068
Petiole moisture	0.010	0.114	-0.029
Petiole dry matter	-0.010	-0.114	0.029

Data pooled for *A. deliciosa* and *A. chinensis*; n = 48.

**TABLE 7** Pearson Correlations Among the Fruit and Leaf Traits

	FM	FDM	LSA	LM	LDM	PL	PM	Petiole dry matter
Fruit volume	0.598	-0.597	-0.091	0.212	-0.206	0.014	0.116	-0.113
Fruit moisture (FM)		-0.959	0.211	0.189	-0.187	0.028	0.111	-0.111
Fruit dry matter (FDM)			-0.284	-0.191	0.191	-0.028	-0.111	0.111
Leaf surface area (LSA)				0.004	-0.004	-0.064	-0.005	0.005
Leaf moisture (LM)					0.954	0.298	0.628	-0.628
Leaf dry matter (LDM)						-0.298	-0.628	0.628
Petiole length (PL)							0.530	-0.530
Petiole moisture (PM)								-0.963

Data pooled for *A. deliciosa* and *A. chinensis*; n = 48.

(Lambers, Poorter, & Van Vuuren 1998; Ryser 1998). When individual horticultural cultivars are considered, the phenotypic variation in vegetative traits may be associated with variation in harvestable yield (Wunsche, Palmer, & Greer 2000).

## CONCLUSIONS

The results supported our hypothesis that two kiwifruit species behaved differently with dehydration stress. *A. chinensis* had higher avoidance than *A. deliciosa*. It is therefore inferred that *A. deliciosa* had higher water loss than *A. chinensis*, and thus the ability for rapid induction of subcellular protection is more vital for *A. deliciosa* than *A. chinensis* during a mild or short period of water stress. On the other hand, *A. deliciosa* showed higher tolerance, indicating that this species had greater advantages under conditions of severe or prolonged water stress. Regardless of species, resistance and avoidance were positively correlated with fruit volume, fruit moisture, and leaf surface area, and negatively correlated with fruit dry matter, while

the reverse was true for tolerance. Because ionic strength is widely used in the determination of stability constant, we investigated dehydration stress in kiwifruit by observing the changes in ionic strength. However, this study demonstrated how avoidance and tolerance abilities are involved in the establishment of total dehydration resistance in the kiwifruit species. Our results should help researchers design better guidelines for risk assessment of kiwifruit under stress conditions. In the future, research should be extended to investigate links between stresses and ionic strength, metal accumulation, secondary metabolites synthesis, heat shock protein, photosynthesis, and carbon assimilation in the kiwifruit at various developmental stages as well as different growing systems.

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